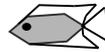


SAMPLING THE SOCIAL ENVIRONMENT IN AN UNCERTAIN WORLD

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We sail within a vast sphere,
ever drifting in uncertainty,
driven from end to end.



- Blaise Pascal

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Stephen Michael Heap: *Sampling the Social Environment in an Uncertain World*, © December 2012

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Dedicated to my parents. This is possible because of them.

ABSTRACT

The world that we inhabit is characterised by variation in the environment over space and time. Subsequently, animals are faced by uncertainty regarding their current and future conditions. Thus, it is critical to understand the nature of responses to uncertainty. Theory suggests that animals incorporate information from their environment through natural selection or personal experience, and use this information to make decisions that anticipate environmental conditions. Animals also possess the ability to improve their estimation of current conditions by sampling for new information, and individuals that incorporate updated information can have an adaptive advantage over those that use older information. However, sampling can be costly and selected against. The use of sampling strategies can also depend on social interactions within a population, the structure of the landscape, and variation in spatial scale. This thesis considers the conditions in which it is adaptive for an individual to sample information from their social environment, and how this behaviour is affected by the landscape and the decisions being made by others. In particular, I explore the use of updated information from the social environment in three contexts in which fitness is dependent on the social environment and phenomena attached to the landscape. In Part I, I report the results of a field experiment on breeding site selection in the terrestrial toadlet *Pseudophryne bibronii*. I collected every calling male in a breeding population, released them into empty habitat patches, and observed the decisions that they made during re-settlement. I found that the decision to sample social cues when selecting breeding sites reflected a predicted relationship between the value of previously gathered information and spatial scale. In Part II, I conceptually explore the interaction between conspicuous features of the landscape, or landmarks, and the adaptive value of sampling the social environment by conducting a literature review on the adoption of landmarks for territorial boundaries. Additionally, I conducted a laboratory experiment on the ability for convict cichlids, *Amatitlania nigrofasciata*, to learn spatial associations between landmarks and contests. The results of these studies indicate that the effect of landmarks on sampling may depend on the process responsible for the adoption of a landmarked boundary and the landmark's reliability for estimating location. Finally, in Part III, I consider the value of sampling during dyadic interactions between individuals. I measured how individual *P. bibronii* changed their calling behaviour in response to a persistent intruder simulated by a playback device, and reveal that males adjust

their behaviour as they gather additional information. Additionally, I analyse a game-theoretic model that considers the functional significance of sampling during contests, which suggests individuals face a trade-off between improving their assessment of opponents and having the capacity to fight for access to fitness-enhancing resources. Furthermore, there can be conflicts over the transfer of information that affect the evolution of sampling. Overall, I conclude that the value of sampling information from the social environment can depend on spatial scale, landmarks and the social interactions within populations. These conclusions may help develop an ecological understanding of how individuals use information.

DECLARATION

This is to certify that

1. the thesis comprises only my original work towards the PhD except where indicated in the Preface,
2. due acknowledgement has been made in the text to all other material used,
3. the thesis is fewer than 100 000 words in length, exclusive of tables, maps, bibliographies and appendices.

Melbourne, December 2012

Stephen Michael Heap

PREFACE

This dissertation is presented as a series of stand alone scientific articles. As such, it contains some repetition between chapters (e.g. methods sections). I am the primary author for the manuscripts that have been published (see page [xi](#)), and the following manuscripts that have been submitted or are in preparation for publication:

- Heap, S. & Byrne, P. Reduction in site-fidelity at smaller spatial scales. Submitted to: *Biology Letters* (March 2013), see [Chapter 2](#)
- Heap, S. & Stuart-Fox, D. Landmarks as spatial cues of agonistic interactions. *In prep.* ([Chapter 5](#))

For these manuscripts, I proposed and developed the original ideas, which were refined by discussion with the co-authors. I shared in the collection of data, and conducted the analysis, literature reviews and wrote the primary drafts of the manuscripts, which were edited and commented upon by the co-authors. All other help is listed in the Acknowledgments (see page [xiii](#)).

For the following manuscript, which is in preparation for submission, I am the shared primary author with Mike Mesterton-Gibbons:

- Mesterton-Gibbons, M. & Heap, S. Variation between self and mutual assessment in animal contests. Submitted to: *The American Naturalist* (February 2013), see [Chapter 7](#)

For this manuscript, I was wholly responsible for conceiving the question, initiating the project and conducting the literature review. Furthermore, in order to address the question, I organised a collaboration with a mathematical expert. Mike Mesterton-Gibbons, the shared author, is wholly responsible for calculating the solutions to a model that we formulated together. I was then responsible for leading the biological interpretation of the results and writing the manuscript. This paper represents a collaboration between a biologist and mathematician, with each party contributing to their area of expertise, to produce a manuscript that could not have been produced by either party alone. For the purpose of this thesis, it is important to note that I was primarily responsible for the biological aspects of the manuscript.

The work contained in this thesis was completed under the following permits and licences:

- Faculty of Science, School of Land and Environment, and Optometry & Vision Sciences Animal Ethics Committee (0911395.1)
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- Monash University (PB)
- the University of Wollongong (PB)
- Florida State University (MMG)

TYPE OF WORK	CHAPTER 2	CHAPTER 3	CHAPTER 4	CHAPTER 5	CHAPTER 6	CHAPTER 7
Project initiation	SH, PB	SH, PB	SH	SH, DSF	SH, PB, DSF	SH
Experimental design/Model formulation	SH, PB	SH, PB	-	SH, DSF	SH, PB, DSF	MMG, SH
Data/Model analysis	SH	SH	-	SH	SH, DSF	MMG
Interpretation	SH, PB	SH, PB	SH, DSF, PB	SH, DSF	SH, PB, DSF	SH, MMG
Writing the manuscript	SH, PB	SH, PB	SH, DSF, PB	SH	SH, PB, DSF	SH and MMG

SH: Stephen Heap

DSF: Devi Stuart-Fox

PB: Phillip Byrne

MMG: Mike Mesterton-Gibbons

PUBLICATIONS

This thesis includes chapters that have appeared previously in the following publications:

- Heap, S. Stuart-Fox, D. & Byrne, P. 2012. Variation in the effect of repeated intrusions on calling behavior in a territorial toadlet. *Behavioral Ecology* 23, 93-100 ([Chapter 6](#))
- Heap, S. Byrne, P. & Stuart-Fox, D. 2012. The adoption of landmarks for territorial boundaries. *Animal Behaviour* 83: 871-878 ([Chapter 4](#))
- Heap, S. & Byrne, P. 2013. Aggregation and dispersal based on social cues as a nest-site selection strategy in a resource-defence polygynandry mating system. *Behavioral Ecology and Sociobiology* 67: 685-697 ([Chapter 3](#))

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To my friends and family, I thank you for keeping me in touch with the social world and the necessary requirements of life. Without you all, I would have, at worst, died of starvation or, at best, turned into some weirdo not fit for public life. Special thanks go to my parents, Bill and Penny, whose emotional and financial support helped me to follow my passions. I could not have done any of this without them, and I owe them everything for putting so much value towards education and allowing me to follow this through to the very end. To my brother Stuart, thanks for the sciency discussions. To Billy, Dave, Ryan, Shaun and Tony; thank you for giving me a life outside of academia. To Dom and Jeremy, thank you for giving me a social life within academia. To Dom again, your hard work and dedication have always been an inspiration to my efforts as a student; trying to keep up with you was always a rewarding challenge. To Beatriz, thank you for your understanding, care and patience. Your companionship has always been there and always treasured. To my conference buddies: Andrew, Ben, Daniel, Dom W, Heidi, I-Ping, Jenny, Krystina, Nori, and all the rest; thank you for making science fun. To Heidi, especially, thank you for your efforts to build our friendship and for your infectious enthusiasm for the natural world. To my friends in the Zoology Department: Bec, Claire, Eunice, Jemma, Lisa H, Maddy, Maggie, Maya, Michelle W, Paul C, Paul O, Rob, Tamara, Zoe and everyone from the Evolution and Behaviour Group; thank you all for making the Department such a nice place to work. I hope that we stay in touch. To those who have taken me with them into the field, no matter how local, thank you. The opportunity to get my hands dirty, or wet, is valued beyond words when most of one's work is at the computer and not in the field. To Matt H, thank you for being the fusion of a science friend and a night-on-the-town friend: the perfect drinking buddy. To all of those at FSU, especially: Abigail, Aki, Allyssa,

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INTRODUCTION

We live in a variable and uncertain world. The landscape and climate change over space and time, which sets a dynamic stage for the patterns of life. Life itself is also inherently variable, owing to the evolutionarily selfish interests of organisms and the chance mutations that are the basis for adaptation. However, our understanding of biology is primarily based on responses to the more predictable aspects of the environment, despite the ubiquity of uncertainty (e.g. [Fretwell and Lucas Jr, 1969](#); [Hamilton, 1963](#); [Maynard Smith and Price, 1973](#); [Stephens et al., 2007](#)). Whilst the assumption that individuals can perfectly predict their environment is necessary for understanding optimal decisions in an ideal context, it does not accurately reflect reality. Furthermore, there is growing evidence for adaptive responses to the level of uncertainty that animals experience in a given situation ([Stephens, 1989](#); [Mangel, 1990](#); [Stephens, 1991](#); [Dall et al., 2005](#); [Dall, 2010](#); [Schmidt et al., 2010](#)). Thus, for a fuller understanding of adaptive behaviour, it is critical to consider how and why individuals can respond to uncertainty.

Environmental uncertainty implies that current conditions can never be determined with complete accuracy. Animals can, however, acquire personal information on environmental conditions through previous experience ([Switzer, 1993](#); [Wagner and Danchin, 2010](#)). Additionally, individuals hold personal information on previous environmental conditions within their genome ([Maynard Smith, 2000](#); [Wagner and Danchin, 2010](#)), which is effectively a history of successful responses to the environment (due to natural selection). In many cases, this information allows an individual to reliably determine its current conditions and respond appropriately (e.g. [Luttbeg and Warner, 1999](#)). For example, animals often re-use the same nest-site, instead of choosing an alternative based on current information, as long as they are consistently able to raise offspring there ([Piper, 2011](#)). In other cases, individuals can benefit by updating their personal information by 'sampling' available environmental cues in order to further reduce uncertainty ([Dall et al., 2005](#); [Dall, 2010](#)). However, gathering new information can be costly and, consequently, investment towards sampling is a strategic decision that has variable fitness consequences ([Dall et al., 2005](#); [Dall, 2010](#)). These costs can include opportunity costs that stem from sampling unproductive options, and the allocation of resources away from growth and reproduction ([Krebs et al., 1978](#); [Stephens et al., 2007](#); [Dall, 2010](#); [Lea et al., 2012](#)). In social con-

texts, individuals face further costs in the form of responding to inaccurate social information, free-riding scroungers that parasitise information, and the costs associated with receiving signals (Dawkins and Guilford, 1991; Giraldeau and Caraco, 2000; Jablonka, 2002; Maynard Smith and Harper, 2003; Laland, 2004).

Theoretically, for sampling to be adaptive, information must both i) reduce uncertainty, and ii) improve fitness (Dall et al., 2005). Thus, sampling is adaptive when reliable information from the environment allows an individual to change its behaviour in a way that gives it a selective advantage over individuals that respond to previously acquired personal information alone (Figure 1). For example, choosing a nest-site based on updated information, rather than remaining in a previously successful site, can be adaptive when there is the possibility for better quality sites to be available (Switzer, 1993).

What explains variation in the functional significance of sampling behaviour? According to the framework outlined by Dall et al. (2005), and summarised in Figure 1, sampling is valuable when animals benefit from responding to current information on their environment. Alternatively, if individuals do not respond to currently available information, then the costs of acquiring new information may outweigh any benefits of responding to the information or constraints may prevent the information from being gathered. Thus, to understand the functional significance of sampling behaviour, we can identify cases in which sampling is adaptive or not, and determine what the environmental conditions were in each case. This then allows us to make inferences regarding the adaptive value of sampling in different environmental conditions.

1.1 THE ECOLOGY OF INFORMATION USE AND INFORMATION FROM THE SOCIAL ENVIRONMENT

Animals use information by making decisions that involve anticipation of environmental circumstances (Stephens, 1989; Mangel, 1990; Dall et al., 2005), and these decisions have consequences for populations, communities and ecosystems (Lima and Zollner, 1996; Kokko and Lopez-Sepulcre, 2007; Schmidt et al., 2010). Furthermore, the environment in which an individual must make decisions is defined by patterns and processes that occur at these higher biological levels. Thus, an animal's use of information, including the conditions in which it is adaptive to sample or not, is intricately tied to broader networks of interactions that extend over space and time (Turner, 1989; Turner et al., 1989; Turner, 1990; Lima and Zollner, 1996; Schmidt et al., 2010). The ecology of information use is a newly defined concept that attempts to extend the study of how animals make informed decisions by considering the ecological consequences of these deci-

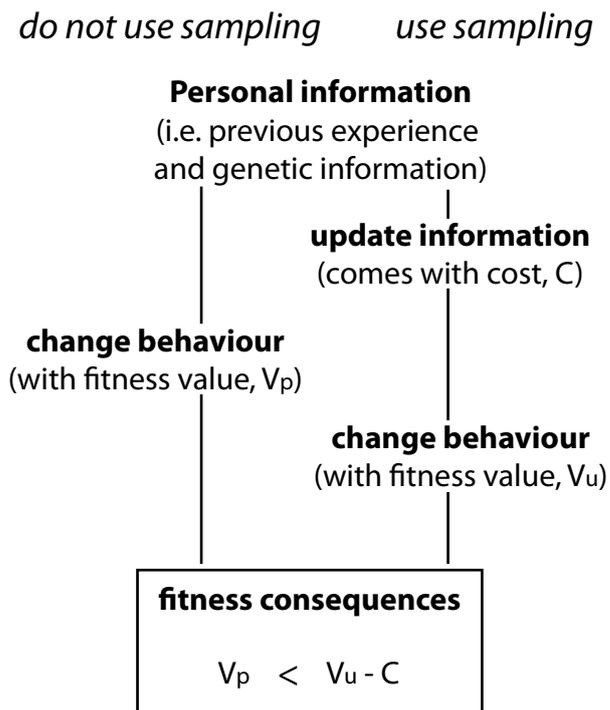


Figure 1: Conditions for updating information (sampling) to be adaptive: the fitness value of responding to sampled information, given the costs of sampling, must outweigh the value of responding only to previously held personal information. Adapted from [Dall et al. \(2005\)](#)

sions and the role of landscapes (i.e. broad spatial scales and structure) and ecosystems in decision making processes (Schmidt et al., 2010). However, at the current stage it is unknown whether the consideration of a broad ecology of information use can provide a general explanation of biological interactions or not. Further development of this concept will require a greater understanding of how information is used over multiple spatial and temporal scales, as well as how interactions within a population affect and are affected by informed decision making by individuals. In this regard, I narrow the focus of this thesis to a consideration of the conditions in which it is adaptive to gather information from the social environment, and how this behaviour is affected by the decisions being made by other individuals and the landscape that an individual inhabits.

Many studies have considered the adaptive value of responding to information from the social environment (Wilson, 1975). For instance, individuals can improve fitness by using information on the properties and behaviours of conspecifics (Danchin et al., 2004; Kokko et al., 2006; Betts et al., 2008), such as when collared flycatchers (*Ficedula albicollis*) choose breeding sites by assessing the reproductive success of conspecifics (Doligez et al., 2002). Additionally, individuals can benefit by changing their behaviour based on the actions of conspecifics when there is competition for limited resources (Fretwell and Lucas Jr, 1969; Krebs, 1971; Huntingford and Turner, 1987). For example, red-winged blackbirds (*Agelaius phoeniceus*) resolve conflicts of territory ownership by signalling their motivation to inhabit the territory (Beletsky and Orians, 1987). Importantly, the social environment can be a significant source of uncertainty because different individuals are differently motivated (Dall, 2010). However, little is known about the costs and benefits of sampling the social environment and the role that the landscape has on sampling behaviour (Lima and Zollner, 1996).

1.2 STUDY ORGANISMS

1.2.1 *Pseudophryne bibronii*

The terrestrial toadlet *Pseudophryne bibronii* (Figure 2), also known as the common brown toadlet or Bibron's toadlet, is a Myobatrachid frog that is endemic to temperate regions of south-eastern Australia (Tyler and Knight, 2009). The species breeds terrestrially, whereby males enter dry creek lines and drainage pans, and establish shallow burrows under leaf litter in moist soil at the beginning of autumn. Males produce acoustic signals, from within their burrows, which advertise their presence to females and mediate competitive interactions (Pengilley, 1971; Woodruff, 1976; Mitchell, 2001; Byrne, 2008;

Heap et al., 2012). Females move through the chorus and select males with whom to mate, presumably based on the quality of acoustic and chemical signals and/or nest-site characteristics, with oviposition occurring in the burrow (Pengilley, 1971; Woodruff, 1976; Byrne and Keogh, 2007, 2009). Females are extremely polyandrous and sequentially split their clutch amongst the nests of two to eight males (Byrne and Keogh, 2009; Byrne and Roberts, 2012). Typically, males remain with their eggs over the course of the breeding season, which continues until winter rainfalls inundate the habitat and eggs hatch into ephemeral pools.

Reproductive success in *P. bibronii* is dependent on suitable moisture conditions. Firstly, egg survival depends on the maintenance of adequate soil water potential (Bradford and Seymour, 1988). Secondly, the development and survival of tadpoles requires flooding to inundate the nest at the appropriate stage of egg development and for the area to remain flooded long enough for metamorphosis to complete (Bradford and Seymour, 1988; Geiser and Seymour, 1989). The maintenance of adequate soil moisture and optimal flooding is determined by the frequency and magnitude of rainfall events, which are spatially and temporally stochastic in Jervis Bay, the region where I conducted the research for this thesis (Figure 3, Figure 4). Thus, individuals are unable to reliably assess the quality of a nest-site during the breeding season and reproductive success can vary substantially between years (Woodruff, 1976). These conditions may have resulted in the evolution of extreme sequential polyandry in females, who split their clutch amongst multiple males to insure against the possibility of nest-site failure in any one nest (Byrne and Keogh, 2009). However, little else is known about how this species has adapted their breeding biology in response to environmental uncertainty, including the conditions in which individuals sample the social environment.

It is the strong selective pressure exerted by environmental uncertainty that makes *P. bibronii* an excellent model system for exploring the effect of uncertainty on sampling behaviour. Furthermore, like most anurans, social interactions among *P. bibronii* are principally mediated by acoustic interactions. Furthermore, unlike many other anurans, male *P. bibronii* rarely engage in physical interactions with their rivals. The ease of quantifying acoustic interactions and their near-exclusive use as a source of social information, allows reliable inferences on the value of socially acquired information to be made from field observations. Research on *P. bibronii* was conducted as a series of field experiments on populations located within remnant *Eucalyptus*, *Banksia* and *Casuarina* woodland in Jervis Bay National Park, on the southeast coast of New South Wales, Australia (Figure 3).



Figure 2: A male terrestrial toadlet of the species *Pseudophryne bibronii*
http://en.wikipedia.org/wiki/Image:Pseudophryne_bibronii.jpg

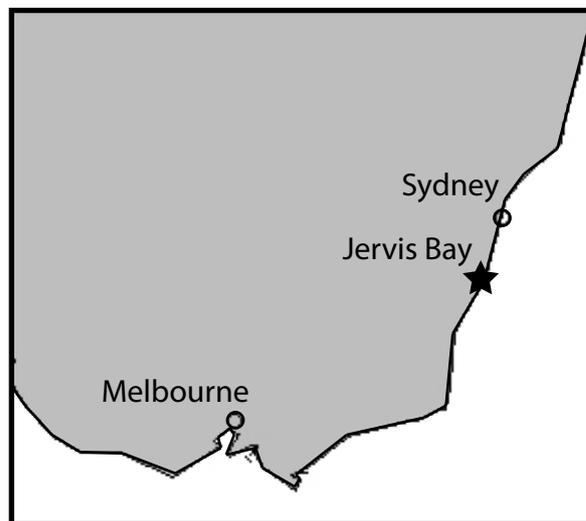


Figure 3: Map of south-eastern Australia showing the location of the study site in Jervis Bay, in comparison to nearby major cities

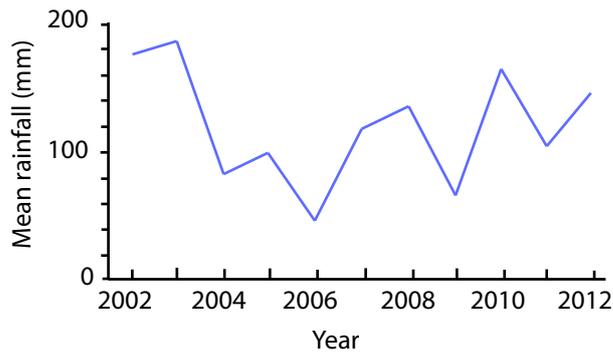


Figure 4: Fluctuation in mean rainfall (mm) over the breeding season (February-May) for the years 2002-2012, measured at the Jarvis Bay Point Perpendicular weather station.

Data courtesy of the Australian Bureau of Meteorology
<http://www.bom.gov.au>

1.2.2 *Amatitlania nigrofasciata*

The convict cichlid, *Amatitlania nigrofasciata*, is native to freshwater flood-lakes and streams in Central America but is a popular aquarium and laboratory species. They are physically characterised by their pale body with black stripes that provide them with their common name (Figure 5). However, there is some sexual di-morphism, with females often expressing variable levels of orange colouration on their body and males occasionally developing a fatty 'nuchal hump' on their head. Individuals also have an extensible jaw that allows them a wide range of foraging options, and which can also be used to excavate the substrate and transport fry (Reebs, 1994; Wisenden, 1995; Hulseley and Garcia De Leon, 2005).

Convict cichlids are principally used as a model organism for understanding questions relating to aggressive behaviour, territoriality, parental care and reproductive decisions (e.g. Mackereth and Keenleyside, 1993; Wisenden, 1995; Alonzo et al., 2001; Leiser et al., 2004; Lehtonen and Lindstrom, 2008; Arnott and Elwood, 2009b, 2010). Both sexes use aggression to establish a position in a dominance hierarchy, which gives them an advantage in breeding (Mackereth and Keenleyside, 1993). In this regard, receptive females tend to select dominant males, who are better able to defend spawning sites, and then compete amongst themselves for access to attractive males (Mackereth and Keenleyside, 1993). Mutual courtship behaviours lead to a pair bond forming, with bonded pairs then selecting a spawning site, which are generally provided for them in the aquarium but tend to be constructed by excavating the substrate underneath rocks in nature (Mackereth and Keenleyside, 1993; Wisenden, 1995). After spawning, the male and female both defend the eggs from predators and use fanning to oxygenate the eggs (Reebs and Colgan, 1992; Wisenden, 1994).



Figure 5: Female (left, with orange colouration) and male (right, with nuchal hump on head) convict cichlids, *Amatitlania nigrofasciata*.
 Photo courtesy of http://commons.wikimedia.org/wiki/File:Convicts_Cichlids.jpg

Bi-parental care continues after the offspring become free-swimming fry, as predation is still a threat (Wisenden, 1994). During this stage of reproduction, both parents aggressively defend their breeding site from rival conspecific breeders and cannibalistic predators.

I sourced convict cichlids from captive breeding stock and commercial suppliers for usage in a lab experiment that investigated the influence of landmarks on an individual's response to territorial aggression. Convict cichlids were used in this study because of their extensive use as a model organism for agonistic interactions and data that suggest individuals respond to landmarks (e.g. Gallagher et al., 1972; Figler and Evensen, 1979; Figler and Einhorn, 1983; Figler et al., 1985; Wazlavek and Figler, 1989; Breau and Grant, 2002; Barley and Coleman, 2010).

1.3 APPROACH AND OUTLINE

In this thesis, I explore sampling behaviour in three different contexts: the selection of breeding habitats, the adoption of landmarked boundaries, and dyadic interactions between competitors. For each of these cases, fitness is strongly tied to the social environment, making them suitable systems in which to study variation in the benefits of sampling social cues. Specifically, the selection of a breeding site depends on competition between members of the same population for reproductive resources and mates, whilst the adoption of landmarked boundaries and dyadic interactions represent two processes that determine the distribution of fitness-enhancing resources amongst a population. Additionally, these three contexts allow me to draw inferences on the manner in which information use interacts with population and landscape level phenomena, as breeding site se-

lection comprises decisions that are made on multiple spatial scales, landmarks are important features of the landscape and dyadic interactions are the basic unit of interaction within populations. The thesis is therefore presented in three parts, followed by a summary and synthesis in [chapter 8](#).

1.3.1 *Part I: Breeding site selection in Pseudophryne bibronii*

Oviparous animals are typically expected to choose the best available habitat in which to lay their eggs by using environmental cues that reveal an area's reproductive suitability (Fretwell and Lucas Jr, 1969; Krebs, 1971; Calsbeek and Sinervo, 2002; Refsnider and Janzen, 2010). The social environment is often an important source of information during breeding site selection, as the presence of conspecifics can affect an individual's reproductive success (Coulson, 1968; Hamilton, 1971; Brown and Bomberger Brown, 1996). This is especially true for breeding site selection in male anurans, such as *Pseudophryne bibronii*, owing to density-dependent acoustic competition and interference between rivals for the attention of females (Gerhardt and Huber, 2002). Furthermore, the cues that an individual uses to select breeding sites can often change depending on whether the individual is choosing a habitat, patch or microhabitat because different factors affect reproductive success at different spatial scales (Orians and Wittenberger, 1991). The level of environmental uncertainty (and thus the value of sampling information) is also expected to vary at different spatial scales (Wiens, 1989; Costanza and Maxwell, 1994). However, it is unclear how responses to uncertainty in breeding site decisions can change according to spatial scale, despite this being a crucial component for understanding habitat selection and the ecology of information use (Lima and Zollner, 1996; Schmidt et al., 2010). Thus, Part I aims to empirically determine the value of sampling the social environment during nest-site selection in the terrestrial toadlet, *P. bibronii*.

A field experiment conducted on *P. bibronii* aimed to determine how individual males adjusted their use of social cues when choosing breeding sites at different spatial scales. This was achieved by performing a patch-swap experiment on an entire population of calling males, whereby every male was collected and released *en masse* into an alternative patch that had all of its prior occupants removed. After males were released, the study site was surveyed every night for 26 consecutive nights until the night of re-capture. A second collection was then conducted for the re-settled population.

In [chapter 2](#), I analyse the distribution of nest-sites between the original population and the population following re-settlement to determine the extent to which current information was used to select a breeding patch, or nest-site within a patch. Specifically, I used the

frequency of individuals that returned to their original site (i.e. site-fidelity) as an indicator for the use of prior information (Switzer, 1993; Piper, 2011), which could then be used to infer the extent of choosing breeding sites on currently available information.

In chapter 3, I conduct a more detailed analysis of nest-site choice within breeding patches. This involved using an information theoretic approach to determine whether males were likely to be sampling their social environment when choosing a breeding site. Observations on the breeding success achieved by males also allowed me to consider the potential ultimate reasons for the use of social cues in breeding site choice. Chapters 2 and 3 together provide insight into the use of prior or updated information on the social environment at different spatial scales.

1.3.2 Part II: The relationship between landmarks and social interactions

The social environment does not exist independently of the landscape, and thus there is the potential for interactive effects between these different aspects of the environment on the value of sampling social cues. However, little is known about the nature of such interactions. An intriguing behaviour expressed by many territorial animals is the adoption of landmarks (i.e. conspicuous features of the landscape) for territorial boundaries (Eason et al., 1999; LaManna and Eason, 2003; Smith, 2011; Heap et al., 2012). In many cases, these landmarks are not produced by the animals themselves, yet their role in the important social process of territoriality attests to an interaction with the social environment. Furthermore, studying the role of landmarks in sampling the social environment allows us to develop our understanding of how individual decisions, territorial populations and the landscape interact with one another to define adaptive information use. Part II aims to conceptually and empirically explore this interaction.

Because individuals can often benefit from sampling social competitors when establishing and maintaining territories, chapter 4 consists of a literature review on the adoption of landmarks for territorial boundaries to better understand the role of the landscape in these decisions. This review highlights the various consequences of adopting landmarked boundaries, classifies different types of landmarks, presents hypotheses for explaining their adoption as territorial boundaries, and emphasises important areas for future studies.

Leading on from the findings of this review, chapter 5 comprises a lab experiment on convict cichlids (*Amatitlania nigrofasciata*) that aimed to test a fundamental assumption for a principal hypothesis that could explain the adoption of landmarked boundaries. Specifically, some landmarks may be used as boundaries because they reduce the uncertainty regarding the location of social interactions (the

clear-boundaries hypothesis). This hypothesis assumes that animals can make learned spatial associations between landmarks and social interactions. I tested this by exposing convict cichlids to costly interactions in the presence of a landmark and comparing their subsequent use of the area near the landmark to a control in which no costly interaction occurred.

1.3.3 *Part III: Uncertainty about opponents during dyadic interactions*

In order to gain access to fitness enhancing resources, individuals must often directly interact with other members of their population. These interactions can take the form of scramble or interference competition, but can also escalate to costly contests if neither individual is willing to concede ownership of the resource (Maynard Smith, 1974; Colegrave, 1994). Uncertainty plays a large role in such interactions, because not only can an individual be uncertain about the external conditions that define the stakes of the interaction, but the qualities and motivations of opponents that are making independent decisions can be difficult to determine. Thus, individuals are expected to invest heavily in sampling their social environment when it comes to direct interactions. The evolution of signals, which are traits that have evolved to function in aiding information transfer between individuals, attests to the value of reducing uncertainty in dyadic social interactions (Bradbury and Vehrencamp, 2000; Maynard Smith and Harper, 2003). Part III aims to address two current research trends in refining our understanding of information use in dyadic interactions: i) gathering information over repeated interactions between the same two individuals, and ii) improving incomplete information during contests. Furthering our understanding in these regards is important for developing a theory for how interactions among a population determines the functional significance of sampling behaviour, and consequently how information is utilised by animal groups.

In [chapter 6](#), I describe a field experiment on the terrestrial frog *P. bibronii* that aimed to empirically determine how territorial residents modify their response to a persistent intruder as they gradually accumulate information. After male *P. bibronii* were captured and released, as outlined above ([page 9](#)), I exposed a number of established resident males to a speaker that simulated a persistent intruder. The speaker was placed within one metre of a male's nest-site and programmed to give six three-minute bouts of calling, each separated by a seven minute period of silence. I measured the resident's change in call rate for each bout and determined whether the resident's response changed over time and whether the response varied among individuals.

In [chapter 7](#), I present a game-theoretical model that considers the functional significance of sampling information during agonistic interactions. This model addresses the next development in understanding contest behaviour by considering the functional significance of self and mutual assessment strategies. These strategies represent the two dominant decision rules that animals can use when deciding on when to withdraw from a contest, and also reflect the use of prior and sampled information, respectively. Specifically, the model considers the value of information on asymmetries in Resource Holding Potential (RHP) for improving the accuracy of decisions to withdraw from a contest. It distinguishes between two sources of information that an individual can use to determine whether it has the potential to win the contest. Firstly, all individuals are assumed to have access to complete and perfect information on the distribution of RHP within the population (general information), which allows them to form a baseline estimation of their ability to win a given contest. This information is used by individuals that adopt a self assessment strategy. Secondly, individuals can invest in gathering information on their current opponent's RHP (specific information) in order to improve their estimation, which reflects the use of a mutual assessment strategy. However, gathering specific information comes at a cost, and can vary in its effectiveness. Furthermore, I consider the possibility for individuals to advertently or inadvertently provide their opponents with information when they gather specific information, as this is often the case in contests. For example, an animal that assesses an opponent visually may provide no information on its own RHP, but an individual involved in a wrestling match simultaneously gathers and provides information through the same action.

I use this model to analyse the functional significance of sampling information with variation in the distribution of RHP in the population, the value of the contested resource, the costs of fighting and the intrinsic cost of sampling. I also consider the effect of sampling efficacy and the amount of information transferred via sampling. Evolutionarily Stable Strategy (ESS) conditions for sampling opponents in a population that consists of weak and strong fighters were then determined. Overall, this model can be used to make inferences regarding the costs and benefits of sampling information from the social environment. The analytical results of this model conclude the thesis by providing formal demonstration of variation in the value of sampling new information in response to environmental uncertainty.

Part I

BREEDING SITE SELECTION IN
PSEUDOPHYRNE BIBRONII

REDUCTION IN SITE-FIDELITY AT SMALLER SPATIAL SCALES

Animals can change the strategy that they use to select breeding-sites at the spatial scales of habitat, patch and microhabitat. The use of a site-fidelity strategy is expected to vary according to the predictability of the environment, which, in turn, is expected to vary according to spatial scale. However, whether animals change their decision to display site-fidelity at different spatial scales remains unclear. We captured and released males of the terrestrial frog *Pseudophryne bibronii* into alternative habitat patches to determine the extent to which site-fidelity influenced individual choices for nest-sites. We found that males preferred to return to their original habitat patch rather than re-settle in an alternative patch. However, males were unlikely to return to their original nest-sites within the patch. We conclude that a site-fidelity strategy in males may be scale dependant because information from previous breeding seasons can predict the quality of habitat patches, but not nest-sites. A relationship between environmental predictability and spatial scale could have implications for decision making processes that, like habitat selection, extend over multiple spatial scales.

2.1 INTRODUCTION

Oviparous animals are typically expected to choose the best available habitat in which to lay their eggs (Fretwell and Lucas Jr, 1969; Calsbeek and Sinervo, 2002; Refsnider and Janzen, 2010), with decisions depending on environmental cues that indicate an area's reproductive suitability (Krebs, 1971). Furthermore, the spatial scale at which cues are gathered can determine whether they are responded to (Orians and Wittenberger, 1991). Because the environment can never be completely predicted, animals often develop an adaptive response to the level of environmental uncertainty. However, it is unclear how responses to uncertainty in breeding-site decisions can change according to spatial scale, despite this being a crucial component for understanding habitat selection (Lima and Zollner, 1996; Schmidt et al., 2010).

Numerous studies have shown that animals can choose to be faithful to a previously used breeding-site, termed site-fidelity (Burger, 1982; Switzer, 1997; Ringler et al., 2009). Regardless of the direct mechanism, theory consistently predicts that site-fidelity allows individ-

uals to exploit patterns that are predictable over multiple breeding seasons by using information on their previous breeding experiences (Johnson and Gaines, 1990; Switzer, 1993, 1997; Doligez et al., 2003; Piper, 2011). Thus, decreases in environmental predictability are predicted to reduce the functional significance of site-fidelity.

Because i) information on previous breeding outcomes corresponds with previous environmental conditions (Johnson and Gaines, 1990; Switzer, 1993, 1997; Doligez et al., 2003; Piper, 2011), and ii) environmental conditions at smaller spatial scales are more closely correlated with recent ecological events rather than those that occurred at a more distant point in time (Wiens, 1989; Costanza and Maxwell, 1994), the functional significance of site-fidelity may decrease at smaller spatial scales. That is, the benefits of responding to previous breeding experiences will decrease as spatial scale narrows because these experiences can no longer predict current conditions. Hence, site-fidelity, which is sub-optimal in unpredictable environments, may be less beneficial at smaller spatial scales.

To determine if the decision to be site-fidel is affected by variation in environmental predictability at different spatial scales, we must first show that an animal's decision to be site-fidel can be scale dependent. However, many studies of breeding-site choice base their conclusions on patterns of distribution and abundance, and are unable to separate the decision to be site-fidel from coarse ecological processes, such as resource limitation or competition, that could also result in nesting patterns that suggest site-fidelity (Parrish and Edelstein-Keshet, 1999; Doligez et al., 2003; Boulinier et al., 2008). Thus, there is an urgent need for manipulative field experiments that have the capacity to distinguish between pattern and process.

We performed a novel patch swap experiment on the terrestrial toadlet *Pseudophryne bibronii*, and measured site-fidelity during re-settlement. Our aim was to determine if individuals choose to be site-fidel if they are presented with an alternative breeding-site. If individuals prefer their original breeding-sites over the alternative, then we can infer that there are fitness benefits associated with site-fidelity. Following toadlet re-settlement, we compared site-fidelity at different spatial scales to determine if there is a decrease in site-fidelity at smaller spatial scales.

2.2 METHODS

2.2.1 Field protocol

The patch-swath experiment was performed on a population of toadlets in Bream Beach NSW Australia between 19 March and 20 April 2010. We divided the breeding habitat into three distinct patches, based

on the intersection of ephemeral streams, referred to as the north, east and south patch (Figure 1). We collected every calling male in a chorus over three nights, approximately 4-6 weeks after the commencement of a 3-4 month breeding season. We collected every calling male from the north patch on night 1 ($N=13$), the east patch on night 2 ($N=23$) and the south patch on night 3 ($N=16$). Nest sites were marked with an ID flag. We placed males into plastic zip-lock bags and brought them to a field station, where they were housed in individual plastic containers (175 x 125 x 50mm). Each container held a moist sponge to ensure that toadlets remained hydrated. Containers were held in a room with windows so that toadlets experienced natural light/dark cycles. We used digital photographs of unique ventral patterns as an identification key.

During toadlet collection, we kept each group of males at the field station for 2 nights. Males from the north and east patches were randomly chosen to be used in the patch swap treatment, whilst males from the south patch were chosen as a control. We released north males into the east patch on night 3, east males into the north patch on night 4 and south males into the south patch on night 5. We released males at a centralised location within their release patch (Figure 6) that was 23 ± 11 m from their original capture site. To release the males, we arranged individual containers into a circle, with the lids facing outwards, and after a 5 minute acclimation period opened each lid sequentially. Exactly 29, 30 and 31 days after the initial collection we re-captured calling males from the north ($N=11$), east ($N=17$) and south ($N=12$) patches, respectively. We repeated the procedure of the original capture and used the identification key of ventral patterns to identify the occupant of each nest site. After all males had been re-captured and returned to the field station, we laid lines of string through the chorus to serve as the axes of a coordinate system and noted the Cartesian coordinates for original and re-settled nest-sites.

2.2.2 Statistical methods

To determine if males toadlets showed site-fidelity, we used Fisher's and χ^2 tests to determine if the proportion of males that settled in their release patch differed between treatment groups. We also conducted these analyses after pooling the two patch-swap groups together. Additionally, we used χ^2 tests to determine the proportion of males that returned to i) their original patch, ii) their original nest-site (strict site fidelity) and iii) within 100cm of their original nest-site (coarse site fidelity) by finding the upper and lower points at which the observed frequencies differ from a particular distribution.

Table 1: Frequency of individual male terrestrial toadlets ($N=52$) that either: established a calling site within the habitat patch in which they were released, or moved to a different habitat patch

RELEASE PATCH	CONTROL	N \implies E		E \implies N
Yes	12 (16.00)	0 (3.25)	(7.11)	1 (3.92)
No	4 (5.33)	13 (1.08)	(2.37)	22 (1.31)

Values in parentheses represent χ^2 components. The values in between N \implies E and E \implies N groups are the χ^2 values when the patch-swap treatments are pooled

2.3 RESULTS

In terms of patch-selection, the frequency of males that settled in the release-patch depended on the treatment (Fisher's test: $p < 0.001$; Table 1). Specifically, males from the control treatment were significantly more likely to settle in the release patch than males from the patch-swap treatment (control vs patch-swap: $\chi_1^2 = 30.81$, $p < 0.001$; Fisher's test: $p < 0.001$; Table 1). Furthermore, if we pool males from all treatment groups together, 38 of the 40 males that were recaptured (84-98%) were recaptured in their original patch (Figure 6, Table 2). This frequency of males expressing site-fidelity could be expected if anywhere from 84-98 % of males express site-fidelity on average. Fisher's tests indicate that there were no significant differences in the proportion of individuals that settled in their original patch when treatments were considered independently ($p=0.739$) or if patch-swap treatments were pooled ($p=1.000$), justifying the pooling of all treatment groups for this comparison.

Within patches, only 3 of the 40 males (3-19%) that had an original nest-site and decided to re-settle close to their original nest-site (Figure 6, Table 2). Even if the criterion for fidelity is relaxed, only eight individuals (11-66%) expressed coarse site-fidelity (Figure 6; Table 2). However, Fisher's tests indicated that there were significant differences in the proportions of males that expressed strict ($p=0.017$) and coarse ($p=0.030$) site fidelity between treatment groups. If the patch-swap treatments are pooled, then there are no significant differences in strict ($p=0.737$) or coarse ($p=1.000$) site-fidelity between control and patch-swap treatments.

2.4 DISCUSSION

Males showed a strong preference for their original patch over an alternative patch. This implies that males display site-fidelity at the patch scale. In contrast, relatively few males returned to within one

Table 2: Proportion and frequency of re-settled individuals ($N=40$) that established their re-settled nest-site in a given location

LOCATION	% MALES	CONTROL	N \implies E		E \implies N
Original patch	84-98 _a	12 (0.03)	10 (0.02)	(0.01)	16 (0.00)
Different patch		0 (0.60)	1 (0.37)	(0.26)	1 (0.03)
Original nest-site	3-19 _b	0 (0.90)	3 (5.73)	(0.39)	0 (1.28)
Different nest-site		12 (0.07)	8 (0.46)	(0.03)	17 (0.10)
< 100cm of original nest-site	11-66 _c	2 (0.07)	5 (3.56)	(0.03)	1 (1.69)
> 100cm of original nest-site		10 (0.02)	6 (0.89)	(0.01)	16 (0.42)

Values in parentheses are χ^2 components. The values in between N \implies E and E \implies N groups are the χ^2 values when the patch-swap treatments are pooled.

Proportions are given for all treatment groups pooled together.

Following are the χ^2 tests for detection of the lower and upper bounds for the proportion of individuals that express a given decision:

_a83%: $\chi^2_1 = 3.77, p=0.052$; 99%: $\chi^2_1 = 1.73, p=0.188$

_b2%: $\chi^2_1 = 2.78, p=0.095$; 20%: $\chi^2_1 = 3.44, p=0.064$

_c10%: $\chi^2_1 = 3.31, p=0.069$; 67%: $\chi^2_1 = 3.49, p=0.062$

metre of their original nest-site. Thus, males did not display site-fidelity within a patch. Together, these results suggest that the use of site-fidelity for choosing breeding-sites is scale dependent.

Breeding habitat selection involves responding to cues that can predict breeding success, over multiple spatial scales (Krebs, 1971; Orians and Wittenberger, 1991). Returning to familiar patches may thus improve reproductive success, but familiarity for nest-sites may provide little benefit. This may be because the benefits of site-fidelity increase with the predictability of the environment (Johnson and Gaines, 1990; Switzer, 1993; Doligez et al., 2003), and environmental predictability is greater at patches than nest-sites (Wiens, 1989; Costanza and Maxwell, 1994). These conditions would imply that males benefit by being faithful to predictable patches, but receive no benefits for being faithful to unpredictable nest-sites within the patch. Thus, there may be an underlying relationship between environmental predictability and spatial scale. This relationship could have implications for behavioural responses to environmental predictability that extend over multiple spatial scales, such as foraging, dispersal and habitat selection.

Information from previous breeding seasons may provide reliable information for the quality of a patch because flooding conditions, which determine reproductive success in *P. bibronii* (page 4), are relatively predictable between breeding seasons. In contrast, this information may not be able to predict reproductive success within patches because flooding conditions within the patch may be more variable

between years. Instead, reproductive success may be more predictable based on factors that vary at shorter time-scales, which is information that males would have to gather during the current breeding season. For instance, male reproductive success may depend on their position in relation to other males, the use of alternative mating strategies, or soil moisture and pH, as well as fine-scale flooding patterns.

Our manipulative field experiment allowed us to determine whether or not males chose to be site-fidel, rather than having to rely on inferences made from patterns of distribution and abundance. Having shown that the site-fidelity decision can change according to spatial scale, it is now necessary to determine if environmental predictability similarly changes with spatial scale. It will also be valuable to identify the cues used to make decisions and the fitness consequences of alternative strategies in order to advance our understanding of how information use in animals interacts with landscapes and within populations (Schmidt et al., 2010).

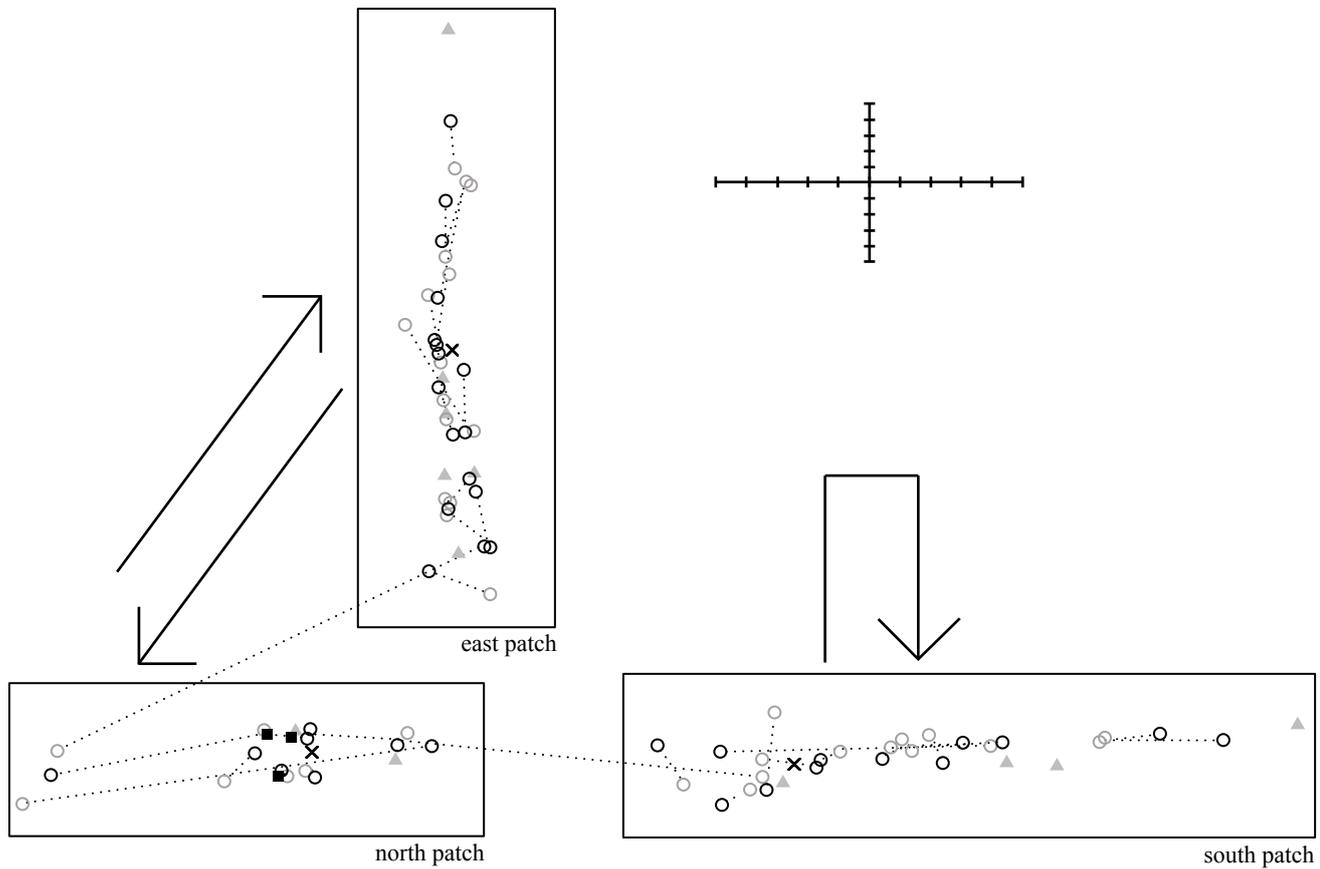


Figure 6: Map of the habitat, showing the three habitat patches (north, east, south). Arrows between patches indicate where captured males were released, with a cross representing the site at which males were released. The location of each male's original nest (grey circle) and re-settled nest (black circle) are connected by a dotted line. Males that returned to their original nest are represented by a black box. Males that did not re-settle are marked with a grey triangle. A scale, with 1m intervals on the x and y axes is provided

SOCIAL CUES FOR NEST-SITE SELECTION

Many animals must choose a nest-site in order to reproduce. However, it is unclear how nest-site selection strategies vary across different mating systems. We must therefore explore nest-site selection strategies in a range of mating systems, including the interaction between resource-defence polygyny and polyandry (i.e. polygynandry). In this study, we imposed a re-settlement event in the terrestrial toadlet *Pseudophryne bibronii* and measured the influence of the spatial position of each male's nest-site with respect to rival males on the likelihood that it would be abandoned or receive eggs. We captured every calling male in a population, measured their breeding success, and released them back into the breeding area. We then recorded the establishment and abandonment of nest-sites by males over 26 consecutive nights. Spatial positioning did not have any significant effects on male-breeding success, supporting claims that females show less discrimination between nest-sites when they are polyandrous and spread their eggs amongst multiple male nests when the chance of nest-site failure is high. However, we found that males consistently selected nest-sites according to a site's spatial position, which suggests that fitness benefits unrelated to male breeding success (e.g. reduced mortality risk) might influence male nesting decisions. Overall, our study provides new evidence that the mating system adopted by a population can influence the cues that individuals respond to when selecting nest-sites.

3.1 INTRODUCTION

Among oviparous animals, the decision of where to establish a nest (nest-site selection) has a direct impact on the survival and development of offspring (Krebs, 1971; Orians and Wittenberger, 1991; Refsnider and Janzen, 2010). It is well established that nest-site selection can be shaped by ecological factors (Fretwell and Lucas Jr, 1969; Petit and Petit, 1996; Muller et al., 1997; Rudolf and Rodel, 2005; Part et al., 2011). Many bird species, for example, will build nests in areas that offer protection from predators or inclement weather (e.g. Ille and Hoi, 1995; Burger and Gochfeld, 2005). However, little is known about the influence of different mating systems (Emlen and Oring, 1977) on nest-site selection. In particular we are only just beginning to understand how factors that characterise a particular mating system, such as conspecific spacing patterns, access to reproductive resources and

frequency of inter-sexual interactions, interact to influence individual nest-site selection strategies (Krause, 1994; Wagner, 1998; Velando and Freire, 2001; Bro-Jørgensen, 2008; Minias et al., 2012).

In systems where males select and defend oviposition sites (resource-defence polygyny), nest-site choice can directly correlate with mate attraction, copulation and oviposition (i.e. breeding success) because females may prefer to lay their eggs in sites that confer fitness advantages (Refsnider and Janzen, 2010). Thus, males can potentially improve breeding success through their choice of nest-site (e.g. Askenmo, 1984). Although the quality of abiotic and biotic resources of a nest-site have been shown to have a strong influence on female preferences for the site and its resident (e.g. Verner and Willson, 1966; Christy, 1983; Balmford et al., 1992), quality (and hence female preference) can also depend on the spatial distribution of males. This is because conspecifics can positively or negatively influence the expected reproductive success associated with a site (Brown and Orians, 1970; Pusey and Packer, 1997) and because males in certain positions may encounter more females (Otte, 1974; Beehler and Foster, 1988; Gerhardt and Huber, 2002; Howard et al., 2011). For instance, competition and disease transmission can increase as individuals get closer together (Yeaton and Cody, 1976; Getty, 1981; Brown and Bomberger Brown, 1996). On the other hand, individuals positioned near conspecifics can benefit from reduced predation pressure, improved exploitation of resources and improved transfer of social information (Hamilton, 1971; Ward and Zahavi, 1973; Wittenberger and Hunt, 1985; Turner and Pitcher, 1986; Brown and Bomberger Brown, 1996; Richner and Heeb, 1996; Donahue, 2006). Thus, males may use social cues pertaining to the distribution of other males when selecting a nest-site, and benefit by choosing nest-sites that improve expected breeding success (Coulson, 1968; Apollonio et al., 1990; Wagner, 1998; Charmantier and Perret, 2004; Bro-Jørgensen, 2008; Minias et al., 2012). Critically, this allows us to explore nest-site selection strategies by identifying correlations between social cues, individual decisions and breeding success (Giraldeau, 1997; Doligez et al., 2003; Dall et al., 2005; Boulinier et al., 2008).

Broadly, three social cues that could potentially influence nest-site selection due to effects on breeding success are i) an individual's location in relation to a group (group position: Coulson, 1968), ii) the spacing between individuals in the group (Doolan, 1981; Arak et al., 1990; Murphy and Floyd, 2005) and iii) the density of individuals in the local area (Fretwell and Lucas Jr, 1969; Doligez et al., 2003; Mariette and Griffith, 2012). In terms of group position, many studies have shown that breeding success can vary depending on whether an individual is situated in a peripheral or central area of a group (Apollonio et al., 1990; Krause, 1994; Fiske et al., 1998; Bro-Jørgensen,

2008; Howard et al., 2011). Spacing between individuals can also be an important cue for nest-site selection because the influence of conspecifics can vary with distance (Brown and Orians, 1970; Farris et al., 1997; Bates et al., 2010; Callander et al., 2011). Similarly, the influence of conspecifics on the environment, the interactions between individuals, and the use of social information are all expected to be density-dependent (Fretwell and Lucas Jr, 1969; Moller, 1987; Moller and Birkhead, 1993; Doligez et al., 2003; Callander et al., 2011).

Despite the potential for group positioning, spacing and local density (i.e. spatial positioning) to affect breeding success (and thus nest-site selection strategies), it is unclear how these effects vary across different mating systems (Westneat and Sherman, 1997; Velando and Freire, 2001; Charmantier and Perret, 2004; Descamps et al., 2009; Minias et al., 2012). Because female preference for nest-sites in certain spatial positions can determine breeding success in a resource-defence polygyny system, the mating strategy adopted by females may have interactive effects on site selection by males. For instance, polyandrous females in socially monogamous systems may prefer nest-sites that increase their opportunities for extra-pair copulations and males may establish nest-sites accordingly (Wagner, 1998). However, Ursprung et al. (2011) have suggested that females show less discrimination against the quality of a nest-site when the likelihood of nest-site failure is difficult to predict and females are polyandrous. In such cases, females appear to mate indiscriminately amongst males that are able to maintain a territory, and only discriminate against non-territorial males. Thus, there may be little variation in breeding success that can be explained by spatial position and, consequently, males may not respond to spatial positioning cues when selecting a nest-site. However, explicit tests of whether males respond to spatial positioning cues in such a polygynandrous mating systems are lacking.

We aimed to test whether spatial positioning affected nest-site decisions in male brown toadlets (*Pseudophryne bibronii* Gunther), and if these nest-site decisions are associated with improved breeding success. In this polygynandrous species, males predominantly adopt a strategy of resource-defence polygyny and select nest-sites that provide suitable juvenile habitat (Woodruff, 1976; Byrne and Keogh, 2009). Females spread their clutches over multiple nests as the suitability of nest-sites for juveniles is difficult to predict (Mitchell, 2001; Byrne and Keogh, 2009). Because females display a strategy of insurance polyandry, we predict that they do not discriminate between males that have chosen different spatial positions (Ursprung et al., 2011). We test this hypothesis using a capture-release approach that allowed us to test whether nest-site abandonment decisions made by settling male toadlets during the first few weeks of re-settlement

corresponded with the expected breeding consequences of those decisions. This approach also allowed us to control for previous experience, abiotic resource quality and nest-site availability within the same breeding season by effectively restarting settlement. We captured every calling male in an established population and measured the correlates of breeding success. We then released males back into the breeding area and recorded the establishment and abandonment of nest-sites during a re-settlement period to serve as an indicator of nest-site choice. If females do not discriminate between males in different spatial positions, males will be unable to improve their breeding success by choosing nest-sites in particular locations. Accordingly, we predict that nest-site abandonment will be unrelated to spatial positioning cues, and that there will be no correlation between breeding success and the spatial position of a male.

3.2 METHODS

3.2.1 *Study species and site*

The brown toadlet, *P. bibronii*, provides a good model to investigate the processes of nest-site selection in a system influenced by sexual selection. Brown toadlets are small (22–36 mm snout-vent length), terrestrial breeding Myobatrachid frogs that are endemic to temperate regions of south-eastern Australia (Tyler and Knight, 2009). At the beginning of autumn, males enter dry creek lines and drainage pans and establish shallow burrows under leaf litter in moist soil. Males produce acoustic signals from within their burrows, which advertises their presence to females and mediates interactions amongst themselves (Pengilley, 1971; Woodruff, 1976; Mitchell, 2001; Byrne, 2008; Heap et al., 2012). Females move through the chorus and select males with whom to mate, presumably based on the quality of acoustic and chemical signals and/or nest-site characteristics, and oviposition occurs in the burrow (Pengilley, 1971; Woodruff, 1976; Byrne and Keogh, 2007, 2009). The breeding season continues until winter rainfalls inundate the breeding habitat and tadpoles hatch into ephemeral pools. Because eggs are maintained at the calling site, it is possible to reliably measure how each male's behaviour and position in the chorus influences breeding success over the course of a breeding season.

The study was conducted on a toadlet population located within remnant *Eucalyptus*, *Banksia* and *Casuarina* woodland in Jervis Bay National Park, on the south-east coast of New South Wales, Australia. All work was conducted between 17 April and 21 May 2010.

3.2.2 *Male collection and measurements for the original distribution*

Within the breeding site, males were distributed amongst three discrete patches, representing three ephemeral creek-lines that converged at the study site. All the males in a patch were classified as belonging to the same group. Triangulation was used to estimate the location of nest-sites to within 20cm, and each nest-site was marked with a unique ID flag. For five consecutive nights, the nest-sites that contained a calling male (active sites) were recorded and new active sites were flagged. Three measurements of each male's maximum calling volume (SPL; sound pressure level relative to 20 μ Pa Root Mean Square) were made on 1-3 consecutive nights, and the mean for each individual was calculated. We used a Digitech QM-1589 SPL meter from a distance of 50cm using slow response speed and A weighting. All calling males from each group were collected over three nights, beginning from the third night after initial observations commenced ($N = 52$ males: group 1=23, group 2=13, group 3=16). When collecting males, the precise location of the nest-site was flagged, the presence of eggs was noted and the saturation of the soil at the nest-site was measured using an ICT soil moisture meter (model MPM-160B). Eggs were then counted and collected, leaving each nest empty. Males were placed in plastic zip-lock bags and brought to a field station (located 400m from the study site) where their mass (± 0.01 g) and snout-vent length (SVL; ± 1.0 mm) were measured. Digital photographs were taken of each male's unique ventral patterns; these photos provided a reliable identification key. After processing, males were placed into individual plastic containers (175 x 125 x 50mm). Each container was lined with moist sponge, to ensure toadlets were kept hydrated, and kept in a room with windows, so that toadlets experienced natural light/dark cycles.

3.2.3 *Male release and re-settlement observations*

Males were held at the field station for two nights and each group was released into the centre of one of the previously occupied (but now empty) patches (23 ± 11 m from their original site). The patch for release was chosen at random, and this resulted in one group being re-released into their original patch, and the other two groups being released into a neighbouring patch. One group of males was released on each of three nights. When releasing males, individual containers were arranged into a circle (with lids facing outwards), and opened sequentially after a five minute acclimation period. Toadlets were then allowed to leave their containers without interference. After approximately one hour, all containers were collected and researchers va-

cated the study site in order to reduce disturbance during the early stages of the re-settlement process.

After males were released, the study site was surveyed every night for 26 consecutive nights until the night of re-capture. During surveys, which lasted between 1 and 12 hrs depending on calling activity, any unmarked 'active sites' were flagged and any calling activity from previously identified 'active sites' was noted.

Observations ended and males were collected, by group, between 1800hrs and 0100hrs on the 31st -34th night after observations began ($N = 44$ males: group 1 = 17, group 2 = 13, group 3 = 14). Observations ended on the 31st night for all males, thus giving a re-settlement period of between 24 and 26 days, depending on the night of release. The procedure used during the original capture was repeated, whereby exact nest-sites were located and the presence of eggs noted. However, soil saturation was not measured, as was done during the original capture, because heavy rain on the night of capture would have inflated soil-moisture readings. Thus, linear interpolation of the moisture measurements from the first capture was used to estimate soil moisture. Any sites that were recorded as active during re-settlement, but were quiet when the chorus was recaptured, were classified as abandoned. Any sites in which males were captured were classified as occupied (non-abandoned), even though the resident may have still been in the process of selecting a site. Each individual was identified based on unique ventral patterns evident in digital photographs. Any individuals that were new to the chorus were photographed for the first time. All individuals were measured to determine mass and SVL. Males were held at the field station for 1-4 nights, after which time they were released at the nest-site from which they were most recently captured.

3.2.4 *Maps of nest-site distribution and calculations for nest-site characteristics*

In the time between the second capture and release, lines of string were laid through the chorus to serve as the axes of a coordinate system. The Cartesian coordinates for every nest-site from which a male was heard calling were recorded (i.e. original, re-settled and abandoned sites; $N = 126$).

To examine the effect of group position, individuals were classified as belonging to either the periphery or centre of their group using the classification system of Krause (1994). Specifically, a minimum convex polygon was drawn around all active sites for each group on each night. Active sites that were on the vertices of this polygon were classified as peripheral sites, and the sites that were not peripheral were classified as central. The group position for each nest-site on the

last day that the site was occupied was recorded (either the day that it was abandoned, or the day that the resident was captured). Because this method required at least 5 individuals in a group, 4 nest sites were unable to have their position classified as they were abandoned during the earliest days of re-settlement before minimum group size was achieved.

The harmonic mean of inter-individual distances (IID) for each frog was used as a measurement of spacing and the number of neighbours within two metres was used to represent local density. The harmonic mean of IID was used instead of the arithmetic mean because smaller distances are given relatively more weight than larger distances, which corresponds with the degradation of acoustic signals over distance and the likelihood that frogs are more influenced by close neighbours than distant neighbours (Wilczynski and Brenowitz 1988; Gerhardt et al. 1989). The data for nest-site location and a matrix of active sites across the nights of observation were used as the input for custom-made functions in R 2.14.1 (R Project contributors, <http://www.r-project.org/>) that calculated the geometric distances between each nest-site and any active sites for each night of the study. This data was used to calculate the mean IID and number of active sites within two metres for each nest-site on each night. We also used these methods to calculate the nearest nest-site that was previously occupied for each of the nest-sites established during re-settlement.

3.2.5 *Statistical analysis*

In order to determine whether our capture-release protocol had any adverse effects on the behaviour of males, we used paired *t*-tests on individuals that were captured twice to test whether they showed any significantly different choices with regards to local density or IID, using the measurements for their final nest-site location. Similarly, we used a χ^2 test for group position. We also compared the number and spread of eggs before and after our treatment, using the average rainfall between weather stations 068088 and 068151 obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au>) to account for differences in climate between the 26 days of our study and the 26 preceding days. Finally, we examined correlations between all of the predictor variables using a combination of *t*-tests, regression analysis, ANOVA and χ^2 tests. We used R 2.14.1 for all analyses.

We investigated the selection of nest-sites within the habitat using an information-theoretic (IT) approach (Burnham, 2004; Mazerolle, 2006; Burnham et al., 2010; Symonds and Moussalli, 2010), in which we compared numerous logistic-regression models that included the effects of local density, group position and spacing on nest-site abandonment during re-settlement and breeding success (whether there

were eggs at the nest) before capture. Comparisons were made on the basis of their corrected Akaike Information Criterion (AICc). We used spacing and local density measurements taken on the night of capture for the original population, under the assumption that the chorus had stabilised, and average values for the re-settlement period due to the dynamic nature of the groups. Average values were based on the mean measurements over the period in which a nest-site was active. In the model for breeding success, we included calling volume, SVL and soil saturation to provide some account of variation in individual and nest-site properties. In the model for abandonment, we included predicted soil saturation, distance to the nearest previously occupied nest-site, the first night at which a site was active and group ID to account for the effects of abiotic properties, settlement patterns and group properties.

Since we were interested in which spatial positioning factors could be important, we defined a set of seven models for each combination of local density, group position and IID. We also included seven models in which the set of non-positioning factors were included with each of these combinations to determine if other factors are necessary to consider. Finally, we included a null model to determine if neither spatial positioning, nor any other measured factors, provided any information for explaining abandonment or breeding success. After removing replicates with missing data (abandonment model=4; breeding success model=2), we tested the fit and suitability of the global model (i.e. all factors included) by following the guidelines of Logan (2010). Four replicates were removed from the abandonment model because we required at least 5 nest-sites within a group to calculate group position and these abandonments occurred in the first night of re-settlement when few other individuals were calling. Two replicates were removed from the breeding success model because these were two frogs that were only detected during the initial collection and thus had no measurements for calling volume. We used pseudo- r^2 (r_p^2) as a measure of the proportion of variance a model could explain in order to illustrate the suitability of our inferences ($1 - [\text{model deviance}/\text{null model deviance}]$). We then used the AICcmodavg package (Mazerolle, 2012) in R 2.14.1 to calculate the AICc for models of nest-site abandonment and QAICc for models of breeding success (QAICc used due to over dispersion). Additionally, we used this package to calculate the natural model average estimates, unconditional standard error and 95% confidence intervals for the effect of each factor. Of important note, inferences made on the basis of the IT approach do not rely on the interpretation of p -values, but on the inclusion of predictor variables in models that provide an explanation for the variables of interest.

3.3 RESULTS

We originally captured 53 males (52 had nest-sites, 1 was roaming the chorus) and re-captured 41 of these males (the remainder were assumed to have left the study site, as all calling males were captured). There were 3 previously unidentified males in the second capture, giving a re-settled population of 44 males. There were 30 sites that were recorded as being abandoned. Almost all individuals that re-settled (39/41) returned to their original patch of capture rather than settling within the release patch, although most (36/39) chose a new nest-site rather than returning to their original site or settling in a previously used site. The locations of nest-sites in the original and re-settled populations, in addition to the locations of abandoned nest-sites, are provided in [Figure 7](#).

3.3.1 Correlations among predictors

Although variance inflation factors for both abandonment and mating models did not exceed 5 for any factor, indicating that multicollinearity among predictors did not severely influence results ([Logan, 2010](#)), there were numerous correlations among the social positioning factors. Nest-sites were significantly closer to other nest-sites in central areas in both the original population ($t_{18.05} = 2.41$, $p = 0.027$), and during re-settlement ($t_{53.24} = 3.40$, $p = 0.001$). Similarly, IID decreased as local density increased in both populations (original population: $F_{1,49} = 17.45$, $r^2 = 0.25$, $p = 0.001$; during re-settlement: $F_{1,68} = 93.63$, $r^2 = 0.57$, $p = 0.001$; [Figure 8](#)). However, local density did not significantly differ between central and peripheral areas in the original population ($t_{32.56} = 1.62$, $p = 0.114$), but did during re-settlement ($t_{61.59} = 3.26$, $p = 0.002$). Of additional note, males called at significantly louder intensity from nest-sites in areas with higher local density ($F_{1,48} = 6.02$, $r^2 = 0.09$, $p = 0.018$; [Figure 9](#)) and less isolated nest-sites ($F_{1,48} = 5.71$, $r^2 = 0.09$, $p = 0.021$) in the original population. The local density of nest-sites was also significantly greater in wetter areas than dry areas ($F_{1,49} = 4.37$, $r^2 = 0.06$, $p = 0.042$). All other correlations were not significant ($p \geq 0.095$), other than those mentioned below.

3.3.2 The effect of capture-release

Individual males did not show any significant differences in their choice of nest-site with regards to local density ($t_{39} = 1.56$, $p = 0.127$) or IID ($t_{39} = 1.90$, $p = 0.064$) between their original choice and their choice after capture-release. Similarly, males were significantly more likely to re-settle in the same group position in which they were

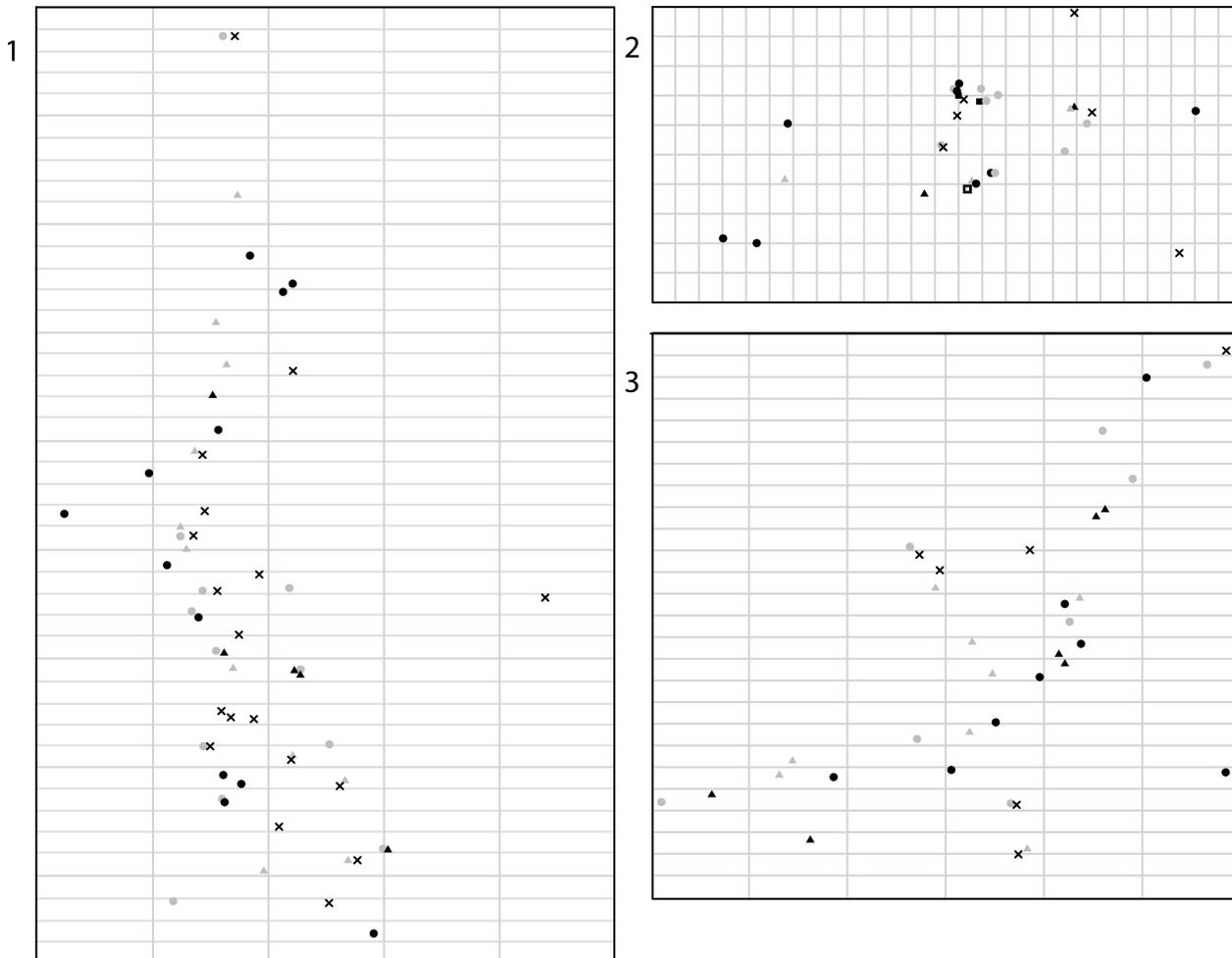


Figure 7: Map showing the distribution of abandoned (crosses) and occupied nest-sites with (triangle) or without (circles) eggs present in groups 1, 2 and 3. The original distribution of nest-sites is in grey, and the re-settled population is in black. Three individuals returned to their original nest-site in group 2, and these nest-sites are represented by black squares. The only male to re-settle on a nest-site in which he had previous breeding success is represented by a hollow black square. Grid-lines indicate 1m intervals. Some points are jittered for clarity

originally captured ($\chi^2_1 = 6.22$, $p = 0.013$). Re-settled nest-sites were also significantly more likely to be established closer to original nest-sites, as the distance of a nest-site from the nearest original nest-site decreased with density ($F_{1,68} = 11.42$, $r^2 = 0.13$, $p = 0.001$), increased with IID ($F_{1,68} = 20.79$, $r^2 = 0.22$, $p = 0.001$) and was greater in central areas ($t_{39,86} = 2.46$, $p = 0.018$). Previous breeding success did not predict breeding success during re-settlement ($\chi^2_1 = 1.07$, $p = 0.301$), indicating that both previously successful and unsuccessful males had the opportunity to mate during re-settlement. Furthermore, there were no significant differences in the final choice of nest-site between males that had previous mating experience and those that did not, with regards to local density ($t_{37,19} = 0.13$, $p = 0.895$), group position ($\chi^2_1 = 1.71$, $p = 0.191$), IID ($t_{37,83} = 0.23$, $p = 0.823$), distance to nearest previously occupied nest ($t_{37,57} = 0.76$, $p = 0.452$), or distance to their original nest-site ($t_{37,21} = 0.85$, $p = 0.403$). Fewer eggs were found in the nests of fewer males during the re-settlement period (original population: 2306 eggs in 44% of nests; re-settled population: 1103 eggs in 35% of nests), which could suggest that capture-release impaired the ability of males to attract females. However, these patterns are also consistent with rainfall patterns during the study period, as calling behaviour correlates with moisture (Mitchell, 2001). Specifically, the 26 days of re-settlement tended to be drier than the 26 days preceding capture-release, as there was 91.2mm of rain over 14 days prior to the study and 15.1mm of rain over 6 days during re-settlement. Furthermore, the $\sqrt{\text{average rainfall/day}}$ tended to be higher prior to capture-release ($0.96\text{mm} \pm 1.64$) than during re-settlement ($0.28\text{mm} \pm 0.72$), although this difference was not significant ($t_{34,39} = 1.95$, $p = 0.060$). Additionally, the breeding population may have been active for at most twice as long as the re-settlement period prior to our study, which is consistent with the number of eggs that we counted. On the basis of this data, and a previous study that indicates males can sometimes change nests without interference (Byrne and Keogh, 2009), we assume that the capture-release protocol did not have any overly detrimental effects on the nest-site selection strategies exhibited by the males of the study population.

3.3.3 Effect of spatial positioning on nest-site abandonment

At best, we could explain up to a quarter of the variance in nest-site abandonment ($r^2_p = 0.24$). The best candidate set of models for explaining nest-site abandonment ($\sum w \leq 0.95$) all include at least one spatial positioning factor (Table 3). Of this set, only the full model ($\Delta\text{AICc} = 4.00$) contains non-positioning factors, but it is more than seven times less likely to be the best candidate model than considering all positioning factors on their own ($\Delta\text{AICc} = 0.00$). Furthermore,

Table 3: The set of models examining the effect of spatial positioning and other factors on the abandonment of nest-sites in a population of brown toadlets

MODEL	K	AIC _c	Δ AIC _c	w	Σw	LL	ER
Pos+Den+IID	4	87.61	0.00	0.32	0.32	-39.50	1.00
Pos+Den	3	88.05	0.45	0.25	0.57	-40.85	1.25
Den+IID	3	88.32	0.71	0.22	0.79	-40.98	1.42
Den	2	89.69	2.09	0.11	0.90	-42.76	2.84
Pos+Den+IID+Other (F)	9	91.61	4.00	0.04	0.94	-35.30	7.38
Pos+Den+Other	8	92.85	5.24	0.02	0.97	-37.24	13.72
Null model	1	94.42	6.81	0.01	0.98	-46.18	30.12
Den+Other	7	95.69	8.08	0.01	0.98	-39.94	56.91
IID	2	95.76	8.15	0.01	0.99	-45.79	58.90
Pos	2	95.99	8.38	0.00	0.99	-45.91	66.16
Pos+IID	3	96.54	8.93	0.00	1.00	-45.09	87.07
Other	6	97.89	10.28	0.00	1.00	-42.28	170.86
Pos+Other	7	98.44	10.83	0.00	1.00	-41.32	224.59
IID+Other	7	100.25	12.65	0.00	1.00	-42.22	557.29
Den+IID+Other	8	100.36	12.75	0.00	1.00	-41.00	588.28
Pos+IID+Other	8	100.36	12.75	0.00	1.00	-41.00	588.28

The full model (F) has $r_p^2=0.24$

Pos: centre or periphery of group; IID: harmonic mean of inter-individual distances (m); Den: number of neighbours within 2m; Other: predicted soil saturation (%)

+ group ID + day of first call + nearest previously occupied nest-site (cm); K: number of factors in the model (includes intercept); w : AIC weight; Σw : cumulative

AICc weight; LL: log-likelihood; ER: evidence ratio

Table 4: Model average estimates for spatial positioning and other factors that predict nest-site abandonment in a population of brown toadlets

FACTOR	ESTIMATE	SE	LOWER CI	UPPER CI	w
Local density ^a	1.82	0.82	0.21	3.43	0.97
Central position ^b	-1.14	0.66	-2.43	0.15	0.64
IID ^a	0.23	0.15	-0.06	0.51	0.59
Group 1 vs 2	-0.92	1.04	-2.95	1.11	0.08
Group 1 vs 3	-0.63	0.72	-2.04	0.78	0.08
First call	-0.03	0.05	-0.12	0.06	0.08
Predicted moisture	0.02	0.03	-0.05	0.08	0.08
Nearest original nest	-0.01	0.00	-0.02	0.00	0.08

Confidence intervals (CI) are for the 95% range; w : AICc weight

^amean value for period of nest-site occupation

^bvalue on night of capture

models containing positioning factors are 30 times more likely to be the best candidate model than the null model that contains no factors. Model averaging estimates provide strong evidence that males are more likely to abandon nest-sites as the local density of males surrounding the site increases (Table 4, Figure 8). Furthermore, there is good evidence to suggest that nest-sites in peripheral positions and more isolated areas (those with greater inter-individual distances) are more likely to be abandoned (Table 4, Figure 8). However, in these latter two cases, the 95% CI for the true value of effect size includes zero (but only by a relatively small degree).

3.3.4 Effect of spatial positioning factors on breeding success

Variation in breeding success could not be substantially explained by considering spatial positioning factors, soil saturation, individual calling volume and SVL ($r_p^2 = 0.11$). Furthermore, inclusion of spatial positioning variables could only provide an equivalent amount of information as a null model that did not consider any measured variables (Table 5). Model averaging indicates that there were no factors that were likely to have had a strong effect on breeding success (Table 6, Figure 9).

3.4 DISCUSSION

We aimed to investigate whether density, group positioning and spacing (spatial positioning) affected breeding success and nest-site selec-

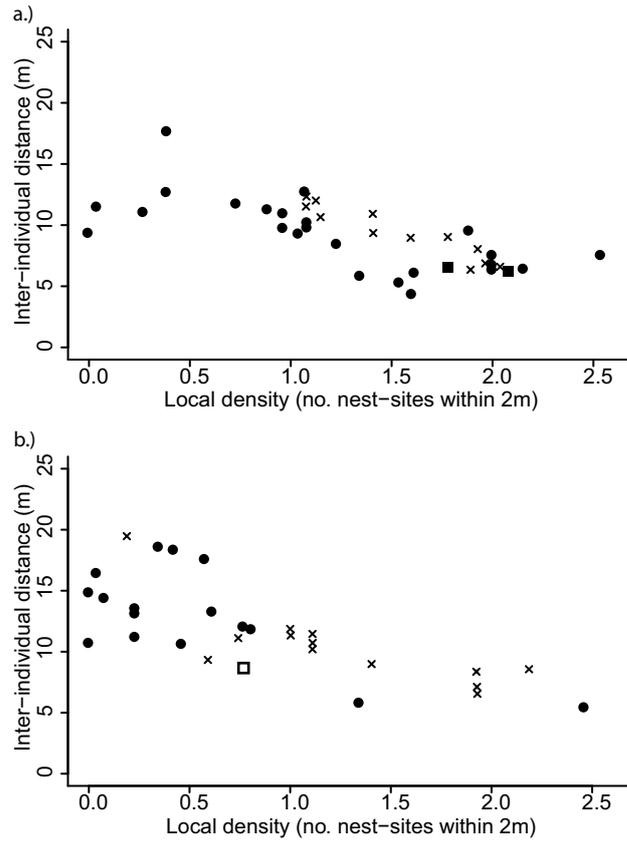


Figure 8: Correlations between spatial positioning cues associated with a nest-site and whether the site was abandoned (crosses) or occupied (circles) by the end of the study period for (a) central and (b) peripheral group positions; site fidel males are represented by squares, with the hollow square as in Figure 7

Table 5: The set of models examining the effect of spatial positioning and other factors on breeding success (whether there were eggs in the nest) in a population of brown toadlets before capture and release

MODEL	K	QAIC _C	ΔQAIC _C	<i>w</i>	∑ <i>w</i>	QLL	ER
Null model	2	64.49	0.00	0.25	0.25	-30.12	1.00
Den	3	65.16	0.67	0.18	0.43	-29.32	1.40
Pos	3	66.16	1.66	0.11	0.54	-29.82	2.30
Pos + Den	4	66.25	1.76	0.10	0.64	-28.68	2.41
IID	3	66.40	1.91	0.10	0.74	-29.94	2.59
Den + IID	4	67.52	3.03	0.06	0.80	-29.32	4.55
Pos + IID	4	67.83	3.34	0.05	0.84	-29.47	5.30
Den + Other	6	68.05	3.56	0.04	0.89	-27.05	5.93
Other	5	68.46	3.97	0.03	0.92	-28.55	7.28
Pos + Den + IID	5	68.71	4.22	0.03	0.95	-28.67	8.23
IID + Other	6	69.90	5.40	0.02	0.97	-27.97	14.90
Pos + Den + Other	7	70.66	6.17	0.01	0.98	-27.00	21.88
Pos + Other	6	71.05	6.56	0.01	0.99	-28.55	26.56
Den + IID + Other	7	72.57	8.08	0.00	0.99	-27.95	56.79
Pos + IID + Other	7	72.57	8.08	0.00	1.00	-27.95	56.79
Pos + Den + IID + Other (F)	8	73.34	8.84	0.00	1.00	-26.91	83.25

The full model (F) has $r_p^2 = 0.11$

Pos: centre or periphery of group; IID: harmonic mean of inter-individual distances (m); Den: number of neighbours within 2m; Other: soil saturation (%) + calling volume (dBA) + SVL (mm); K: number of factors in the model (includes intercept and correction for over-dispersion); *w*: QAIC weight; ∑*w*: cumulative QAICc weight; QLL: quasi-log-likelihood; ER: evidence ratio

Table 6: Model average estimates for spatial positioning and other factors that predict breeding success (whether there were eggs in the nest) in a population of brown toadlets before capture and release

FACTOR	ESTIMATE	SE	LOWER CI	UPPER CI	<i>w</i>
Local density ^a	-0.33	0.26	-0.84	0.17	0.43
Central position ^a	0.61	0.73	-0.81	2.04	0.32
IID ^a	0.04	0.08	-0.13	0.20	0.26
Calling volume	0.33	0.24	-0.14	0.80	0.13
SVL	-0.02	0.32	-0.65	0.61	0.13
Moisture	0.01	0.02	-0.03	0.06	0.13

Confidence intervals (CI) are for the 95% range; *w*: QAICc weight

^avalue on night of capture

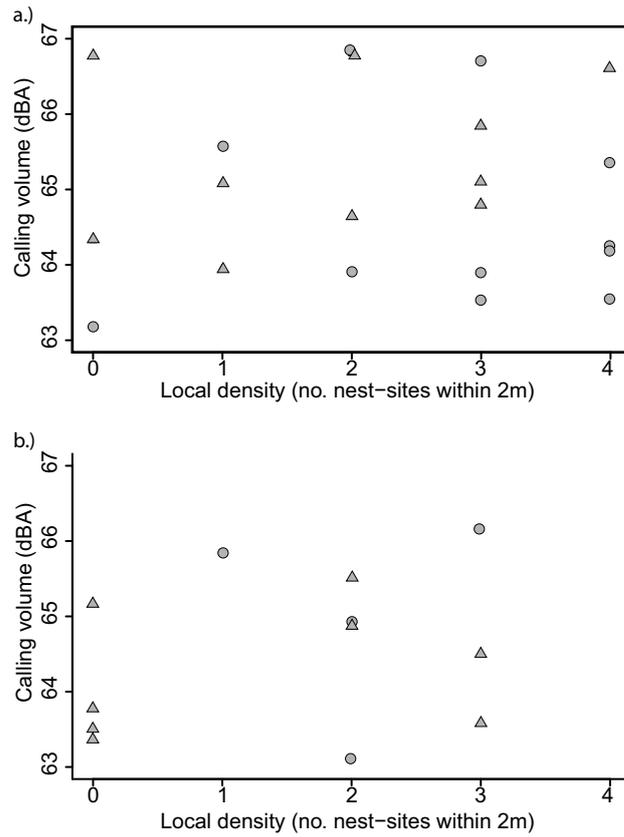


Figure 9: Correlation between local density (number of nest-sites within 2m) and calling volume (dBA) for nest-sites in the (a) centre or (b) periphery of the original population, showing nest-sites that had eggs present (triangles) and no eggs present (circles)

tion in a resource-defence system, in which females spread their eggs amongst multiple nests that are difficult to assess and males choose sites associated with suitable juvenile habitat (Geiser and Seymour, 1989; Chambers et al., 2006). Because the study ended before the termination of breeding, our results are primarily applicable to the first few weeks of re-settlement. We tested the hypotheses that, in this breeding system, i) males do not have preferences for nest-sites in certain spatial positions, and ii) there is no predictable variation in breeding success across different spatial positions. Correspondingly, we found that spatial positioning factors did not predict breeding success. Therefore, resource-defending males may not be able to improve breeding success with preferences for nest-sites in certain spatial positions when females do not strongly discriminate between different nest-sites. However, in contrast to this result, males were more likely to abandon nest-sites as local density increased. Furthermore, males may be more likely to abandon nest-sites on the periphery of a group and in more isolated areas. These results indicate that males arranged themselves according to the placement of other males. Thus, there must be ultimate explanations for these nest-site selection criteria that are independent of breeding success.

These results are consistent with those of Ursprung et al. (2011), who found that polyandrous females of the frog species *Allobates femoralis* do not discriminate among males based on spatial positioning, providing that the male can be discriminated from the background noise. Both *P. bibronii* and *A. femoralis* share a similar mating system, in which females split their eggs amongst multiple males (who display resource-defence polygyny) as a response to unpredictable environments (Byrne and Roberts, 2012). Together, these studies suggest that males are unable to improve their breeding success by choosing nest-sites in particular spatial locations when females benefit from spreading their clutch over multiple nest-sites. This pattern is in contrast to other resource-defence mating systems, in which females show strong bias towards particular nest-sites and males can thus improve their breeding success by choosing nest-sites that females prefer (Verner and Willson, 1966; Wells, 1977; Yasukawa, 1981; Christy, 1983; Kodric-Brown, 1983; Askenmo, 1984; Balmford et al., 1992; Bensch and Hasselquist, 1992; Gerhardt and Huber, 2002; Refsnider and Janzen, 2010). Thus, the mating system adopted by a population can influence the cues that individuals respond to when selecting nest-sites.

The lack of a strong effect from positioning factors on breeding success conforms to the prediction that these factors have limited influence on breeding success when polyandry reduces the costs of nest failure (Ursprung et al., 2011). However, our results imply that males were more likely to abandon nest-sites in certain spatial position, which suggests that spatial positioning can still be associated

with fitness. Specifically, our findings clearly indicate that males were more likely to abandon nest-sites as local density increased. Additionally, there are trends for males to abandon peripheral and isolated nest-sites. These decisions could be made according to a direct influence of spatial positioning on a more complete index of fitness than breeding success, or due to environmental constraints that limit a male's available choices.

Spatial positioning may directly influence the survival of both males and their offspring (Coulson, 1968; Hamilton, 1971; Gross and MacMillan, 1981; Krause, 1994; Descamps et al., 2009; Refsnider and Janzen, 2010; Minias et al., 2012; Molloy et al., 2012). For instance, the abandonment of peripheral and isolated nest-sites may function to reduce the predation pressure on males. According to the selfish-herd hypothesis, more isolated individuals, and those on the periphery, can face greater predation risk (Hamilton, 1971). Although these toadlets possess toxic skin compounds that make them distasteful to predators (Daly et al., 1990), solitary or peripheral individuals may be more susceptible to attack from the parasitoid fly, *Batrachomyia* spp. These flies have been observed to parasitize *P. bibronii* and other *Pseudophryne* species (Lemckert, 2000; Schell and Burgin, 2001), and although not directly fatal, may reduce fitness by impairing the male's condition and ability to call and attract females. However, we do not know the level of parasitism experienced by *P. bibronii* in our study population and thus can not currently determine whether this pressure is enough to explain the observed preferences for grouping. Similarly, nest-sites on the periphery or in isolated areas may be associated with lower offspring survival if, for instance, peripheral pools are quicker to dry or experience greater tadpole-predation pressure (e.g. Coulson, 1968). In any case, we require tests that determine whether offspring survival is the ultimate reason for male nest-site selection by observing the fate of eggs and tadpoles that were deposited in different spatial locations.

Alternatively, spatial positioning may correlate with competition, as males were more likely to abandon nest-sites in dense areas and thereby show some degree of local dispersal. In particular, male frogs that occupy nest-sites in dense areas can suffer from higher levels of male-male competition and have less distinctive (and hence less attractive) advertisement signals (Gerhardt and Huber, 2002; Wells, 2007). This interpretation is supported by an extensive literature concerning the reproductive costs of competition and masking interference in frogs (Gerhardt and Huber, 2002). Furthermore, our results suggest that males can compete against neighbours by calling louder, as individuals significantly increased their calling volume as the local density increased. Because calling loudly is energetically costly and can increase the risk of desiccation (Taigen and Wells, 1985; Prestwich

et al., 1989; Prestwich, 1994; Mitchell, 2001), males may incur physiological costs from competition. Furthermore, energy and moisture resources are critical for participating in the chorus over extended periods of time, and the ability to participate in the chorus directly influences breeding success in many frogs (Gerhardt and Huber, 2002; Wells, 2007). Therefore, males that suffer more physiological costs may have lower breeding success, but only over longer periods of time than that considered in this study (as we found no effect of local density on breeding success). Thus, males may be using a cue that correlates with the number of nearby neighbours to evaluate the quality of a nest-site in terms of expected competition and masking interference.

Males may also be constrained by uncertainty regarding the abiotic quality of their nest-site. In *P. bibronii*, the survival of offspring is principally determined by local flooding conditions (Woodruff, 1976; Bradford and Seymour, 1988; Geiser and Seymour, 1989; Mitchell, 2001), which may be difficult for breeding males to predict over the period of a single season (Brissonette, 1997; Byrne and Keogh, 2009). However, males may be able to use information gathered from previous breeding seasons to make nest-site decisions that better reflect the local abiotic environment (Switzer, 1993, 1997). If a sufficient number of males have information on abiotic quality and make informed choices, then the abandonment of nest-sites in peripheral and isolated areas may reflect males that are less informed choosing to settle near conspecifics that are perhaps more informed (conspecific attraction: Stamps, 1988). Simulations suggest that individuals can benefit from using conspecific attraction in weakly predictable environments because settling near others can allow individuals to effectively copy the decisions of more informed individuals (Doligez et al., 2003). Such copying behaviour is also predicted to occur when there are high costs associated with decision making (Frommen et al., 2008), such as the cost of choosing a nest-site that fails. Thus, males may increase the likelihood of settling in an area of sufficient abiotic quality by using group position and spacing as independent cues for conspecific presence. However, this hypothesis assumes that there are a sufficient number of informed individuals in the population. Testing this hypothesis would require long-term observations of nest-site selection and environmental variability to determine if experienced males make better nesting decisions. Manipulations that show individual males are attracted to occupied areas and groups converge upon more predictable areas are also required. If this hypothesis is supported, it would suggest that abiotic uncertainty can drive male spacing patterns, in addition to and independently from, driving sequential polyandry.

A limited availability of suitable nest-sites could also constrain nest-site selection (Stewart and Pough, 1983; Donnelly, 1989a; Newton, 1994; Heying, 2004). That is, males may have abandoned sites that were unsuitable for the establishment of a nest-site in terms of abiotic or biotic quality, and this could result in the aggregation or dispersal of males depending on the distribution of limited environmental resources. Under certain resource distributions, such a process could correlate with spatial positioning factors (Donnelly, 1989b). For instance, if there is a decreasing gradient of resource quality from a central area, individuals on the periphery may be more likely to abandon a nest-site because of limited resources rather than their position in relation to a group that inhabits the resource patch. This hypothesis could be tested by the addition of suitable nest-site locations, as has been done in other systems (Stewart and Pough, 1983; Donnelly, 1989a,b).

In conclusion, our data support the hypothesis that insurance polyandry homogenises breeding success within a group, rather than driving competition for certain positions that improve breeding success (Ursprung et al., 2011). However, males still used spatial positioning cues for selecting nest-sites, which suggests that a male's spatial position (or a factor that correlates with spatial position) has direct fitness consequences that are independent of breeding success. Thus, we require studies that incorporate a more complete measure of fitness (e.g. tadpole survival) to improve our understanding of nest-site selection by males. Additionally, further investigations into the influence of polygamy on the use of spatial positioning cues in nest-site selection strategies will add to our understanding of the factors influencing the evolution and ecological influence of different mating systems. This understanding will then allow us to make better predictions concerning the distribution and skew of reproductive success in populations based on their breeding ecology.

Part II

THE RELATIONSHIP BETWEEN LANDMARKS
AND SOCIAL INTERACTIONS

THE ADOPTION OF LANDMARKS FOR TERRITORIAL BOUNDARIES

Although behaviours associated with territory maintenance are extensively studied, little is known about the establishment of territorial boundaries, a key process influencing individual fitness and population demography. In this regard, conspicuous features of the landscape and constructions such as scent-marks (landmarks) can have an effect on whether and where boundaries are established. Landmarked boundaries have also been associated with altered social interactions, particularly contests that take place on boundaries. Some of these landmarks physically constrain a resident's perception or movement and may thus make the use of space beyond the landmark too costly. Other landmarks are purely conspicuous and appear to have no constraining effect, yet still have strong influences on boundary location by affecting social interactions. Factors that may influence whether a landmark is adopted for a boundary include the properties of the resident, properties of the landmark and the rate of encounter between neighbours. The purpose of this review is to consolidate and explicitly describe hypotheses relating to landmarked boundaries and highlight areas most in need of research. Ultimately, understanding the decision to adopt landmarked boundaries and the implications of these decisions on territorial populations is critical for understanding the link between landscapes, individual decisions and population ecology.

4.1 INTRODUCTION

Territoriality, or site-specific intolerance of others, has evolved numerous times in a diversity of taxonomic groups (Alexander, 1961; Brown, 1964; van den Assem, 1967; Dyson-Hudson and Smith, 1978; Davies, 1980; Hart, 1987; Stamps, 1988; Ostfeld, 1990). Functionally, territoriality provides individuals with the benefits of having exclusive or priority access to resources within a given space (e.g. food, mates, shelter). Thus, territoriality will evolve when these benefits outweigh the costs of maintaining dominance in the area through aggression and display (Brown, 1964). The existence of territoriality within a population has important spatial, social and demographic consequences that lead to variation in mortality and reproductive success (Patterson, 1980; Elliott, 1990; Calsbeek and Sinervo, 2002). These fitness consequences of territoriality have important implications for

the evolution of other phenomena such as aggression, communication and reproductive strategies (e.g. Tinbergen, 1957; Beletsky and Orians, 1987; McGregor, 1993; Sinervo and Lively, 1996; Morbey and Ydenberg, 2001; Kokko et al., 2006).

An important feature of a territory is the boundary, within which the resident is intolerant of other individuals. Boundaries spatially define the territory and determine the effect that the territory and its resident have on a population. Therefore, much of the research into territoriality has focused on the spatial location of boundaries in response to environmental and social pressures (Adams, 2001). However, we know little about how the location of the boundary depends on the interactions between individuals (Maynard Smith, 1982; Stamps, 1994; Adams, 2001; Pereira et al., 2003). These interactions appear to be influenced by conspicuous features of the landscape, or landmarks. Additionally, some animals construct landmarks to delineate territorial boundaries. Exploring the relationship between landmarks and territorial boundaries is therefore important for understanding the decisions involved in boundary formation and maintenance and for how the landscape influences the division of space between individuals (St. Louis et al., 2004; Smith, 2011). Understanding these processes is then crucial for explaining variation between and within territorial populations and, ultimately, the evolution of territoriality.

In this review, we outline the manner in which landmarks affect territoriality through their influence on the location of boundaries and the interactions that take place there. We consider landmarks that do not constitute complete physical barriers to movement, but rather act as barriers due to the consequences of crossing them. To avoid confounding landmarks with other types of territorial resource, we do not explicitly consider landmarks that provide or diminish reproductive and survival benefits (e.g. food, reproductive opportunities, improved visibility, shelter). We focus instead on landmarks that have no cost or value beyond their use as a boundary. The review begins with a synthesis of current research on the adoption of landmarked boundaries. This includes both direct and indirect evidence for an effect of landmarks on territorial boundaries and their individual and population level consequences. We then define two types of landmark, based on whether or not they impose a physical constraint on an individual's perception or movement. Even when boundaries impose no physical constraint, animals may sacrifice potentially larger territories in order to have a conspicuously marked boundary. We discuss how this behaviour could have evolved in terms of spatial associations or conventions to avoid agonistic costs. We then highlight the potential factors that could influence whether or not a given landmark is adopted for a boundary. We conclude with a brief summary and highlight key areas requiring greater research focus.

4.2 ADOPTION OF LANDMARKED BOUNDARIES

Anecdotal reports, correlations and territorial maps suggest that boundaries can be significantly more common along natural or artificial features and features constructed by territorial residents than other areas [Table 7; McCartan and Simmons, 1956; Kalleberg, 1958; Barlow, 1961; Ficken, 1962; Miller, 1964; Baylis, 1974; Itzkowitz, 1974; Finck, 1990; Tupper and Boutilier, 1995]. Red grouse (*Lagopus lagopus scoticus*), for example, consistently establish boundaries along features such as hillocks, ridges, walls, steep banks and streams (Watson and Miller, 1971). Similarly, St. Louis et al. (2004) objectively determined the territorial borders of ovenbirds (*Seiurus aurocapilla*) and black-throated blue warblers (*Dendroica caerulescens*), as well as changes in vegetation, rocks, topography, water and trails. Results showed that the areas that were associated with a sharp decline in space use (i.e. territory boundaries) occurred in the same areas as sharp changes in the presence of bare rocks and slopes in topography, which are features unlikely to be used as internal territorial resources. This suggests that some landmarks are valuable for use as a boundary even if they are of no value in other circumstances. Experiments that manipulate the presence of landmarks have since demonstrated that a relationship between landmarks and territorial boundaries is not a coincidence, but can be due to individuals modifying their behaviour (Table 8). For example, Eason, Cobbs & Trinca (1999) placed dowels in an established neighbourhood of cicada killer wasps (*Sphecius speciosus*) and showed that the wasps adjusted the arrangement of their territories to utilise the dowels for their boundaries within 24 hours. Although explicit studies on landmarked boundaries are limited, there are a number of hypotheses relating to the effects of landmarked boundaries on individuals and populations, the types of landmark used and the conditions under which a landmark is adopted for a boundary. Below is a consolidation and explicit description of these hypotheses, with notes on the areas most in need of research.

4.3 THE EFFECT OF LANDMARKED BOUNDARIES ON INDIVIDUAL BEHAVIOUR AND POPULATIONS

4.3.1 Individual behaviour

The adoption of landmarks for boundaries has been associated with altered social interactions between individuals, of which reductions in the frequency and intensity of contests are relatively common (Table 7: 3, 9, 10, 14; Table 8: 1, 5, 6, 7, 8, 9, 11). For example, cicada killer wasp (*S. speciosus*) contests can be less frequent and of shorter duration along boundaries marked by dowels compared to non-landmarked

Table 7: Species in which there is non-experimental evidence for landmarked boundaries, with IDs that are cited in the text

ID	SPECIES	DATA AVAILABLE		LANDMARK TYPES		SOURCE
		C	M	C	N	
MAMMALS						
1	Golden jackals, <i>Canis aureus</i>	X	X		X	Macedonald 1979
2	Wolf, <i>Canis lupus</i> and <i>Canis simensis</i>	X	X		X	Sillero-Zubiri and Macedonald 1998; Zub et al. 2003
3	European badger, <i>Meles meles</i>	X	X		X	Kruuk 1978
4	Oribi, <i>Ourebia ourebi</i>	X			X	Brashares and Arcese 1999
5	Tiger, <i>Panthera tigris</i>	X	X		X	Smith et al. 1989
6	Vicuna, <i>Vicugna vicugna</i>		X		X	Kotford 1957
BIRDS						
7	Black-throated blue warbler, <i>Dendroica caerulescens</i>	X	X		X	St. Louis et al. 2004
8	Red grouse, <i>Lagopus lagopus scoticus</i>		X			Watson and Miller 1971
9	Pukeko, <i>Porphyrio porphyrio melanotus</i>		X			Craig 1979
10	Savannah sparrow, <i>Passerculus sandwichensis</i>		X		X	Potter 1972; Welsh 1975; Reid and Weatherhead 1988
11	Willow warbler, <i>Phylloscopus trochilus</i>		X			May 1949
12	Ovenbird, <i>Seiurus aurocapilla</i>	X	X		X	Ortega and Capen 1999; St. Louis et al. 2004; Bayne et al. 2005
13	Rufous-collared sparrow, <i>Zonotrichia capensis</i>		X			Laiolo 2011
REPTILES						
14	Rainbow lizard, <i>Agama agama</i>		X		X	Harris 1964
FISH						
15	Bream, <i>Abramis brama</i>		X		X	Fabricsius 1951
16	Black surfperch, <i>Embiotoca jacksoni</i>		X			Hixon 1981
17	Redlip blennies, <i>Ophioblennius atlanticus</i>		X		X	Nursall 1977
18	White Cloud Mountain minnow, <i>Tanichthys albonubes</i>		X		X	Fabricsius 1951
19	Mozambique tilapia, <i>Tilapia mossambica</i>		X		X	Barlow 1974

The data available can be either (C) quantitative correlations between landmarks and boundaries, or (M) maps that note both territorial boundaries and landmark positions.

The types of landmark observed, if identifiable, could have been (C) constraining or (N) nonconstraining

Table 8: Species in which there is experimental evidence for landmarked boundaries, with ID's that are cited in the text

ID	SPECIES	LANDMARK TYPES		SOURCE
		C	N	
MAMMALS				
1	Mouse, <i>Mus musculus</i>	X	X	Mackintosh 1973
BIRDS				
2	Ovenbird, <i>Seiurus aurocapilla</i>			Machtans 2006
3	Forest-dependent birds			St. Clair 2003
REPTILES				
4	Bronze anole, <i>Anolis aeneus</i>	X		Eason and Stamps 1992
FISH				
5	Mudskipper, <i>Boleophthalmus boddarti</i>	X		Clayton and Vaughan 1986; Clayton 1987
6	Pupfish, <i>Cyprinodon sp.</i>	X	X	Kodric-Brown 1978
7	Three-spined stickleback, <i>Gasterosteus aculeatus</i>	X		van den Assem 1967
8	Rose bitterling, <i>Rhodeus ocellatus</i>		X	Smith 2011
9	Blockhead cichlid, <i>Steatocranus casuarius</i>		X	LaManna and Eason 2003
ARTHROPODS				
10	Mantis shrimp, <i>Gonodactylus oerstedii</i>		X	Hazlett 1978
11	Cicada killer wasp, <i>Sphecius speciosus</i>		X	Eason et al. 1999

The types of landmark observed, if identifiable, could have been (C) constraining or (N) nonconstraining

boundaries on the same territory (Eason et al., 1999). In such situations, landmarks have value as a boundary because they increase the tactical defensibility of the territory: the efficiency at which it can be defended (Eason et al., 1999). In addition to being less costly, contests may be more (Table 7: 10) or less (Table 7: 9; Table 8: 11) likely to occur at landmarked than non-landmarked sections of the boundary and the rate of interactions unrelated to boundary defence may also be reduced (Table 7: 13).

4.3.2 Populations

The use of landmarks for boundaries can be expected to have an effect on territorial populations, since adopting landmarks for boundaries can influence the size, shape and defensibility of territories (Table 7: 8, 18; Table 8: 1, 6). For example, the presence of landmarks has been shown to reduce territory size (Table 7: 18; Table 8: 1, 6, 7, 9, 10; Kalleberg, 1958; Baylis, 1974) and affect territory shape (Table 8: 4; Grant, 1968). Consequently, these properties can influence how many individuals a habitat is able to support (Fretwell and Lucas Jr, 1969; Patterson, 1980; Stamps and Krishnan, 1990; Adams, 2001). Specifically, the adoption of landmarked boundaries has been associated with increases in the number of individuals settling in an area (Table 7: 15, 18, 19; Table 8: 1, 5, 6, 7, 9; Miller, 1964; Baylis, 1974). This may be because territories do not need to be as big as they would otherwise, due to the decreased costs of sharing space (Baylis, 1974; Clayton, 1987; LaManna and Eason, 2003). For instance, competing pairs of blockhead cichlids (*Steatocranus casuarius*) were able to maintain exclusive territories when there was a row of unimposing, yet conspicuous, rocks at the mid-point between their nests, but rarely (<7% of cases) when the rocks were absent, despite the available area being identical (LaManna and Eason, 2003). On the other hand, the adoption of landmarked boundaries may have little influence on population abundance or even reduce it (Table 7: 10, 12). This could occur if adopting landmarked boundaries results in larger territories due to the reduction in defence costs or wide spacing between landmarks (Reid and Weatherhead, 1988). Additionally, the arrangement of landmarks may make areas of the habitat unsuitable (Bayne et al., 2005). Despite the apparent association between landmarked boundaries and population abundance, factors that influence whether this relationship is positive, negative or neutral have not been adequately explored.

In addition to affecting population abundance, landmarked boundaries may increase the long-term stability of an arrangement of territories and thus a territorial population (Reid and Weatherhead, 1988; Eason et al., 1999; LaManna and Eason, 2003; Mesterton-Gibbons and

Adams, 2003). Landmarked boundaries have been observed to persist longer than non-landmarked boundaries, although strong evidence is still lacking (Table 7: 3, 9; Table 8: 5, 6, 9). For instance, competing pairs of blockhead cichlids (*S. casuarius*) could maintain a stable boundary for at least three hours when boundaries occurred over a row of rocks but not when the rocks were absent (LaManna and Eason, 2003). Similarly, communal swamphen (*Porphyrio porphyrio melanotus*) boundaries were better defined and more resilient to intrusion when they were over drains and fences than when they were in open paddocks (Craig, 1979). In addition to being more persistent over time for individual owners, landmarked boundaries can persist through multiple owners (Table 7: 10; Table 8: 6). For example, when the same rock was presented to different populations of pupfish (*Cyprinodon sp.*), the location and configuration of boundaries over topographical features was remarkably consistent between independent settlement events (Kodric-Brown, 1978). These results imply that the adoption of landmarked boundaries may result in less variation in population abundance over time because the size and occupancy of territories remains constant. In contrast, Nursall (1977) found that redlip blennies (*Ophioblennius atlanticus*) constantly re-defined their boundaries over different topological features. Clearly, long-term comparisons of populations that differ in their use of landmarked boundaries are needed to determine the effect that landmarked boundaries have on the stability of a territorial neighbourhood.

4.4 TYPES OF LANDMARK

The effects outlined above can be caused by two main classes of landmark that are characterised by whether or not the landmark imposes a physical constraint on an individual's perception or movement. Within these two classes, landmarks can be constructed by the animals themselves (e.g. walls, scent-marks, middens, scratchings) or be a feature that exists without effort from the territorial resident (e.g. topography, rocks, rivers, fences, walls, roads, sticks). We include features that are constructed by animals (Table 7: 1, 2, 3, 4, 5, 19; Table 8: 1, 5; Baylis, 1974) as landmarks because they are likely to serve a similar function to natural landmarks when used as boundaries. For example, European badgers (*Meles meles*) build paths along their boundaries, which are rarely crossed by neighbouring groups (Kruuk, 1978). A shared function between natural and constructed features is supported by an association between constructed landmarks and areas that do not contain natural landmarks (Table 7: 2, 3, 19; Baylis, 1974) as well as by concentrations of constructions at boundary zones (Table 7: 2, 3, 4, 5).

In the context of this review, the type of landmark can be confidently inferred in many cases (Table 7: 1, 2, 3, 4, 5; Table 8: 1, 4, 5, 8, 9, 10, 11), but there are some situations in which the presence of a constraint is uncertain (Table 7: 8, 9, 11, 13, 16; Table 8: 2, 3). For instance, it is unclear whether some topographical features are physically constraining to birds or fish that are able to move in three-dimensions. Below, we discuss constraining and non-constraining landmarks in more detail.

4.4.1 *Constraining Landmarks*

Many cases of the adoption of landmarked boundaries can be explained if the landmark impedes the perception or movement of an animal (Table 7, Table 8; Landmark Type = C). This concept is supported by studies that show landmarks being used for boundaries in the absence of competitors (e.g. van den Assem, 1967). Constraints to perception are best represented by reduced vision (Table 7: 8, 10, 15, 18; Table 8: 1, 4, 7; Kalleberg, 1958), although constraints to other sensory modalities are not impossible. Animals may not defend areas beyond a landmark that limits vision because it is more costly to detect and respond to intruders, predators, prey and mates beyond the landmark (Watson and Miller, 1971; Reid and Weatherhead, 1988; Eason and Stamps, 1992; Breau and Grant, 2002). Thus, in terms of visual constraints, defending the space beyond the landmark may be less beneficial than terminating the territory at the landmark, making it adaptive to adopt the landmark for a boundary. However, intentionally imposing visual constraints can also be adaptive; such is the case for mudskippers (*Boleophthalmus boddarti*) that build mud walls around their territories. In this species, close proximity coupled with visual stimuli of conspecifics results in aggressive behaviour. Therefore, when population density is high, individuals build walls around their territories that reduce visual stimulation and thereby allow the associated social costs to be reduced (Clayton, 1987). Some landmarks can also constrain the movement of animals by acting as a physical barrier that establishes energetic and time costs to traverse (Table 7: 6, 8, 9, 10, 12, 15; Table 8: 6, 7). There may also be costs associated with increased predation risk when crossing some areas, such as rivers (Table 8: 3; Lima and Dill, 1990). Hence, animals may adaptively decide not to defend past landmarks where the costs of gaining access to desirable areas outweigh the benefits.

4.4.2 *Non-constraining landmarks*

Many landmarks used as territorial boundaries are unlikely to physically impede animals and seem only to be utilised based on their

conspicuousness (Table 7, Table 8; Landmark Type = N). In other words, landmarks can be no more than a 'line in the sand', yet still affect an individual's behaviour. For instance, mantis shrimp (*Gonodactylus oerstedii*) kept in an enclosure with a line of gravel surrounding their burrow only attacked an intruder once the gravel line was crossed, regardless of the line's distance from the burrow (Hazlett, 1978). Such patterns imply that there must be strategic benefits for adopting purely conspicuous landmarks as a boundary, since doing so can come at the cost of sacrificing the potential to defend a larger territory (assuming larger territories are more beneficial).

One likely functional explanation for the adoption of non-constraining landmarks as boundaries is a reduction in defence costs (Eason et al., 1999; LaManna and Eason, 2003; Mesterton-Gibbons and Adams, 2003; Smith, 2011). Empirical studies have shown that animals can invest less in defence over landmarked boundaries that are visually conspicuous than for non-landmarked boundaries (Table 8: 7, 8, 9, 11). For example, interactions between blockhead cichlids (*S. casuarius*) were of lower intensity, shorter duration and were less frequent when a row of rocks was adopted for the boundary compared to when the boundary was non-landmarked (LaManna and Eason, 2003). Furthermore, the reduction in the frequency of high intensity contests in the presence of landmarks appeared to be associated with an increase in the frequency of low intensity contests. Thus, high intensity contests may have been replaced by low intensity contests (although the overall frequency of contests was still lower when landmarks were present). Theoretically, boundaries marked by olfactorily conspicuous scent marks or visually conspicuous marks such as scratches are also associated with lower defence costs (Gosling and Roberts, 2001; Lewis and Moorcroft, 2001; Moorcroft and Lewis, 2006; Hamelin and Lewis, 2010). Reduced investment toward territory defence may have a suite of other benefits to a resident, such as an increased ability to invest in exploitation of the territory (Schoener, 1987; Ydenberg and Krebs, 1987), decreased stress (Young and Monfort, 2009) and more time to become familiar with their own space (Stamps, 1995). Furthermore, according to the rubber disc hypothesis of territoriality, individuals may be able to use the savings made on defence of one boundary to expand in other directions (Huxley, 1934). Although a decrease in defence costs associated with landmarked boundaries is well supported, the reason it occurs remains unclear (Eason et al., 1999; Smith, 2011).

4.5 LANDMARKED BOUNDARIES AND DEFENCE COSTS

At least two, non-mutually exclusive, hypotheses could explain how and why the adoption of landmarked boundaries is associated with a reduction in costs. First, landmarks may provide animals with a clear

and easily defended boundary, provided the landmark can be used as a component in a spatial referencing system (the clear-boundaries hypothesis; Eason et al., 1999). Second, landmarks may be used as a convention that allows a cost-effective way for boundaries to be established, assuming that boundary formation is normally a costly process (the landmarks-as-convention hypothesis; Mesterton-Gibbons and Adams, 2003). These hypotheses, although not mutually exclusive, differ in the way that residents benefit (Mesterton-Gibbons and Adams, 2003). For the clear-boundaries hypothesis, individuals benefit unilaterally, in that any individual that adopts a landmarked boundary will experience some benefit. In contrast, the landmarks-as-convention hypothesis stipulates that settlers must mutually adopt the same landmark for their boundary in order for either to benefit.

4.5.1 *Clear-boundaries hypothesis*

There are at least three, non-exclusive ways in which having clear boundaries could reduce the frequency and intensity of agonistic interactions (Kodric-Brown, 1978; Eason et al., 1999; LaManna and Eason, 2003). First, the resident may restrict its activity (i.e. movement and defence) to within the landmarked boundary, thereby reducing its intrusions into areas defended by other individuals (Eason et al., 1999). Second, potential intruders into the resident's territory (either neighbours or non-territorial individuals) will recognise the landmark as a boundary and avoid accidentally or intentionally crossing it because intrusion is reliably associated with an aggressive response from the resident. A reduction in intruder pressure may additionally diminish the resident's need to patrol boundaries or devote time to vigilance in addition to decreasing agonistic interactions (Eason et al., 1999). Third, landmarks may increase the stability of the boundary and reduce the need for contests that function to re-establish it, although this stability could come at the cost of reduced flexibility in territory size when conditions change (Eason et al., 1999).

In order for a non-constraining landmark to be utilised as a clear boundary, animals need to associate the landmark and/or the area beyond it with the interactions that take place there. In other words, territorial animals may be required to make spatial associations in order to determine which areas to avoid, exploit, or treat as a boundary (Stamps and Krishnan, 1999; Sih and Mateo, 2001) and landmarks could be used to make or facilitate spatial awareness of these areas, including boundaries (Eason et al., 1999; Gosling and Roberts, 2001; St. Louis et al., 2004; Smith, 2011). Support for using landmarks as spatial references for boundaries comes from studies that demonstrate the use of landmarks as spatial references for navigation and foraging (e.g. Tinbergen, 1968; Warburton, 1990; Benhamou, 1997; Collett and

Collett, 2002; Odling-Smee and Braithwaite, 2003a; Kelly et al., 2009; Bruck and Mateo, 2010). Additionally, familiarity with the arrangement of landmarks in a novel area appears to affect contest behaviour and territory settlement (de Boer and Heuts, 1973; Heuts and DeBoer, 1973; Figler et al., 1975, 1976). Finally, individuals involved in contests near landmarks may be unwilling to return there, lest another contest takes place (Stamps and Krishnan, 1999; Gosling and Roberts, 2001; Zub et al., 2003). For instance, a map of pupfish (*Cyprinodon sp.*) territories suggests that neighbours mutually avoid some conspicuous features, even patches of algae that are otherwise used for food (Kodric-Brown, 1978).

4.5.2 *Landmarks-as-convention hypothesis*

The landmarks-as-convention hypothesis suggests that animals use landmarks as arbitrary boundary locations instead of using costly interactions to determine a location that better represents the asymmetry in individual abilities (Mesterton-Gibbons and Adams, 2003). If the cost of boundary settlement is sufficiently high and competitors are uncertain about each other's abilities, then a resident may benefit from adopting a landmarked boundary even when the outcome is a territory that is smaller than it would have been if the convention was ignored. In other words, it can be better to accept an arbitrary convention than risk a potentially rewarding, but also potentially costly interaction. Consequently, the model formulated to test this hypothesis suggests that individuals are more likely to accept a landmarked boundary if it provides them with a large territory, boundary establishment through contests is costly or the uncertainty regarding their opponent's abilities is high. Furthermore, in order for the use of landmarks-as-convention to evolve, a species must already be influenced by landmarks in some way (Mesterton-Gibbons and Adams, 2003). For instance, the landmark would have to physically constrain an individual, exploit a pre-existing sensory bias or have the potential to be used as a spatial reference in navigation or territorial defence.

4.5.3 *Identification of the clear-boundaries and convention hypotheses*

The clear-boundaries and landmarks-as-convention hypotheses are not mutually exclusive and make many of the same predictions (Mesterton-Gibbons and Adams, 2003). However, each hypothesis is associated with explicit testable assumptions and predictions, which allow one or the other to be ruled out (or considered unlikely). The landmarks-as-convention hypothesis can be ruled out when different individuals choose different landmarks for their boundaries, since the hypothesis requires that both individuals will converge on a single bound-

ary location. The landmarks-as-convention hypothesis also predicts that the tendency to accept a landmarked boundary increases with the skew and declines with the variance of the distribution of fighting abilities in a population (Mesterton-Gibbons and Adams, 2003). On the other hand, the clear-boundaries hypothesis requires that animals make spatial associations between contests and landmarks, even when the landmark is not being used as a boundary. This assumption can be tested by determining whether individuals exposed to contests in the presence of a landmark show changes in behaviour when subsequently exposed to the same landmark. Additionally, associations made near landmarks should be more precise than those made elsewhere. In other words, an individual exposed to a negative stimulus near a landmark is expected to avoid a smaller area (directly around the landmark) than if it were exposed to the stimulus in the absence of a nearby landmark owing to uncertainty regarding the location of the negative experience. Finally, removal of a landmark that is being used as a boundary should result in residents becoming less efficient at using space and more likely to be involved in costly interactions because the spatial association has been removed.

4.6 CONDITIONS INFLUENCING THE USE OF LANDMARKS AS BOUNDARIES

Species and individuals vary in their use of landmarks for territorial boundaries (Table 7: 3, 8, 9, 10, 12, 16; Table 8: 3; Harris and Reed, 2002; Mesterton-Gibbons and Adams, 2003). For example, in a manipulative experiment involving 41 bird species, only ovenbirds (*S. aurocapilla*) adopted narrow linear clearings for territorial boundaries (Machtans, 2006). Thus, there must be variation in the costs and benefits associated with accepting a landmarked boundary, yet the factors that explain this variation have not been adequately explored (Smith, 2011). Current evidence suggests that the propensity to adopt or construct landmarked boundaries can be influenced by the properties of available landmarks, the properties of the individuals involved and the risks of encounter between individuals, each of which we discuss below.

4.6.1 *The properties of available landmarks*

The properties associated with the landmarks present in a habitat are likely to affect their utility as a boundary and thus whether or not an individual will choose to adopt one as such (Mackintosh, 1973; Kodric-Brown, 1978). This includes variation in their placement, conspicuousness, dimensions and the type of constraint that they pose. Individuals may also choose to construct a landmarked boundary

when it is more cost-effective than adopting a natural landmark that is unsuitable in these properties (Barlow, 1974; Baylis, 1974; Kruuk, 1978). This can be tested by observing an individual's response to the addition or removal of natural features with suitable properties. Despite the potential importance of variation in landmark properties, studies investigating this are rare (Table 8: 1, 5, 6; Mesterton-Gibbons and Adams, 2003) in comparison to those that simply test for an effect of landmark presence.

In terms of boundary placement, the location of a landmark is likely to influence whether it is used for a boundary since the location of boundaries determine the territory's value. A model that shows settlers only using landmarks for boundaries if the benefits of adopting the landmark outweigh the costs of a territory that is too small supports this concept (Mesterton-Gibbons and Adams, 2003). Observationally, when the movement of plant fronds used as a boundary by an individual minnow (*Tanichthys albonubes*) resulted in a territory that was too small, the individual abandoned its territory and usurped the territory of another (Fabricius, 1951; see also Barlow, 1961, for a similar observation). In contrast, mice (*Mus musculus*) did not opt to defend a non-landmarked over a landmarked boundary, which was gradually shifted in one direction, once their territories got too small. Instead, the individuals with the smaller territories became submissive to their opponents (Mackintosh, 1973). However, this could have been due to shifts in dominance relationships associated with the experimental methods. In any case, there is little reliable data concerning the effect of landmark placement on whether the landmark will be adopted for a boundary. The preference for a landmark in a given location may also be affected by the number of alternative landmarks to choose from. For instance, a landmark that is being used as a boundary may not be used if another landmark is added in a preferable location.

Variation in the conspicuousness of the landmark is likely to determine when a non-constraining landmark will be adopted for a boundary, since features that are more conspicuous may provide a clearer boundary. In addition to conspicuousness, the dimensions of a landmark are likely to be important since larger landmarks are likely to be more obvious and provide greater utility when being utilised as a conspicuous feature (Eason et al., 1999). For instance, a long, linear feature may provide a more effective clear boundary than a smaller feature. In terms of constraining landmarks, the costs associated with the landmark are likely to increase with its dimensions, thus making them preferable as a boundary (Reid and Weatherhead, 1988; Harris and Reed, 2002; Lees and Peres, 2009). Finally, the type of constraint that a landmark imposes on a territorial resident may be important in determining whether it is used as a boundary (Eason and Stamps,

1992). For instance, a resident may be unwilling to defend areas beyond a landmark that constrains vision but would defend those areas if the landmark constrained movement (Clayton, 1987).

4.6.2 *The properties of individuals and species*

Differences between individuals and species are likely to account for some variation in the use of landmarks due to variation in fighting abilities, behavioural strategies and ecology. Theoretical evidence suggests that variation in fighting ability can be important, in that better fighters may be less willing to adopt landmarked boundaries because they are more certain that they can claim larger territories than landmarks would allow (Mesterton-Gibbons and Adams, 2003). This also implies that the distribution of fighting abilities within a population is an important factor for predicting the adoption of landmarked boundaries (Mesterton-Gibbons and Adams, 2003). Additionally, Smith (2011) found that variation in how strongly rose-bitterlings (*Rhodeus ocellatus*) responded to landmarked boundaries was correlated with the individual's natural propensity to intrude. Thus, variation in behavioural strategies such as the time of arrival to a habitat, aggression and tendency to intrude could affect the likelihood of a landmark being adopted. Such strategies are also expected to vary between populations and species. Ecologically, landmarked boundaries may be more common in populations that have high costs associated with boundary maintenance or establishment (Smith et al., 1989; Eason et al., 1999; Lewis and Moorcroft, 2001; Mesterton-Gibbons and Adams, 2003; Hamelin and Lewis, 2010). Furthermore, optimal territory size is strongly dependent on resource availability (Adams, 2001), implying that landmarks will only be adopted for boundaries if an individual does not need to extend its territory beyond the landmark in order for the territory to be economical. The adoption of landmarked boundaries has been observed to vary across seasons and years (Watson and Miller, 1971; Kruuk, 1978; Reid and Weatherhead, 1988), which may be associated with changes in resource availability. Additionally, factors associated with the natural history of a species may affect the costs and benefits associated with crossing landmarked boundaries; this is implied by correlations between the ecological niche filled by woodland birds and their willingness to cross constraining landmarks (Harris and Reed, 2002; Lees and Peres, 2009). Habitat specialists, for instance, appear more likely to restrict their movements within habitat gaps than generalists. However, this could be associated with the ability of the guilds to use the gap for foraging. Finally, the evolutionary history of a species may influence whether it uses a given landmark for a boundary (King et al., 1996; St. Clair, 2003). For example, some woodland birds tend to use rivers

as boundaries, possibly because crossing rivers is associated with a predation risk. Roads, in comparison, are not used as boundaries despite being associated with equivalent risks. This may be because the birds had adapted to avoid rivers, but have not yet done so for roads due to their recent introduction (St. Clair, 2003).

4.6.3 *Risk and consequences of encounter*

Under the clear-boundaries hypothesis, a landmark's effectiveness is determined by the conditioned association between the agonistic response of the resident to intrusions over the landmark. Thus, an individual will be less likely to cross a landmarked boundary as the chance and costs of encountering the resident increase (Smith et al., 1989; Stamps and Krishnan, 2001). The risk of an intruder encountering a resident when ignoring a landmark may increase with factors such as population abundance, the number of territory owners, proximity between territories, limitations to visibility, shared use of resources and the mobility of resources (Lewis and Moorcroft, 2001; Moorcroft and Lewis, 2006; Hamelin and Lewis, 2010).

The nature of the association between crossing a boundary and the resident's response may explain why constructed landmarks (such as scent marks, middens and scratchings) are used instead of natural landmarks in complex habitats or extensive territories (Table 7: 1, 2, 3, 4, 17, 19; Table 8: 1). In such conditions, the visibility of boundaries is limited, thereby prohibiting residents from responding to every intrusion. Therefore, residents may signal how likely they are to be found in an area by marking it on each visit (Smith et al., 1989). Like natural features in appropriate conditions, these constructions may allow intruders to recognise areas that are more costly to use (Smith et al., 1989; Gosling and Roberts, 2001; Zub et al., 2003). For instance, models of scent marking behaviour in wolves demonstrate that individuals that retreat from conspecific scent marks and produce their own scent marks along borders have a reduced risk of encountering their neighbours, providing a selective advantage when the costs of encounter are sufficiently high (Lewis and Moorcroft, 2001; Hamelin and Lewis, 2010). This hypothesis predicts that the effectiveness of a constructed landmarked boundary will increase with the density and decrease with the age of constructions (Smith et al., 1989).

4.7 CONCLUSIONS AND FUTURE DIRECTIONS

The adoption of constraining or non-constraining landmarks for territorial boundaries is, under certain conditions, associated with changes in the interactions between neighbours and the size, shape and defensibility of territories. Consequently, the use of landmarked bound-

aries has important implications for territorial populations and ultimately the links between landscapes, individual decisions and population dynamics. In particular, landmarks bear directly on processes involved in boundary establishment and maintenance. Due to this link, it may be necessary to consider the topography of the landscape, in addition to resource availability and intruder pressure, to gain a complete understanding of territorial behaviour. However, explicit studies into landmarked boundaries are rare and we lack data on factors causing variation in the adoption of landmarked boundaries and their population level consequences.

Although some research has begun to focus on landmarked boundaries, more work is needed to identify factors that influence variation in whether landmarks are adopted as boundaries within and between species. This will involve bettering our understanding of the costs and benefits associated with non-constraining landmarks used for boundaries, including explicit tests of the clear-boundaries and landmarks-as-convention hypotheses. In terms of understanding the population level consequences of landmarked boundaries, future research should focus on the costs and benefits associated with landmarked boundaries over extended periods of time and the conditions in which population size increases or decreases in response to landmarked boundaries. Finally, to develop both individual and population based hypotheses, we require data on how individuals behave when they have multiple landmarks to choose from. There is clearly wide scope for further empirical and theoretical development and this review provides the initial framework for these advances by identifying testable hypotheses relating to the causes and consequences of adopting landmarked boundaries.

LANDMARKS AS SPATIAL CUES OF AGONISTIC INTERACTIONS

Territorial boundaries are occasionally defined by conspicuous landmarks, yet the value of landmarked boundaries is unclear. The clear boundaries hypothesis proposes that landmarks provide a distinctive feature that reliably indicates the location of a boundary. Intrinsic to this hypothesis is the assumption that animals are capable of forming learned spatial associations between landmarks and the agonistic interactions that occur at boundaries. However, it is unclear whether animals are able to quickly and efficiently form such associations with landmarks in order for them to be effectively utilised as a clear boundary. In this study, we aimed to determine whether convict cichlids (*Amatitlania nigrofasciata*) were able to form a learned spatial association between a landmark and agonistic interactions with an established resident. We conditioned individuals in an enclosure that contained a landmark and either an empty shelter or an inhabited shelter for 15 minutes and then removed all fish. After a 5 minute period of isolation, we removed a barrier that separated the conditioning chamber from an alternative shelter that had a distinctively different landmark. We returned subjects to the enclosure, alone, and timed how long they spent within the area bordered by the conditioned landmark. In half of the trials, we swapped the position of the conditioned landmark with the alternative landmark to separate the use of the landmark cue from the use of cues associated with the enclosure. We found that individuals exposed to an established resident only showed significantly greater avoidance of the conditioned landmark than individuals conditioned in an empty environment when landmarks were not swapped, and only when the landmark was in the northern end of the aquarium. In all other cases, there was no difference between treatment groups. These results suggest that convict cichlids are unable to form a reliable spatial association between a landmark and agonistic interactions in a short time-frame, and that the use of landmarks for clear boundaries may be better tested by manipulating the likelihood and costs of territorial interactions at boundaries.

5.1 INTRODUCTION

Conspicuous features of the landscape, or landmarks, are occasionally used to define territorial boundaries (Heap et al., 2012). Intriguingly,

ingly, even landmarks that are physically unobtrusive, such as a change in the colour of the substrate, can be used for territorial boundaries (Hazlett, 1978; LaManna and Eason, 2003). This behaviour requires explanation because individuals can be willing to accept small territories that have a landmarked boundary over a larger territory without a landmarked boundary (Eason et al., 1999; Smith, 2011). For example, LaManna and Eason (2003) showed that blockhead cichlid (*Steatocranus casuarius*) pairs were willing to split territorial ownership of an aquarium tank with another pair when a row of rocks was present in the centre of the tank. In contrast, one pair of fish would aggressively establish dominance over the other and take control of the entire aquarium when the rocks were absent. Despite the use of landmarks for territorial boundaries being well supported (reviewed in Heap et al., 2012), it is unclear why landmarked boundaries are valued over non-landmarked boundaries.

One explanation is that landmarks are used as 'clear boundaries' that facilitate the spatial awareness of boundaries for territorial residents and potential intruders (Kodric-Brown, 1978; Eason et al., 1999; LaManna and Eason, 2003; Smith, 2011). Increased awareness of a boundary's location may then translate into fitness benefits for both residents and intruders, due to a reduction of agonistic interactions associated with territorial defence or negotiation of the boundary's location (Eason et al., 1999; Smith, 2011). However, in order for purely conspicuous (and not obstructive) landmarks to be utilised as clear boundaries, animals are required to associate visiting the landmark and/or the area beyond it with territorial contests (Heap et al., 2012). Specifically, territorial animals may make spatial associations between different areas, and the social consequences of using each area, in order to determine which areas to avoid, exploit or treat as a boundary (Stamps and Krishnan, 1999, 2001). Landmarks could be used to make or facilitate spatial awareness of these areas, including an awareness of boundaries (Eason et al., 1999; Gosling and Roberts, 2001; St. Louis et al., 2004; Smith, 2011).

The use of landmarks for navigation and foraging is well supported, implying that many different animals are able to notice landmarks and incorporate them into their behavioural strategies (Tinbergen, 1968; Warburton, 1990; Benhamou, 1997; Collett and Collett, 2002; Odling-Smee and Braithwaite, 2003b; Kelly et al., 2009; Shettleworth, 2009; Bruck and Mateo, 2010). Additionally, several studies have shown that familiarity with the arrangement of landmarks in a novel area affects contest behaviour and territory settlement (de Boer and Heuts, 1973; Heuts and DeBoer, 1973; Figler et al., 1975, 1976). Thus, there is good reason to expect animals to be able to make the necessary spatial associations between landmarks and agonistic interactions. However, there is little definitive evidence of how animals

incorporate information on landmarks and contests together when they are establishing and maintaining boundaries.

In some cases, landmarks are adopted for boundaries in a short period of time (e.g. within three hours for blockhead cichlids, LaManna and Eason, 2003). Additionally, transient non-territorial floaters or settlers can encounter established residents in unfamiliar spaces and may benefit from quickly recognising the location of territorial boundaries (Stamps and Krishnan, 1990; Adams, 2001). Thus, the use of landmarks for clear boundaries may require associations to be made relatively quickly and at minimal cost for the landmarked boundary to be cost-effective. The aim of this experiment was to test whether a one-off exposure to agonistic interactions in the vicinity of a landmark can result in a learned association between the two stimuli in the convict cichlid fish, *Amatitlania nigrofasciata*. Specifically, we tested whether non-territorial individuals are able to quickly associate landmarks with agonistic interactions and use this information to make future decisions regarding space use. Support for learned associations between landmarks and agonistic interactions would indicate that landmarks have the potential to be used as clear boundaries in such encounters.

5.2 METHODS

5.2.1 Study species

Convict cichlids (*Amatitlania nigrofasciata*) are bi-parental, Central American fish that establish territories in defence of shelters for eggs and fry (Wisenden, 1995; Alonzo et al., 2001; Lehtonen and Lindstrom, 2008). Individuals also use shelters for their own protection. Both sexes can be territorial, and are aggressive to conspecifics in order to establish a dominance hierarchy and to defend sheltering sites, although males often have the primary role in territory establishment (Lehtonen and Lindstrom 2008).

Landmarks are important cues for territoriality and contest behaviour in cichlid fish, including convict cichlids (e.g. Gallagher et al., 1972; Figler and Einhorn, 1983; Figler et al., 1985; Wazlavek and Figler, 1989). For instance, landmarks can influence aggression and be necessary for territorial residents to have a prior residency advantage in contests (Figler and Evensen, 1979; Barley and Coleman, 2010). Furthermore, the cichlid *Hemichromis bimaculatus* has a contest advantage in novel environments that have a similar arrangement of landmarks to a previously inhabited area (de Boer and Heuts, 1973; Figler et al., 1975, 1976). Landmarks have also been used as territorial boundaries by convict cichlids (Breau and Grant, 2002) and another cichlid species, *S. casuarius* (LaManna and Eason, 2003). However, re-

search typically considers the behaviour of territorial or dominant individuals, and the manner in which non-territorial individuals and intruders respond to contests and landmarks is less well understood.

We housed fish across multiple stock tanks that separated individuals by sex. This controlled for pre-trial social conditions by reducing the influence of breeding experience. The aquarium room, housing all stock tanks and the experimental tank, was kept at a light: dark cycle of 10: 14h, and maintained at a constant temperature of 24°C. Fish were fed five days a week on flake food and Tetracolor Tropical Granule pellets.

5.2.2 *Experimental conditions*

We used two treatment groups to test for the effect of agonistic interactions on subsequent space use for a subject by testing whether exposure to an unconditioned stimulus (established resident) became associated with a conditioned stimulus (shelter surrounded by a landmark). Trials consisted of two phases: i) a conditioning phase, in which subjects were exposed to either an unoccupied chamber (control; $N = 21$) or a chamber inhabited by a resident (treatment; $N = 21$); ii) a choice phase, in which the separation between chambers was removed and focal fish were given the opportunity to choose a shelter, one of which was within the conditioned landmark and the other within a different landmark (Figure 10).

We collected three size and sex matched fish from different stock tanks and randomly assigned each fish to be either a focal fish in the control or experimental treatment, or a resident fish for the experimental treatment. Subjects were matched for size and sex to increase the likelihood that the resident will act aggressively toward the focal fish in the experimental treatment and to maximize the intensity of these interactions. Additionally, this procedure ensured that size and sex were evenly distributed between treatment groups. We used fish from different stock tanks to control for prior experience between the subjects. We recorded the weight of each fish by placing them in a water-filled beaker on a tared balance (Sartorius BL3100; $d = 0.1g$), after drying the fish with a paper towel to remove excess water. We then placed the resident in a pre-assigned chamber of the experimental tank and placed focal fish in separate isolation tanks (600 x 300 x 300mm) that contained an undergravel filter and a shelter (terracotta pot). Isolation tanks were covered in dark garbage bag plastic on the outside (but not the ceiling) to reduce exposure to outside cues. The purpose of the isolation was to control for pre-trial social experiences, and to increase the likelihood of aggression in the experimental group Figler et al. (as short term isolation tends to increase aggression 1986); Ratnasabapathi et al. (as short term isolation tends

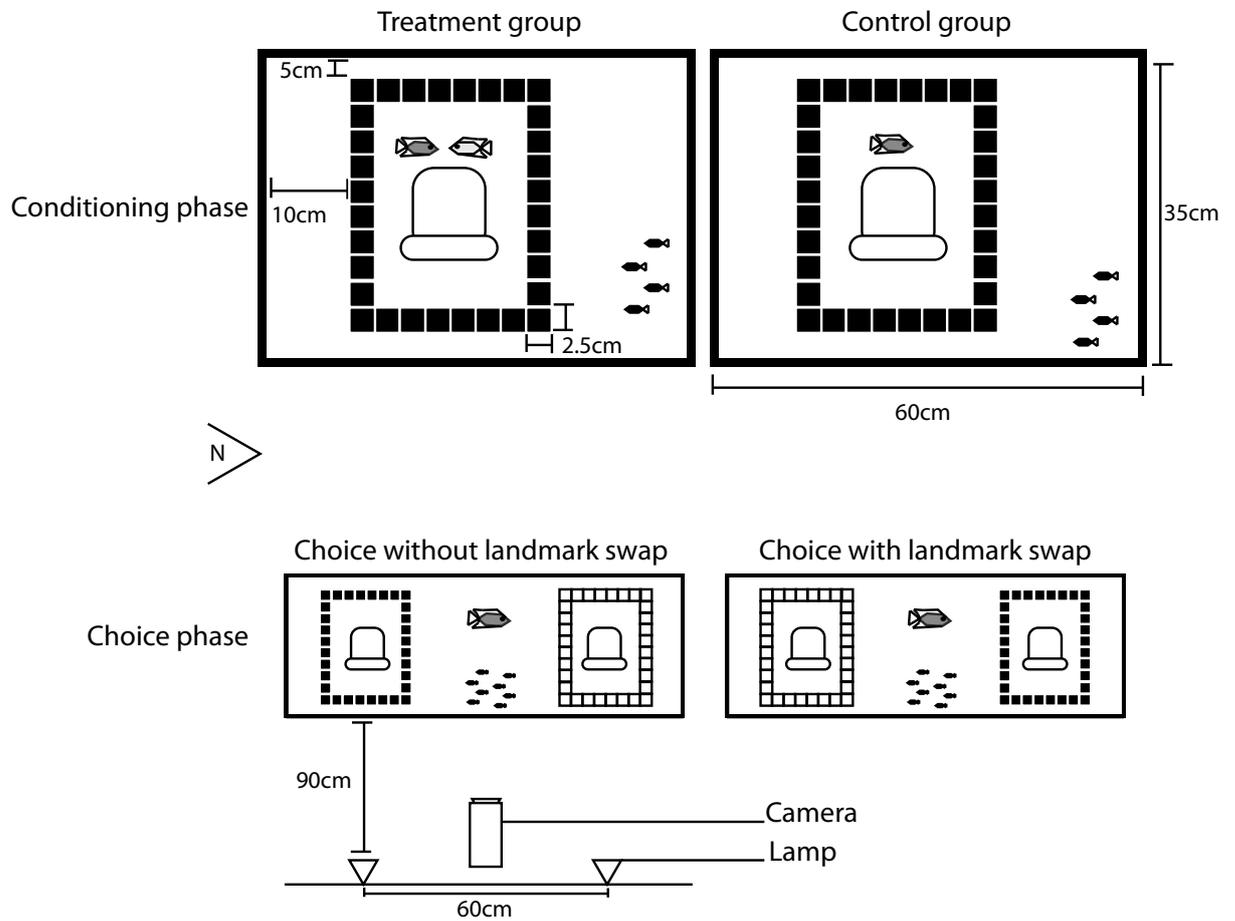


Figure 10: The experimental tank and its configuration, showing the different treatment groups. The focal fish is presented in dark shade, and the established resident is presented in light shade. The smaller fish are dithers. The chamber used during the conditioning phase (in this example, the south) is either the northern or southern end of the tank having being enclosed with an opaque partition. The choice phase consists of removing the partition and either leaving the conditioned landmark (in this example, the dark face-up type) in place or swapping it with the landmark in the other end of the tank. Chambers contain a terracotta pot for shelter, surrounded by dark or white tiles. The height of the tank was 45cm, with 6cm of coarse gravel substrate and water filled to 24cm above the substrate. Not to scale

to increase aggression 1992). We allowed 24 hours of isolation for resident fish to establish residency in the chamber.

For the conditioning phase, we removed the focal fish from isolation and placed it into the conditioning chamber, which either contained a resident or not. We recorded the conditioning chamber for 15 minutes, using a Panasonic SDR-H250GN-S digital video recorder, and then placed the focal fish in a bucket and the resident in a stock tank. We removed the partition between chambers and, in half of the trials for each treatment, swapped the landmarks between chambers (Figure 10). Five minutes after the end of the conditioning phase, we began the choice phase by placing the focal fish into the centre of the experimental tank. We then filmed the experimental tank for 15 minutes. At the conclusion of the trial, we removed the focal fish and placed it in a stock tank. For the conditioning phase, we recorded time spent within the landmark boundary (i.e. the square defined by the tiles) and the number of threat displays (frontal and lateral), chases, bites and mouth-wrestles (see Baerends and Baerends-van Roon, 1950, for a description of actions) that occurred within a dyad for subjects that were exposed to a resident. For the choice phase, we measured the time spent within the landmark boundary for each option.

The landmarks were polished marble stone tiles arranged into a rectangle surrounding the terracotta pot and buried so that they were not projecting above the substrate. One landmark was face-up, exposing the dark, mottled marble. The other landmark was face down, exposing the white mesh that binds the tiles together. The terracotta pots (internal diameter: 75mm) served as a shelter resource for the cichlids, thereby improving the value that individuals attach to the chamber. Improving the value of the chamber encourages residents to defend the site and increases the incentive for focal fish to claim a site. Pilot studies indicated that aggression from residents was less consistent when no terracotta pot was present. Each chamber also included four Buenos Aires tetras (*Hyphessobrycon anisitsi*) to function as 'dither fish', whose schooling behaviour provides convict cichlids with a cue for safety (Barlow, 1968). When dither fish are not present, isolated convict cichlids are typically less active. Apart from the rare threat display, the convict cichlids and tetras rarely interact with one another.

We ran one trial for each treatment in a day, starting the trial between 1100 and 1800. Because the resident inhabited one chamber overnight, we ran the treatment trial followed by the control trial but stirred the water between trials to minimise any effect of chemical cues (see below). No fish was used in more than one trial. We randomized the order of sex and size for subjects in trials to reduce order effects. Furthermore, we replicated the trials over all possible combinations of the conditioning chamber that was used, whether

the landmark was swapped between chambers and whether subjects were conditioned to a dark or white landmark. We removed the potential for handling to confound the results by handling fish from both treatment groups in the same way and randomising individuals across groups. The experimental and stock tanks were maintained at the same temperature with similar pH, ammonia and nitrate levels. Additionally, all individuals had prior experience with handling. Prior to an experimental trial, individuals were unfamiliar with the landmarks.

The design of the experiment loosely follows the Conditioned Place Preference (CPP) experimental paradigm (Carboni and Vacca, 2003); but differs in two respects. Firstly, we did not establish base-line preferences, because we wanted to test for the effect of a landmark when individuals had no prior experience with a location. Secondly, we swapped the location of the landmark in half of the trials, because we wished to distinguish between the use of the landmark and/or cues in the conditioning chamber as the conditioning stimulus. In other words, because we can not assume that the fish perceived the landmark as the conditioned stimulus (i.e. they could use other cues to make spatial associations), we assumed that the conditioning chamber was a separate conditioned stimulus in addition to the landmark and accounted for this by swapping the landmark location in half of the trials.

5.2.3 *Minimising availability of non-landmark cues*

Because we wanted to determine whether convict cichlids were able to use landmarks as a cue for forming learned spatial associations, we reduced the likelihood that any other cue could be used. In addition to using landmarks as spatial cues, fish have also been observed to use water movements, electrical senses, olfaction, dead reckoning, social cues, environmental geometry and compasses based on the sun, polarised light or geo-magnetism (Odling-Smee and Braithwaite, 2003b; Sovrano et al., 2007; Wisenden and Dye, 2009). However, evidence for some of these abilities is limited to specific taxa, and most are not well understood (Odling-Smee and Braithwaite, 2003b). To reduce the use of non-experimental landmark visual cues, we surrounded the experimental tank with opaque black polyethylene boards from the inside, which completely obscured outside visual cues from all sides. We took care to leave no gaps between the boards, in order to reduce the likelihood that stray light could be used as a visual cue. One of these boards was also used for the opaque divider that separated the two tank chambers. We angled a mirror across the length of the tank to make observations from a birds-eye view. For illumination, we had two 60W lamps that were positioned across from

the centre of each chamber. Additionally, we used the inbuilt lamp on the video camera, which was positioned in the centre of the tank. Thus, although the overhead light would be visible, their symmetry across the aquarium reduced the ability for individuals to use them as a compass. We further reduced available visual cues by smoothing and homogenising the gravel substrate before each trial. To reduce the use of chemical cues, we stirred the water between experimental phases and after each trial. We also replaced the terracotta pots and landmarks for each phase and each trial and rinsed all terracotta pots and landmarks each day. Furthermore, we changed a quarter of the water, vacuumed and redistributed the gravel, scrubbed polyethylene boards, and removed algae from the aquarium glass every four days. We also used undergravel filters and air-stones to circulate the water each day. During experimental trials, the head of the filter (i.e. the part above gravel) and the airstone were removed to prevent them, or the water-flow they produce, from being used as spatial cues.

5.2.4 *Data analysis*

We tested whether there were differences in the time that individuals spent within the conditioned landmark that depended on their treatment conditions. Because the conditioned landmark was swapped in half of the trials, we considered two response variables: i) the time spent within the conditioned landmark during the choice phase, $T_{landmark}$ and ii) the time spent within the landmark in the conditioning chamber (irrespective of landmark colour) during the choice phase, $T_{chamber}$. The latter allowed us to assess whether individuals were using uncontrolled cues associated with the conditioning chamber as a spatial cue, rather than the colour of the landmark within the chamber. We used generalised linear models (GLM), with residuals fitted to a negative binomial distribution to account for over-dispersion (Logan, 2010), to test for any differences due to the conditioning treatment or the landmark swap treatment. Specifically, we considered four treatment groups, based on the location of the conditioned landmark in each phase: $N \rightarrow N$; $N \rightarrow S$, $S \rightarrow S$, $S \rightarrow N$ and used planned comparisons to compare groups that involved a swap or not (i.e. $N \rightarrow N + S \rightarrow S$ vs $N \rightarrow S + S \rightarrow N$), those that involved conditioning in the southern or northern chamber (i.e. $N \rightarrow N + N \rightarrow S$ vs $S \rightarrow S + S \rightarrow N$), or those in which the conditioned landmark was present in the southern or northern chamber during the choice phase (i.e. $N \rightarrow N + S \rightarrow N$ vs $N \rightarrow S + S \rightarrow S$). In cases where GLM's were not appropriate due to un-removable over-dispersion, we used an ANOVA with Type III SS to test for differences in square root transformed response variables. We also used

ANOVAs to test for any effect of the colour of the landmark (dark or white).

To gain an understanding of how an individual's specific experience during conditioning affected its subsequent space use, we tested whether the time spent within the conditioned landmark (or chamber) depended on i) the time spent within the landmark during the conditioning phase, or ii) the frequency of agonistic interactions that occurred between the subject and resident. For the former, we used a multiple regression model that included the effects of conditioning treatment and landmark swap in addition to the \sqrt{time} spent within the landmark during conditioning. For the latter, we used an IT-AIC approach (Burnham, 2004; Mazerolle, 2006; Burnham et al., 2010; Symonds and Moussalli, 2010) using the AICcmodavg package (Mazerolle, 2012) in R.2.14.1 to compare the set of linear models that considered each additive combination of agonistic interactions (out of threats, chases, bites and mouth-wrestles). A null model that considered the absence of predictor variables was also included in this comparison. Natural model averaging was used to determine if any agonistic behaviours had a significant effect (in terms of whether the 95% CI range did *not* include zero). R 2.14.1 was used for all analyses.

5.3 RESULTS

5.3.1 *Time spent within the conditioned stimuli*

Time spent within the conditioned landmark (Table 9) or landmark within the conditioned chamber (Table 10) depended on significant interactions between the treatment, the chamber used for conditioning (northern or southern chamber) and the placement of the landmark during the choice phase in terms of whether the landmark was swapped, and to which chamber it was moved to (north or south end of the tank). Thus, we separated analysis by whether the landmark was swapped or not because this allows us to determine how individuals behaved when the conditioned landmark was within the conditioned chamber and when the conditioned landmark was within the non-conditioned chamber.

5.3.1.1 *Landmarks not swapped*

When the conditioned landmark was present within the conditioned chamber ($N = 21$; 10 treatment trials, 11 control trials), the time spent within the conditioned landmark ($T_{landmark}$) between individuals exposed to a resident and those in the control was dependant on a significant interaction between the treatment group and the chamber in which the individual was conditioned ($z = 5.43$, $p < 0.001$). Specifically, there was no significant difference between treatment groups

Table 9: Planned comparisons for the time spent within the conditioned landmark, as compared between treatment groups, whether the landmark was swapped or not, the chamber used for conditioning, or the chamber in which the conditioned landmark was present during the choice phase ($N = 42$)

FACTOR	ESTIMATE	z	p
Treatment	-0.32	1.56	0.118
Landmark swap	-0.83	2.03	0.042
Conditioning chamber	0.61	1.51	0.130
Choice chamber	0.23	0.56	0.576
Treatment: swap	-0.78	1.92	0.055
Treatment: conditioning	0.91	2.24	0.025
Treatment: choice	-1.64	4.03	<0.001

Table 10: Planned comparisons for the time spent within the landmark in the conditioned chamber, as compared between treatment groups, whether the landmark was swapped or not, the chamber used for conditioning, or the chamber in which the conditioned landmark was present during the choice phase ($N = 42$)

FACTOR	ESTIMATE	z	p
Treatment	-0.29	1.46	0.145
Landmark swap	-0.67	1.67	0.094
Conditioning chamber	-0.45	1.13	0.260
Choice chamber	-0.84	2.10	0.036
Treatment: swap	-0.83	2.08	0.038
Treatment: conditioning	1.33	3.32	< 0.001
Treatment: choice	-1.22	3.05	0.002

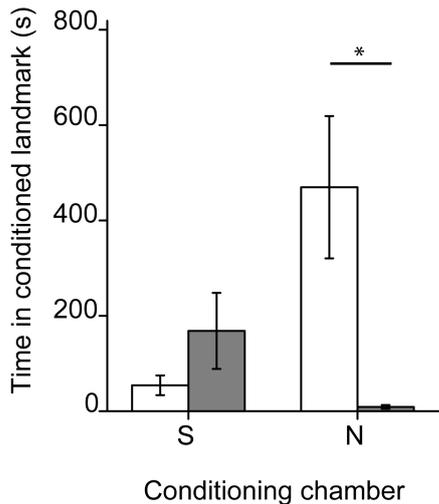


Figure 11: Mean \pm SE time (s) spent within the conditioned landmark during the choice phase for individuals that were conditioned to the presence of an established resident (grey) or an empty shelter (white) within the landmark, in cases where the conditioned landmark was not moved to the opposite end of the tank for the choice phase. Measurements are split depending on whether subjects were conditioned in the southern (S) or northern (N) chamber. Significant differences are given by a bar with an asterisk (see text for statistics)

when they were conditioned in the southern chamber ($z = 1.64$, $p = 0.102$), but individuals conditioned to an established resident in the northern chamber had significantly less $T_{landmark}$ than control individuals ($z = 6.53$, $p < 0.001$; Figure 11). These patterns were also present when considering an ANOVA on $\sqrt{T_{landmark}}$ (Treatment: chamber interaction: $F_{1,17} = 16.70$, $p < 0.001$; effect of treatment in the southern chamber: $F_{1,9} = 1.71$, $p = 0.223$; effect of treatment in the northern chamber: $F_{1,8} = 17.77$, $p = 0.003$). Whether individuals were conditioned to a dark or white landmark had no significant effect on $\sqrt{T_{landmark}}$ ($F_{1,17} = 0.01$, $p = 0.910$), nor was there any significant interaction with the conditioning treatment ($F_{1,17} = 2.12$, $p = 0.163$).

5.3.1.2 Landmarks swapped

When the conditioning stimuli (landmark and chamber) were separated by moving the landmark to the opposite chamber ($N = 21$; 11 treatment trials, 10 control trials), an ANOVA indicated that there were no significant interactive effects between treatment and conditioning chamber ($F_{1,17} = 0.95$, $p = 0.343$), or any main effects (Treatment: $F_{1,17} = 1.56$, $p = 0.229$; Chamber: $F_{1,17} = 2.19$, $p = 0.158$), on $\sqrt{T_{landmark}}$. We were unable to conduct the previous test using a GLM, due to over-dispersion. Similarly, when considering $T_{chamber}$, there was no significant difference between the two treatment groups

($z = 0.39$, $p = 0.696$). However, individuals that were conditioned in the southern chamber had significantly less $T_{chamber}$ compared to those conditioned in the north ($z = 1.97$, $p = 0.049$; Figure 12). The effect of the chamber is also present when conducting an ANOVA on $\sqrt{T_{chamber}}$ ($F_{1,17} = 6.02$, $p = 0.025$). There were no significant effects of the landmark type ($F_{1,17} = 2.29$, $p = 0.149$), or its interaction with treatment ($F_{1,17} = 0.89$, $p = 0.359$) on $\sqrt{T_{chamber}}$. Nor was there any effect of the landmark type ($F_{1,17} = 0.03$, $p = 0.856$), or its interaction ($F_{1,17} = 0.32$, $p = 0.582$), on $\sqrt{T_{chamber}}$.

Experience-dependent effects

Individuals that spent more \sqrt{time} within the landmark during the conditioning phase spent more \sqrt{time} within the conditioned landmark ($T_{landmark}$) during the choice phase ($t = 2.45$, $p = 0.019$). This was unaffected by conditioning to a resident ($t = 1.51$, $p = 0.139$) or the swap treatment ($t = 0.85$, $p = 0.400$), according to a multiple regression analysis ($F_{3,38} = 2.34$, $r^2 = 0.14$, $p = 0.035$; Figure 13). However, the \sqrt{time} an individual spent within the landmark during conditioning only had a tendency to be correlated with $\sqrt{T_{chamber}}$ ($t = 1.92$, $p = 0.062$), regardless of whether the individual was conditioned to a resident ($t = 0.98$, $p = 0.332$) or whether the landmark was swapped ($t = 0.42$, $p = 0.674$). Furthermore, the overall explanatory power of the model (i.e. r^2) for $\sqrt{T_{chamber}}$ is lower than that for $\sqrt{T_{landmark}}$ ($F_{3,38} = 1.71$, $r^2 = 0.05$, $p = 0.181$).

In the case of convergent conditioned stimuli, individuals that were conditioned to a resident spent significantly more \sqrt{time} within the conditioned landmark ($\sqrt{T_{landmark}}$) if they were involved in more \sqrt{chases} ($\hat{\beta} \pm SE = 1.41 \pm 0.57$, 95% CI range: 0.29–2.54), although the model involving \sqrt{chases} is no better at explaining $\sqrt{T_{landmark}}$ than the null model (Table 11). However, neither $\sqrt{T_{landmark}}$, nor $\sqrt{T_{chamber}}$ could be predicted based on agonistic interactions during conditioning when the landmark was swapped (Tables 12, 13). For all observed chases, the subject was the one being chased by the resident. There were no significant differences in the frequency of displays ($t_{5,3} = 0.03$, $p = 0.980$), chases ($t_{7,8} = 0.78$, $p = 0.460$), biting ($t_{7,8} = 1.41$, $p = 0.198$), or mouth wrestles ($t_4 = 1.00$, $p = 0.374$) between the northern and southern chambers. However, there were only three trials that involved mouth wrestling, and each of these trials involved conditioning in the northern chamber.

5.4 DISCUSSION

Convict cichlids conditioned to an established resident showed a tendency to avoid conditioned cues, but only when conditioned in the

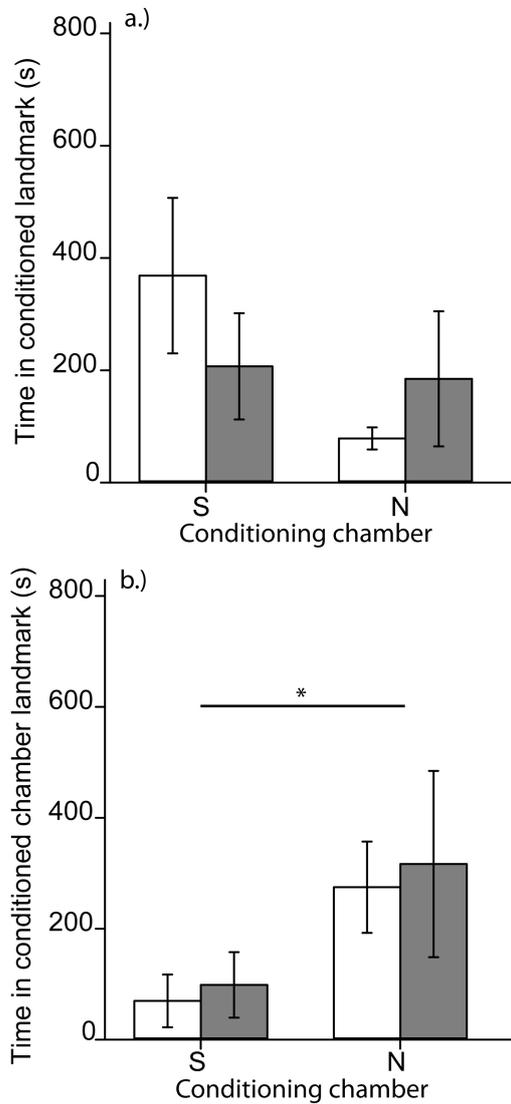


Figure 12: Mean \pm SE time (s) spent within the a.) conditioned landmark or b.) landmark in the conditioned chamber during the choice phase for individuals that were conditioned to the presence of an established resident (grey) or an empty shelter (white) within the landmark, in cases where the conditioned landmark was moved to the opposite end of the tank for the choice phase. Measurements are split depending on whether subjects were conditioned in the southern (S) or northern (N) chamber. Significant differences are given by a bar with an asterisk (see text for statistics)

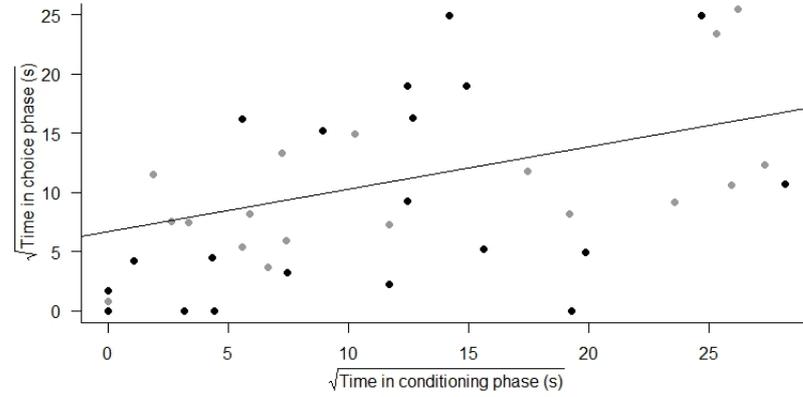


Figure 13: There is a significant correlation between the \sqrt{time} spent within the landmark during the conditioning phase and the \sqrt{time} spent in the conditioned landmark during the choice phase for individuals conditioned to residents (black circles) or an empty chamber (grey circles)

Table 11: The $\sum w < 0.95$ set of linear models containing agonistic interactions for explaining the \sqrt{time} spent within the conditioned landmark in cases where the landmark was not swapped

MODEL	AIC_C	ΔAIC_C	w	$\sum w$	LL	κ
Chases	70.15	0.00	0.49	0.49	-30.08	3
Null	71.62	1.47	0.23	0.72	-32.95	2
Chases + Wrestles	74.24	4.09	0.06	0.78	-29.12	4
Wrestles	74.63	4.48	0.05	0.83	-32.32	3
Bites	74.93	4.78	0.04	0.88	-32.47	3
Chases + Bites	75.50	5.34	0.03	0.91	-29.75	4
Display + Chases	75.71	5.56	0.03	0.94	-29.85	4

All agonistic variables are square root transformed. The full model has $r^2 = 0.44$

Table 12: The $\sum w < 0.95$ set of linear models containing agonistic interactions for explaining the \sqrt{time} spent within the conditioned landmark in cases where the landmark was swapped to the opposite chamber during the choice phase

MODEL	AIC_C	ΔAIC_C	w	$\sum w$	LL	κ
Null	86.01	0.00	0.58	0.58	-40.25	2
Display	89.40	3.39	0.11	0.69	-39.99	3
Bites	89.54	3.53	0.10	0.78	-40.05	3
Wrestles	89.86	3.85	0.08	0.87	-40.21	3
Chases	89.90	3.89	0.08	0.95	-40.24	3

All agonistic variables are square root transformed. The full model has $r^2 < 0.01$

Table 13: The $\sum w < 0.95$ set of linear models containing agonistic interactions for explaining the \sqrt{time} spent within the landmark in the conditioning chamber in cases where the landmark was swapped to the opposite chamber during the choice phase

MODEL	AIC_C	ΔAIC_C	w	$\sum w$	LL	κ
Null	85.21	0.00	0.52	0.52	-39.86	2
Bites	87.31	2.09	0.18	0.70	-38.94	3
Wrestles	88.69	3.47	0.09	0.79	-39.63	3
Chases	89.14	3.92	0.07	0.86	-39.85	3
Display	89.14	3.93	0.07	0.93	-39.86	3
Display + Bites	92.11	6.89	0.02	0.95	-38.72	4

All agonistic variables are square root transformed. The full model has $r^2 < 0.01$

northern end of the tank and when the landmark was not swapped. In all other cases, those conditioned to a resident did not respond differently to individuals conditioned to an unoccupied (by conspecifics) chamber. However, individuals spent more time within the conditioned landmark, but not within the landmark in the conditioned chamber, the longer they spent within the landmark during conditioning. This gives some indication that the subjects may have recognised the conditioned landmark as familiar. Whilst the one case of a conditioning effect suggests that individuals may be able to form learned spatial associations within a single 15 minute exposure, the uniqueness of this case does not allow us to determine whether individuals were using the landmark or some other feature in the chamber as a cue. However, the specificity of the behavioural response indicates that the use of landmarks as spatial cues for territorial contests may involve more elements than simply a landmark and a fight, which could have implications for the use of landmarks as clear boundaries.

Swapping the landmark did not enable us to determine whether the cichlids were conditioned to the landmark or cues associated with particular chambers because the changes in space use between swapped and non-swapped treatments were inconsistent. Additionally, the effects of conditioning were only apparent for subjects conditioned in the northern chamber when no swap occurred, and not present when conditioned in the south. Further complications arise from the confounding effect of which chamber was used for conditioning and which housed the conditioned landmark during the choice phase. That is i) subjects conditioned to a resident only avoided the conditioned landmark if they were conditioned in the northern chamber and the conditioned landmark was present in the northern chamber during the choice phase, and ii) subjects conditioned in the northern chamber (regardless of treatment) spent more time within the northern chamber landmark than subjects conditioned in the southern chamber spent within the southern chamber landmark when the landmarks were swapped. This was despite efforts to reduce or prevent alternative cues (other than the landmark) that could enable an individual to determine whether it was in the same chamber as it was during conditioning.

One possibility for explaining these results is that individuals did not distinguish between the different types of landmark (i.e. dark or white), and instead were conditioned to associate all terracotta pots and landmarks with a resident. However, this could not explain why the landmark, or conditioned chamber, was avoided in one case. Future studies could test this hypothesis by conditioning individuals to a resident in the presence of one landmark and also conditioning them to an uninhabited area with another landmark.

Fish possess a number of structures and behaviours that allow them to orientate and navigate (Odling-Smee and Braithwaite, 2003b), including the ability to assess the geometry of their environment; that is, the ability to assess the lengths and angles of boundaries in their surroundings, as well as a concept of left and right (Sovrano and Vallortigara, 2006). Geometric cues are important for orientation and spatial learning in many taxa, and interactions between the use of geometric and landmark cues in spatial learning are well documented, but not well understood (Odling-Smee and Braithwaite, 2003a; Sovrano et al., 2007; Doeller and Burgess, 2008; Ratliff and Newcombe, 2008). Importantly, the geometric cues available to cichlids in our study would have varied between the conditioning and choice phases. For instance, two walls would appear to be extended. Hence, an individual that is assessing whether a nearby shelter is the same one from conditioning would encounter a mis-match in cues that were independent of the landmark. In addition to geometric cues, some fish may also have access to a compass based on polarised light or geo-magnetism (Odling-Smee and Braithwaite, 2003b). Although we attempted to account for variation in geometric and compass cues by including every variation of conditioning chamber and landmark location during the choice phase, the cichlids appear to have assessed the available information in such a way that they responded differently to cues encountered in the northern and southern ends of the aquarium. This could be because individuals paid more attention to cues in a particular direction, because of a bias for particular orientations, or some other mechanism.

In any case, conflicts between the cues encountered during conditioning and those encountered during the choice phase that were imposed by our methods may have disturbed any spatial associations made between the landmark and agonistic interactions with a resident. Specifically, theory suggests that the avoidance of particular areas is the product of the fitness consequences of territorial contests and the likelihood of a contest occurring within the area (Stamps and Krishnan, 2001; Dall, 2010). That is, individuals may use available spatial cues to assess the likelihood that they will encounter a territorial resident and weigh this against the costs of such an encounter. If an individual learns that an area is risky, it will avoid it, but will not avoid areas associated with low risk (Stamps and Krishnan, 2001). Thus, our results can be explained by considering the costs of encounters with a territorial resident, the perceived likelihood of an encounter occurring and how our methods affected this interaction.

In terms of encounter costs, a single 15 minute conditioning period may not have been sufficiently costly for individuals to decide on avoiding spatial cues associated with a resident. Although 15 minutes is generally a sufficient amount of time for convict cichlids to

form a dominance relationship (Wazlavek and Figler, 1989), it may not be enough for an intruder to associate an area with a high level of costs. In support of this hypothesis, convict cichlids substantially increase their aggressive response to an intruder after 48 hours of residency, compared to the 24 hours of residency we used (Figler et al., 1986), and thus the aggression received by the subjects may not have been consistent with a truly established resident (despite subjects being submissive in 90% of encounters). Accordingly, subjects may have assessed the resident to be relatively weak, and possibly even as a potential opportunity for territory usurpation. Alternatively, individuals may actually value areas associated with residents for a number of reasons, and thus not avoid them. Firstly, it may be beneficial for an individual to be in a group, even if it is submissive. For instance, non-receptive females can benefit from grouping with more attractive females to reduce the costs of male harassment (Brask et al., 2012), or individuals can benefit from reduced predation pressure on themselves and their offspring (Hamilton, 1971; Turner and Pitcher, 1986; Wisenden and Keenleyside, 1992). Secondly, non-territorial individuals are often able to gain control of space by persistently interacting with a resident (Sih and Mateo, 2001; Stamps and Krishnan, 2001; Morrell and Kokko, 2005). If the subjects could have benefited from gaining space in this way, they may not have assessed the conditioned areas as costly and necessary to avoid. In support of this hypothesis, we found that individuals that were chased more often spent more time within the conditioned landmark, which could suggest that they were following a strategy of territory acquisition through persistence (e.g. Stutchbury, 1991). However, these hypotheses alone can not provide an explanation for why individuals tended to avoid the conditioned landmark in one case but not others.

In terms of the perceived likelihood of an encounter with a territorial resident, research in spatial cognition across a variety of taxa indicates that individuals gather information from a variety of cues that can correlate with spatial location, which are each given weightings according to their reliability and then combined to form an updated estimate of location (Odling-Smee and Braithwaite, 2003a; Newcombe and Ratliff, 2007; Sovrano et al., 2007; Ratliff and Newcombe, 2008). Individuals may use this process to estimate their own location, or the location of other objects, such as food, conspecifics or predators. Hypothetically, the weight that individuals assign to specific cues can be significantly influenced by the individual's ecology, sensory acuity, and even their personal experiences. For example, Odling-Smee & Braithwaite (2003a) have demonstrated that three-spined sticklebacks (*Gasterosteus aculeatus*) sourced from rivers and streams pay less attention to landmark cues in a navigation task than individuals sourced from lakes and ponds. This result is consistent with landmarks being

less reliable as navigational cues in a flowing environment, since the landmarks are more likely to move compared to landmarks in a stable environment. Consequently, Odling-Smee & Braithwaite (2003a) conclude that the cues used by individuals for spatial memory tasks may depend on the reliability of the cue for providing spatial information. Furthermore, studies suggest that the reliability of landmark cues for providing spatial information can depend on interactions with the use of other cues, especially geometry (Sovrano et al., 2007; Doeller and Burgess, 2008; Ratliff and Newcombe, 2008). Additionally, the size of an enclosure can have an effect on these interactions (Sovrano and Vallortigara, 2006; Ratliff and Newcombe, 2008). Sovrano et al. (2007), for example, demonstrated that red-tail splitfins (*Xenotoca eiseni*) tested in a small aquarium made more geometric errors in a spatial re-orientation task than fish tested in a large aquarium. With respect to our experiment, fish were conditioned in a smaller enclosure than that presented during the choice phase and consequently, their use of landmark, geometric and other cues may be affected. For example, human (*Homo sapiens*) adults typically use geometric cues in small rooms and landmark cues in large rooms for spatial re-orientation tasks. However, individuals trained to a spatial re-orientation task in a large room (where they use landmarks) showed an increase in the use of landmark cues when tested in a small room (where they normally use geometry). Conversely, those trained in a small room showed no change in geometric cues when tested in a large room (Ratliff and Newcombe, 2008). Despite such patterns, there may be differences in how different cues integrate that depend on the species being considered (Sovrano et al., 2007), their environment (Odling-Smee and Braithwaite, 2003a), and their previous experience (Doeller and Burgess, 2008; Ratliff and Newcombe, 2008), implying that we can not generalise the same changes in cue use to convict cichlids.

If such interactions occur in convict cichlids, then an individual's perception of danger from an established resident in each of the choice trials may have been dependent on the methodology that we applied and in only one case did the available cues provide reliable information that an area was associated with an established resident. In other cases, we propose that individuals conditioned to an established resident did not perceive the conditioned landmark as sufficiently reliable information for a resident's presence to justify avoiding the landmark, especially if the costs of being wrong about this assessment (e.g. being chased by the resident) were not severe. In such cases, the reliability of the landmark cue may have been affected by changes in the size of the enclosure and the resulting effects on how information from landmarks and other cues were integrated. Under this explanation, the correlation between chases and time spent

within the conditioned landmark may reflect subjects exploring the tank and updating their assessment of the threat posed by a possible resident. In other words, when faced with cues that do not match their previous experience, individuals may update their assessment by testing whether an area is associated with a resident or not. However, further lab experiments would be required to test this hypothesis explicitly.

If the use of landmarks in forming spatial associations with territorial interactions is strongly contingent on the availability of other cues and their relative importance in providing an individual with reliable information on its location, then the use of landmarks as clear boundaries would be dependent on a range of factors beyond those involved in a simple case of classical conditioning. Factors such as prior experience with landmarks and social interactions, and the availability of other ecological, compass-related or geometric cues are likely to be important. Furthermore, the cost of encounters with territorial residents may determine the strength of any associations made between an encounter and a landmark. Whilst lab experiments such as this are typically useful for identifying specific learning mechanisms and important stimuli, the clear boundaries hypothesis may be better tested by manipulating the likelihood and cost of encounters associated with a landmarked boundary. Furthermore, tests of the clear boundaries hypothesis may benefit from borrowing concepts from the study of scent-marked boundaries, as models indicate that the functional significance of scent-mark signals is also dependent upon the likelihood and consequences (i.e. risk) of encounter with territorial residents (Smith et al., 1989; Gosling and Roberts, 2001; Lewis and Moorcroft, 2001; Hamelin and Lewis, 2010).

Part III

UNCERTAINTY ABOUT OPPONENTS DURING
DYADIC INTERACTIONS

VARIABLE RESPONSES TO REPEATED INTRUDERS

Territorial animals must optimise their investment towards exploiting their territory and defending it from competitors. However, the manner in which territorial investment changes in response to repeated interactions with a rival remains unclear. We experimentally exposed nest-defending terrestrial toadlets (*Pseudophryne bibronii*) to playback that simulated an intruder that called and retreated six times. We measured the change in a resident's investment toward calls that function to advertise their presence to mates (territory exploitation) or threaten competitors (territory defense) over successive interactions. We found significant independent effects of repeated interactions on each call type, but no trade-off between them. Aggressive call response was initially high, decreasing significantly after the first bout. In contrast, advertisement calls increased linearly over successive bouts. However, the magnitude and direction of changes over time were not consistent among individuals. Instead, individuals appeared to change their calling behavior according to their initial response. Furthermore, there was a decrease in the variability of responses over successive interactions. Together, these results suggest that residents independently optimise their exploitative and defensive behaviors in response to intruders as they gain information over successive interactions. This process will be important to consider when there is variation in the number of times a given intruder will be encountered.

6.1 INTRODUCTION

Intruder pressure from non-territorial individuals (floaters) is arguably one of the most important factors influencing the behavior of a territorial resident (e.g. [Brown, 1964](#); [Boutin and Schweiger, 1988](#); [Chapman and Kramer, 1996](#); [Jablonski, 1996](#); [Manteuffel and Eiblmaier, 2008](#)). Many models of territoriality assume that intrusion attempts are independent of one another and that residents simply respond to the absolute level of intrusion (for a review and criticism, see [Adams, 2001](#)). However, residents can face the same intruder on multiple occasions and it is becoming increasingly apparent that this has important implications for how the resident should respond, because both the resident and the intruder have the opportunity to gain information about each other ([Sih and Mateo, 2001](#); [Morrell and Kokko, 2003, 2005](#)). For instance, residents may reduce future intrusion pressure by attacking, and thus 'teaching', intruders to avoid their territory

(Switzer et al., 2001). Additionally, residents may learn about the likelihood of future intrusions and base decisions regarding space use on this information (Stamps and Krishnan, 1999, 2001; Díaz-Uriarte, 2001). Floaters, on the other hand, can learn about the likelihood of being met with aggression as well as signal their intentions to settle in an area by repeatedly returning to it in a process analogous to a war of attrition (Stutchbury, 1991; Stamps and Krishnan, 1999, 2001). Finally, individuals can learn about each others fighting abilities the more they interact (Enquist et al., 1990; Leiser et al., 2004; Kemp et al., 2006). Information gained during agonistic contests may thus be important for a range of territorial behaviours (e.g. patrolling, advertising, foraging, space use, aggressive display) beyond deciding when to withdraw from a contest. For example, experiments conducted on birds have demonstrated that simulated intrusions can influence an individual's advertisement of territory ownership hours after the intrusion and aggressive behaviour during later intrusions (Amrhein and Erne, 2006; Schmidt et al., 2007).

The territorial behaviours that may be affected by repeat intrusions can be broadly classified as being either exploitative (i.e. deriving fitness benefits from territory ownership through mating, predator avoidance or foraging) or defensive (i.e. minimising resource loss to intruders). A common assumption is that there is a trade-off between the two (Schoener, 1987; Ydenberg and Krebs, 1987; Morrell, 2004). Theoretically, residents that focus on exploiting their territory may be more vulnerable to having their resources stolen (Díaz-Uriarte, 2001; Switzer et al., 2001; Hinsch and Komdeur, 2010). On the other hand, residents that invest excessive time and energy in defense may incur the cost of missed opportunities for exploiting their own space (Schoener, 1987). Therefore, we expect that a resident's response to repeated intrusions will represent shifts along a continuum between exploitative and defensive behaviors. For example, great tits (*Parus major*) exposed to an intruder reduced their foraging efforts to spend more time being vigilant, whereas those that were not exposed foraged at closer to maximum efficiency (Kacelnik et al., 1981; Ydenberg and Krebs, 1987).

A resident's familiarity with an intruder increases with repeated interactions and can be an important determinant of its defensive behavior (e.g. Wich and Sterck, 2007; Briefer et al., 2008; Rosell et al., 2008; DelBarco-Trillo et al., 2009). Individuals that are more familiar with one another are expected to be less aggressive because they have accurate information on the costs and consequences of interaction and are hence less motivated to engage in costly fights (the familiarity hypothesis: Ydenberg et al., 1988; Getty, 1989). However, an intruder's familiarity can also indicate the threat it poses to a resident's resources (i.e. likelihood of stealing resources or taking over

the entire territory). Consequently, residents can be less, or more, aggressive toward familiar intruders than unfamiliar intruders, depending on which is more threatening (the relative threat hypothesis; Temeles, 1994). Overall, residents are expected to reduce their defensive behaviors toward an intruder as it becomes more familiar (the dear enemy phenomenon), except in cases where the intruder is sufficiently threatening, in which case the resident will increase its defensive behaviours (Temeles, 1990; Müller and Manser, 2007; Schradin et al., 2010). Although the relationship between familiarity and defensive behavior is well studied, our understanding of how exploitative behaviors are affected is limited. This understanding does not generally extend beyond the expectation of a negative correlation between exploitative and defensive behaviors.

Anuran amphibians (frogs and toads) have provided an excellent model system for exploring changes in exploitative and defensive behaviours in response to intruder pressure (Rose and Brenowitz, 1997; Owen and Perrill, 1998; Brenowitz and Rose, 1999; Bee, 2003b; Marshall et al., 2003; Humfeld et al., 2009). This is largely because anuran calling behavior reflects investment toward these competing interests. Typically, males form dense breeding aggregations and defend patches of space required by females for oviposition. They advertise their presence and quality to females using acoustic signals (advertisement calls), which can be considered as investment toward exploiting their territory (through breeding). In this regard, residents must maintain a sufficient rate of advertisement calling in order to offset any reproductive interference imposed by nearby callers (Telford, 1985; Schwartz and Gerhardt, 1989; Dyson and Passmore, 1992; Burmeister et al., 1999). Additionally, males benefit from maintaining an exclusive space surrounding their calling site, and males of many species use an aggressive call to deter rivals from settling too close (Wells, 1977; Gerhardt and Huber, 2002; Wells, 2007). Thus, aggressive calling generally reflects investment toward territory defense. These call types are also expected to be involved in a trade-off, since females prefer males that give a high rate of advertisement calls, the production of which is impaired by giving aggressive calls (Taigen and Wells, 1985; Schwartz et al., 1995; Rose and Brenowitz, 1997; Brenowitz and Rose, 1999; Marshall et al., 2003). Frogs have also been shown to respond to familiarity and persistent exposure to an unfamiliar intruder. Although by no means the rule (Bee, 2003a), frogs in a chorus often exhibit the dear enemy phenomenon, whereby residents respond less aggressively to the calls of a familiar rival than an unfamiliar rival (e.g. Owen and Perrill, 1998; Lesbarreres and Lode, 2002; Feng et al., 2009), or become less aggressive toward an unfamiliar intruder with continued exposure (e.g. Rose and Brenowitz, 1997; Bee, 2003b; Humfeld et al., 2009). This is thought to benefit residents by allowing them

to focus their efforts on attracting females rather than on spacing conflicts with males (Brenowitz and Rose, 1999).

The aim of this study was to determine how exploitative and defensive behaviors vary in response to repeated intrusions. This was achieved by conducting a playback experiment on the terrestrial brown toadlet, *Pseudophryne bibronii*. We exposed resident males to a speaker that played pre-recorded calls presented at intermittent intervals to simulate repeated intrusions by an unfamiliar male. The response of the resident was gauged by the number of calls given in reaction to each simulated intrusion. We expected that aggressive calling would decrease over successive intrusions because the simulated intruder was not a large threat (Temeles, 1994). Similarly, we expected that advertisement calling would increase in order for the resident to remain attractive in the face of a new competitor (Burmeister et al., 1999). We also tested whether there was inconsistency among individuals in the direction of change in order to determine if all individuals respond in the same manner. We predicted that any variation in the direction of change for individual responses would be consistent with the relative threat and familiarity hypotheses (Temeles, 1994). Finally, we tested the hypothesis that shifts in calling behavior reflect a trade-off between exploitative and defensive behaviors (Schoener, 1987; Ydenberg and Krebs, 1987; Morrell, 2004).

6.2 METHODS

6.2.1 Study organism and field site

The brown toadlet, *Pseudophryne bibronii*, is a small (22-36mm Snout-Vent Length) terrestrial, breeding Myobatrachid frog endemic to temperate regions of southeastern Australia (Tyler and Knight, 2009). During the prolonged, 4-5 month breeding season, males aggregate along dry creek lines and drainage pans that seasonally inundate. Males construct shallow burrows (nest sites) in moist soil and use advertisement calls to attract females, who deposit their eggs at the call site (Pengilley, 1971; Woodruff, 1976; Mitchell, 2001). Males are territorial and defend the nest site using a distinct aggressive call that is longer and more pulsatile than the advertisement call (Byrne, 2008; Figure 14). Most territorial disputes are resolved acoustically, and physical interactions between males are rarely observed (unpublished data). Critically, this means that acoustic investment provides a reliable indicator of exploitation and defense of the nest site. The study was conducted on two choruses within a population in remnant *Eucalyptus*, *Banksia* and *Casurina* woodland in Jervis Bay National Park, on the south-east coast of New South Wales in Australia. All work was conducted between May 4 and May 20, 2010.

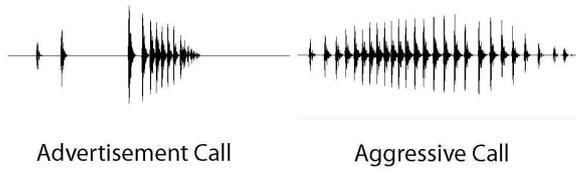


Figure 14: Advertisement and aggressive call types used by *Pseudophryne bibronii* can be distinguished based on their waveform

6.2.2 Experimental design and procedure

Acoustic playback devices were used to simulate the presence of a novel male that repeatedly calls and retreats from a location within the exclusive space surrounding a focal resident (stimulus callers; [Figure 15](#)). Playback experiments were conducted in two choruses, less than a kilometer apart. Resident males were located by triangulating on their advertisement calls. A random male was chosen to be a subject from within a subset of residents that had not been within five meters of a stimulus caller for at least two days and that had not been previously used as a subject. A playback trial was conducted by placing an mp3 player (SanDisk Sansa Shaker and attached Cygnett Micro 2x2W speaker), loaded with one of four stimulus call recordings chosen at random, within 100 cm of a subject in space unoccupied by any current neighbor. We ensured that the stimulus caller used was not based on a recording from any individuals within 5 m of the subject. Multiple stimulus callers were used in order to generalize the results across a range of rival identities and calling patterns rather than a specific individual or calling pattern. Playbacks of stimulus calls were conducted at a volume of 60-70 dB Sound Pressure Level (SPL; sound pressure relative to 20 μ Pa RMS) at the location of the resident's nest. This value approximates the SPL of a caller located 0.5-2.5 m from the resident (unpublished data), which is consistent with observed distances between natural neighbors and not within the range a resident considers to be a large threat (residents produce a third type of call, which was not recorded, during contests over nest-site ownership). Trials were conducted during the first half of the night (1900-2300 hours). We recorded the resident and its interactions with the stimulus caller for a one hour period using a Marantz PMD660 recorder and Rode NTG-2 directional microphone. Experimenters were not present during trials. Overall, subjects were exposed to six, three-minute long exposures to a stimulus caller (a bout period), separated by seven minutes of silence (silent period) to simulate the withdrawal of the intruder. Additionally, each trial began with a seven-minute silent period before the first bout period to act as a baseline measurement ([Figure 15](#)). Seven minutes of silence is a rel-

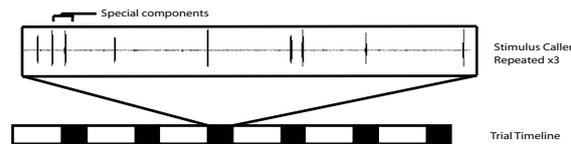


Figure 15: Playback scheme. Each trial lasted for 60 minutes. White periods represent a seven minute silent period. Black periods represent a three minute bout period with one of four stimulus callers (only one stimulus caller is presented here as an example). The audio track that comprises a stimulus caller lasts for one minute but is repeated to produce a three minute bout. Two special components, comprising either aggressive calls or grouped advertisement calls, are included in the stimulus caller in order to stimulate the resident to respond

atively long break from calling in *P. bibronii*, compared with the mean call rate of 7.2 ± 4.1 calls/min observed during baseline recordings. A silent period of this duration is thus likely to be representative of the simulated intruder withdrawing from the interaction. Furthermore, a seven minute break may give the resident ample time to readjust its calling behavior to account for the simulated intruder's most recent withdrawal.

Because the calling behavior of anurans is temperature dependent (Oseen and Wassersug, 2002; Saenz et al., 2006; Canavera et al., 2008; Navas et al., 2008; Steelman and Dorcas, 2010), we measured ambient air temperature at the beginning and end of each trial and calculated the mean. We also noted the number of days since it last rained and the start time for each trial because both the moisture and the time of day are important determinants of anuran calling behavior (Mitchell, 2001; Oseen and Wassersug, 2002; Saenz et al., 2006; Canavera et al., 2008; Steelman and Dorcas, 2010). Following the trial, we measured the volume of three of the speaker's calls from directly above the subject's nest, recording the greatest of these values. In 11 cases, we were able to capture the resident male and measure his weight. These values can be used to determine how threatening the speaker was in relation to the resident because speaker volume correlates with the perceived distance of the intruder and a male's weight correlates with its attractiveness and energy stores. In total, we conducted 21 playback trials, 17 from one chorus and 4 from the other. The experiment was conducted according to the guidelines on animal experimentation produced by the Association for the Study of Animal Behaviour and the Animal Behaviour Society. All of our activities were approved by the Monash University Animal Ethics Committee (permit number BSCI/2007/14) and the NSW National Parks and Wildlife Service (permit number S12552).

6.2.3 *Stimulus calls*

To create the stimulus calls, four independent nest-holding males were recorded for three minutes each. Recordings were made using a Marantz PMD660 portable solid-state recorder and a Rode NTG-2 directional microphone. Recordings were made in mp3 mono format at a sampling rate of 44 kHz and 16bit (CD quality). Each recording was then edited using the software program Audacity v1.3.5 (<http://audacity.sourceforge.net/>) to create four unique, but similar, stimulus calls. This was done by cutting nine calls from each recording. Nine advertisement calls were cut from three of the recordings, whereas seven advertisement and two aggressive calls were cut from the remaining recording. These calls were then arranged into a one-minute timeline and normalized to 100% amplitude. Calls from different individuals were not mixed together in the same track, so that each track represented a different individual. Each track began with a call being made in the first second and had two 'stimulating components', as pilot studies indicated that residents often ignored stimuli that did not contain at least one slightly aggressive signal. For one of the stimulus callers, two aggressive calls were used as the stimulating component. For the other three stimulus callers, two advertisement calls given within 1.5 seconds of each other were used, as grouped calls of this nature appear to stimulate aggression. The remaining six calls were distributed randomly throughout the one minute timeline so as to generalize results across a range of calling patterns and to limit the possibility for residents to be responding to some quirk in calling pattern (for instance, a specific arrangement of calls may act as some kind of signal, which could confound results). The interval between calls for individual residents and stimulus during competitive interactions was not significantly different in terms of mean (residents: 6.30 ± 2.71 ; stimulus callers: 6.69 ± 0.1 ; $t_{20.3} = 0.65$, $p = 0.522$) or standard deviation (residents: 4.68 ± 2.67 ; stimulus callers: 4.11 ± 0.50 ; $t_{22.9} = 0.91$, $p = 0.373$). This sequence was made to repeat three times, giving a three-minute period of calling (Figure 15). Seven minutes of silence was inserted before the calling period. Each ten-minute sequence was loaded onto separate portable mp3 players (SanDisk Sansa Shaker) for use in playback trials. The call rate (9/min), quality (i.e. duration and number of pulses) and type (number of advertisement and aggressive calls) of calls were chosen to reflect slightly below average individuals, based on results reported by Byrne (2008). This was done in order to reduce the threat posed by the intruder to a resident, reducing the risk of the resident abandoning its nest or calling activity.

6.2.4 *Statistical analysis*

6.2.4.1 *Resident responses*

The number of aggressive and advertisement calls given in each three minute bout period (exposure-count) and in each of the three minute periods immediately preceding a bout (preceding-count) were counted from the waveform of the recordings using SoundRuler v0.9.6.0 (<http://soundruler.sourceforge.net/main/>). Advertisement and aggressive calls were treated separately. We calculated exposure-count minus preceding-count for each of the six bout periods to give values that represented the changes in advertisement and aggressive calling behavior attributable to the stimulus call (these values were termed the call-responses). In other words, the call-response variables reflect the magnitude (i.e. the difference in call number between the exposure and preceding periods) and direction (i.e. whether this change was positive or negative) of the resident's response to the stimulus caller. The call-response variables also control for inter- and intra-individual changes in calling behavior (such as those attributable to individual quality, responses to other neighbors and time). These values were divided by the number of minutes in a bout (three) to give the response in units of mean calls/minute.

6.2.4.2 *Do resident calls change over successive interactions?*

We used a mixed model, repeated measures analysis of variance (ANOVA) on each call-response variable according to the guidelines of Littell et al. (1996) and Logan (2010) and using SAS 9.2 (SAS Institute, <http://www.sas.com/>). For analysis, the stimulus caller, bout period and their interaction were the fixed factors, with bout period being the repeated measure within each individual toadlet (the blocking factor). Additionally, we included temperature, days without rain, speaker volume and the starting time of the trial as covariates. We used a restricted maximum likelihood estimation method with Kenward-Roger fixed effects and degrees of freedom approximation. We determined the covariance structure for each model based on the lowest corrected AIC (out of unstructured, correlated symmetry, Toeplitz and first order auto correlative). This method resulted in a Toeplitz structure being chosen for the advertisement call-response and a first order autocorrelation structure for the aggressive response. We used planned comparisons to investigate the nature of any differences in the mean call-responses at each bout period. For advertisement calls, we used polynomial contrasts (i.e. testing for linear, quadratic, etc., relationships over successive interactions). For aggressive calls, we compared each bout period with the following bout period (i.e. 1 vs. 2, 2 vs. 3 . . . 5 vs. 6).

6.2.4.3 *Is there individual variation in the direction of change in call-response?*

To explore variation in the direction of responses throughout the population, we used a Tukey's test of additivity to determine if there was an interaction between individual toadlets and the effect of bout period (Logan, 2010). Additionally, we subtracted each individual's first call-response from its last call-response (for both advertisement and aggressive calls) as a measure of the direction and magnitude of their ultimate change in behavior (termed delta response indices). To determine if there were any predictors for an individual's change in response or initial reactions to the speaker, we tested for any correlations between delta response indices, call-responses in the first bout, temperature, days without rain, resident mass, speaker volume and trial start time. We also used an ANOVA to test whether the stimulus caller used affected delta response indices or initial call-responses. Finally, to determine if responses became more or less similar over successive bouts, we tested for a correlation between the standard deviation of responses and bout period. Note that there is no assumption regarding homogeneity of variance for the mixed model ANOVA, as the covariance structure is able to compensate for a relationship between mean and variance (Littell et al., 2006; Myers et al., 2010). Thus, a correlation between variability and bout period does not invalidate any of the results. All of these tests were conducted using R 2.12.0 (R Project contributors, <http://www.r-project.org/>).

6.2.4.4 *Is there a trade-off between advertisement and aggressive calls?*

To determine whether there was a trade-off between advertisement and aggressive calls, we tested for a negative correlation between advertisement and aggressive call-responses at each bout period and for the call-responses given by an individual averaged across all six bout periods. Additionally, we tested for a correlation between advertisement and aggressive delta response indices. This analysis was conducted using R 2.12.0.

6.3 RESULTS

6.3.1 *Do resident calls change over successive interactions?*

Residents changed their advertisement and aggressive call-rates in response to simulated intrusions by significantly different amounts across successive intrusion attempts (Table 14; Figure 16). Planned contrasts indicated that there was a significant linear increase in the mean advertisement call-response over successive intrusion attempts ($F_{1,18.8} = 13.96, p = 0.001$). In contrast, the mean rate of aggressive

Table 14: Mixed model ANOVA testing for differences in advertisement and aggressive call-responses (change in call-rate in response to intrusion) over successive intrusions

CALL RESPONSE	FACTOR	F_{df}	p
Advertisement	Stimulus call	1.96 _{3,13}	0.170
	Bout period	4.24 _{5,36.6}	0.004
	Call x Bout period	1.16 _{15,47.9}	0.333
	Speaker volume	0.40 _{1,13}	0.537
	Start time	1.31 _{1,13}	0.273
	Temperature	1.46 _{1,13}	0.249
	Days without rain	0.79 _{1,13}	0.390
Aggressive	Stimulus call	0.90 _{3,17.8}	0.461
	Bout period	2.34 _{5,79}	0.049
	Call x Bout period	1.01 _{15,80.2}	0.458
	Speaker volume	1.13 _{1,18.5}	0.301
	Start time	0.86 _{1,18.5}	0.367
	Temperature	3.66 _{1,18.5}	0.071
	Days without rain	1.35 _{1,18.5}	0.261

calls given in response to an intruder declined after the first bout period ($F_{1,76.7} = 8.96$, $p = 0.004$) and thereafter remained steady (p range=0.273 - 0.844). The stimulus call used had no significant effect on the results, nor did temperature, speaker volume, time and days since rain (Table 14).

6.3.2 *Is there individual variation in the direction of change in call-response?*

Individuals that substantially increased their call-rate when first encountering the intruder gave comparatively lower shifts in call-rate during the ultimate bout. Similarly, individuals that reduced their calling effort in response to the first intrusion gave greater call-responses in the ultimate bout compared with their initial response. This pattern is described by a significant correlation between initial call-responses and delta response indices for both advertisement and aggressive call-responses (Table 15; Figure 17). This correlation also shows that the amount an individual changed its calling behavior depended on the magnitude of its initial response, so individuals that showed the most extreme initial responses also showed the most extreme changes. The nature of this variation appears to have led call-responses across the population to become more similar over time, as indicated by significant negative decreases in the standard deviations of advertisement

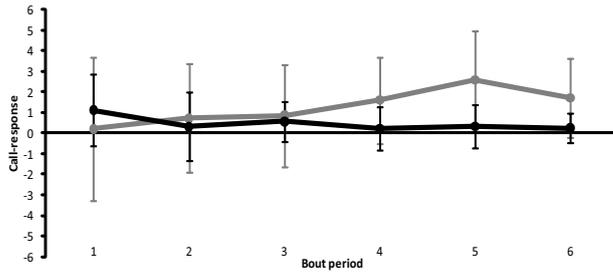


Figure 16: The relationship between unadjusted mean changes in call-rate due to intrusion (call-response; calls/min \pm SD) and successive intrusion instances (bout period). Advertisement calls are given by grey circles and the grey line; aggressive calls are given by black circles and the black line

($F_{1,4} = 12.85$, $p = 0.023$, $r^2 = 0.70$) and aggressive ($F_{1,4} = 18.46$, $p = 0.013$, $r^2 = 0.78$) call-responses over successive bout periods (Figure 16). No variables other than initial call-responses were found to affect delta response indices, as there were no significant correlations with any covariate (Table 15) and the stimulus call used had no significant effect (advertisement calls: $F_{3,17} = 0.73$, $p = 0.548$; aggressive calls: $F_{3,17} = 0.81$, $p = 0.508$). Despite the influence of initial call-response, neither resident mass, speaker volume nor environmental variables (temperature, days since rain and trial start time) could explain how it varied (Table 16). Furthermore, there were no significant differences in initial call-response attributable to the stimulus caller used (advertisement calls: $F_{3,17} = 2.36$, $p = 0.108$; aggressive calls: $F_{3,17} = 0.27$, $p = 0.846$). Thus, although residents increased their advertisement call-response and decreased their aggressive call-response on average Figure 16, there was significant variation in these directions between individuals for both advertisement (Tukey's test of additivity: $t = 2.87$, $p = 0.004$) and aggressive ($t = 5.21$, $p < 0.001$) call-responses.

6.3.3 Is there a trade-off between advertisement and aggressive calls?

Although residents increased their advertisement call-response and decreased their aggressive call-response on average (Figure 16), there were no significant negative correlations between advertisement and aggressive call-responses at any period, or averaged across all six bout periods (Table 17). Furthermore, the delta response indices for advertisement and aggressive calls were independent of one another ($F_{1,19} = 0.43$, $p = 0.518$, $r^2 < 0.01$). Therefore, investment into either call

Table 15: Correlations between advertisement and aggressive delta response indices (difference in change in call-rate between last and first interactions) and covariates

DELTA RESPONSE INDEX	FACTOR	F_{df}	p	r^2
Advertisement	Volume of stimulus call	0.10 _{1,19}	0.759	< 0.01
	Resident mass	2.00 _{1,10}	0.188	0.08
	Start time	0.11 _{1,19}	0.747	< 0.01
	Temperature	0.30 _{1,19}	0.591	< 0.01
	Days without rain	1.11 _{1,19}	0.305	< 0.01
	First advertisement response	45.31 _{1,19}	< 0.001	0.69
	First aggressive response	0.77 _{1,19}	0.392	< 0.01
Aggressive	Volume of stimulus call	0.63 _{1,19}	0.436	< 0.01
	Resident mass	< 0.01 _{1,10}	0.923	< 0.01
	Start time	< 0.01 _{1,19}	0.977	< 0.01
	Temperature	0.87 _{1,19}	0.445	< 0.01
	Days without rain	4.97 _{1,19}	0.708	< 0.01
	First advertisement response	1.18 _{1,19}	0.291	< 0.01
	First aggressive response	94.14 _{1,19}	< 0.001	0.82

Table 16: The correlations between advertisement and aggressive call-responses (change in call-rate in response to intrusion) in the first bout period and covariates

DELTA RESPONSE INDEX	FACTOR	F_{df}	p	r^2
Advertisement	Volume of stimulus call	0.06 _{1,19}	0.807	< 0.01
	Resident mass	1.54 _{1,10}	0.243	< 0.01
	Start time	0.19 _{1,19}	0.664	< 0.01
	Temperature	0.42 _{1,19}	0.523	< 0.01
	Days without rain	0.34 _{1,19}	0.570	< 0.01
Aggressive	Volume of stimulus call	1.19 _{1,19}	0.290	< 0.01
	Resident mass	< 0.01 _{1,10}	0.974	< 0.01
	Start time	0.13 _{1,19}	0.721	< 0.01
	Temperature	0.74 _{1,19}	0.401	< 0.01
	Days without rain	0.08 _{1,19}	0.779	< 0.01

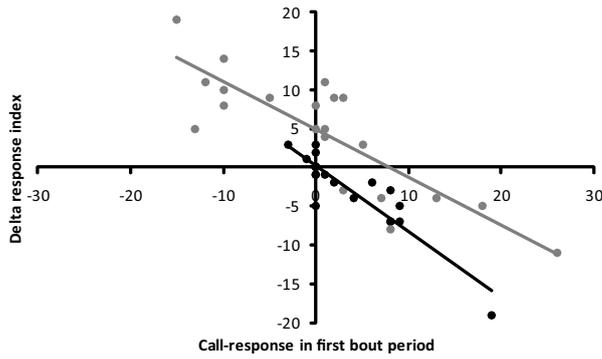


Figure 17: The relationship between an individual's change in call-rate upon initial contact with a simulated intruder (call-response in the first bout; calls/min) and its change in response over multiple interactions (delta response index; calls/min) for advertisement (grey) and aggressive calls (black). Positive values for call-response in the first bout represent individuals that increased their call-rate during the first playback, whereas negative values represent individuals that reduced their call-rate. Positive values for delta response index represent individuals that showed a greater shift in call-rate during the final bout compared with the first, whereas negative values represent individuals that showed a greater shift in the first bout period compared with the last

type was not reduced by investment into the other, nor did changes in one call type over time correlate with changes in the other.

6.4 DISCUSSION

We aimed to determine whether advertisement and aggressive calling responses increased or decreased over successive interactions with a repeat intruder, whether individuals responded differently and whether there was a trade-off between the different call types.

In regards to the changes observed in call-responses, the mean advertisement call-response linearly increased over successive interactions whereas the mean aggressive call-response decreased after the first bout period. These patterns conformed with our expectations and the results of previous studies of male frogs responding to a persistent caller (Bee, 2003b; Marshall et al., 2003; Humfeld et al., 2009). The implication is that individuals benefit from minimizing the costs of aggressive calling after the intruder has signaled its intention to remain in the area. In other words, the intruder has become a neighbor and the resident benefits from having a 'dear enemy' relationship with it. Accordingly, the increase in advertisement calling suggests that residents increased their effort toward attracting females in order to compensate for the reproductive interference imposed by their new neighbor. However, contrary to the dear enemy interpre-

Table 17: The correlation between advertisement and aggressive call-responses (change in call-rate in response to intrusion) given by an individual at each bout period and for all bout periods pooled together

PERIOD	F_{df}	p	r^2
1	1.41	0.249	0.02
2	0.24	0.632	< 0.01
3	0.32	0.580	< 0.01
4	0.40	0.535	< 0.01
5	0.01	0.915	< 0.01
6	0.01	0.933	< 0.01
Pooled	1.55	0.228	0.03

tation, there was significant individual variation in the direction of change for both advertisement and aggressive calls, indicating that different individuals showed different patterns of response. Also unexpected was the correlation between an individual's first response and the direction of its subsequent change. Specifically, individuals that responded strongly in the first interaction reduced the magnitude of their call-response by the ultimate interaction, whereas those that responded weakly increased their efforts. This resulted in a convergence of call-responses toward a similar level by the ultimate bout. The establishment of a dear enemy relationship is not sufficient for explaining these three important findings (individual variation in the direction of shifts in calling behavior, a correlation between these shifts and an individual's first call-response and convergence of calls over time).

A large body of work suggests that territorial residents alter their aggressive behavior in response to an intrusion based on the threat posed by the intruder and that the perceived threat of the intruder varies with repeated interactions (the relative threat hypothesis; [Temeles, 1994](#); [Wich and Sterck, 2007](#); [Briefer et al., 2008](#); [Akçay et al., 2009](#); [Booksmythe et al., 2010](#)). This would suggest that although most individuals were not threatened by the intruder (and hence decreased their aggressive signaling), some were threatened enough to attempt expelling the intruder by increasing aggressive call-rate. However, we did not detect any effect of resident mass (although the sample size was only 11) or speaker volume, which should both be related to the threat of the stimulus in relation to the resident, on the changes in call-responses. Additionally, the relative threat hypothesis can not explain the correlations between initial call-responses and their subsequent change, nor the convergence of call-responses to a similar level. The familiarity hypothesis (which is often associated with rel-

ative threat) is also insufficient for explaining the results, as it only predicts aggression to decrease with increasing familiarity (Ydenberg et al., 1988; Getty, 1989).

One explanation for the variation in response direction is that residents were initially uncertain about the intruder's quality and intentions, but were able to more accurately assess the intruder with each interaction and thus gradually adjust their calling behavior to an optimal level. That is, a resident may need to give a certain number of advertisement and aggressive calls in response to an intruder in order to remain attractive and maintain adequate spacing while minimizing calling costs (Burmeister et al., 1999; Marshall et al., 2003; Wells, 2007; Byrne, 2008; Humfeld et al., 2009). For instance, chorusing frogs have been observed to gradually match the number of calls produced by rivals in order to optimize their calling behavior (Ayre et al., 1984; Gerhardt et al., 2000). However, residents may initially be uncertain about the optimal response (this would explain the large degree of variation in, and lack of predictor for, call-responses in the first bout period). Residents may thus require information gathered over repeated interactions in order to determine how best to alter their behavior. The ability to gather information and use it as the basis for behavioral changes is suggested by the familiarity hypothesis (Ydenberg et al., 1988; Getty, 1989) and some models of contest behavior (Parker and Rubenstein, 1981; Hammerstein and Parker, 1982; Enquist and Leimar, 1983). Furthermore, resident frogs are expected to continually assess their opponents and alter their calling appropriately in order to remain closer to optimal levels. For instance, spring peepers (*Pseudacris crucifer*) have been observed to reduce their aggression over time toward speakers that give purely advertisement calls, but immediately respond with aggressive calls once the playback changes to a mixture of advertisement and aggressive calling (Humfeld et al., 2009). Overall, the call adjustment hypothesis can explain why the initial call-response predicted the ultimate change in response because individuals that gave too many calls to begin with benefited by giving fewer, whereas those that responded weakly benefited by giving more. Furthermore, initial reactions with the greatest error required the greatest adjustment. It would also explain why resident calls tended to converge because residents may have ultimately made similar assessments of the quality and threat posed by the simulated intruders. Therefore, variation in the direction of change in call-responses may not be due to an increase or decrease in the perceived threat of the intruder over successive interactions, but differences in how calling had to be adjusted from initial uncertainty in order to give an optimal response.

Fatigue is an alternative to optimization for explaining changes in behavior related to repeated intrusions (Peeke, 1984). Specifically, the

observed decreases in call-response may have reflected prohibitively high metabolic costs of sustaining call production. By contrast, individuals that increased call-response with each interaction may have been able to do so because they were initially conservative. However, even though calling is energetically expensive for frogs (Taigen and Wells, 1985), reduced call rate is not necessarily indicative of depleted metabolic resources (Schwartz et al., 1995). Instead, frogs are expected to manage energy allocation to enable them to maintain calling throughout the night (Schwartz et al., 1995) and to give intense displays when the situation demands it (Byrne, 2008). Furthermore, other playback experiments conducted on frogs have ruled out fatigue as a contributing factor by demonstrating that individuals are able to respond at full intensity if the stimulus is changed (Owen and Perrill, 1998; Bee, 2003b; Humfeld et al., 2009). Furthermore, if fatigue was important, we would expect a relationship between call rate and environmental factors such as days since rain, temperature or the starting time of the trial as these are all expected to influence fatigue thresholds. However, we found no effect of these factors on either call-response. Taken together, this evidence suggests that fatigue is unlikely to explain the observed changes in calling behavior in terrestrial toadlets.

Finally, our expectation that shifts in behavior would reflect a trade-off between exploitative and defensive interests was not supported. This trade-off is expected to occur in frogs because an individual that gives an aggressive call does so at the cost of not producing an advertisement call and vice versa (Brenowitz and Rose, 1999; Marshall et al., 2003). There are at least three alternatives to the lack of a trade-off to explain why we did not detect any correlation. First, advertisement and aggressive calls may have some functional overlap (i.e. advertisement calls may weakly repulse males and aggressive calls may weakly attract females). For example, Marshall et al. (2003) found evidence that suggests preference for advertisement over aggressive calls in female spring peepers (*P. crucifer*) depends on the frequency and volume at which the calls are given in relation to one another. However, in species that produce these two types of call, each call type is superior to the alternative at performing the hypothesized function, so some degree of trade-off is still expected. The second potential explanation is that residents were not calling at their maximum output, allowing them to vary each call type independently. Finally, the trade-off may be reflected in the quality of calls (e.g. call duration, call volume and energetic requirements) rather than in quantity. In any case, changes in calling behavior in this species and at the observed competitive intensity do not necessarily reflect a shift along a continuum between exploiting and defending a territory.

In conclusion, our results suggest that changes in a resident's response to a repeated intruder over successive interactions may reflect corrections made to an initially uncertain response. Frogs benefit by responding to changes in their social environment by minimizing the costs of calling and reproductive interference imposed by others, such as the simulated intruder in this study. Our results imply that a learning period is necessary for residents to assess the relative costs and benefits of interacting with an intruder and to arrive at this optimal level of calling. This is important to consider in cases where there is variation in the number of times a given intruder will be encountered. Additionally, unlike the predictions of the familiarity hypothesis, the results of this study imply that the optimal shift in an aggressive response to increasing familiarity is not always negative. Instead, individuals may tune their aggressive response to an appropriate level, which could be greater or less than their initial investment. Therefore, we may need to reconsider the prediction that increasing familiarity leads to a decrease in aggression when the threat of the intruder is low. Instead, we may consider that increasing familiarity leads to decreased uncertainty regarding the threat of the intruder. Finally, models of contest behavior have long incorporated increasing accuracy of opponent assessment over time as contestants gain more information about their relative abilities (Parker and Rubenstein, 1981; Hammerstein and Parker, 1982; Enquist and Leimar, 1983; Enquist et al., 1990). Our study highlights that a similar process is likely to influence the structure of long-term competitive interactions. Furthermore, behaviors related to territory exploitation, in addition to aggressive behaviors, can be influenced by the gradual acquisition of information through interaction.

VARIATION BETWEEN SELF AND MUTUAL ASSESSMENT IN ANIMAL CONTESTS

Limited resources lead animals into conflicts of interest, which are resolved through contests that are determined by the withdrawal of one of the contestants. Current theory suggests that the decision to withdraw can be based on a threshold derived from an individual's own state (self assessment) or on a comparison between their own state and their opponent's (mutual assessment). The observed variation between these assessment strategies in nature does not conform to theory, which suggests mutual assessment should be predominant. Thus, we require theoretical developments that explain the functional significance of different assessment strategies. We consider a Hawk-Dove game with two discrete classes that differ in fighting ability, in which the players strategically decide on their investment towards mutual assessment. Analysis of the model indicates that there are simultaneous trade-offs relating to assessment strategies. Firstly, weaker individuals in a population must decide on whether to acquire information about their opponents at the cost of providing opponents with information about themselves. Secondly, all individuals must decide between investing in mutual assessment and being persistent in contests. Our analysis suggests that the potential for individuals to make errors during contests, and differences in the consequences of sharing information within a population, may serve as fundamental concepts for explaining variation in assessment strategy.

7.1 INTRODUCTION

Animals can have conflicts of interest over access to resources, which can be decided by a contest (Maynard Smith, 1974). Individuals engaged in a contest are faced with a strategic decision of when to withdraw, rather than persist (Arnott and Elwood, 2008, 2009a). We expect that this decision can be improved by responding to information that can help to predict the outcome (Giraldeau, 1997; Dall et al., 2005). One such factor is the resource holding potential (RHP) of each individual, which represents their ability to persist in the contest. RHP can be determined from cues such as size, mass or energy stores (Arnott and Elwood, 2009a). Therefore, if an individual's RHP affects its expected payoffs in a contest, then an asymmetry in RHP between the contestants will affect their decision to withdraw or persist (Parker and Rubenstein, 1981).

There are at least two sources of information on RHP: private information on an individual's own RHP and public information regarding the RHP of an opponent. Furthermore, there are at least two sources of public information on opponent RHP. Individuals may firstly have access to information on the distribution of RHP within the population (general information), and secondly to cues or signals that indicate the RHP of a given opponent (specific information). Provided that an individual has some private and public information, it can compare its own RHP to its opponent's RHP (based on either general or specific information) in order to determine if there is an RHP asymmetry that can influence the outcome of the contest. The individual can then benefit by basing its decision of whether to withdraw or persist in an encounter on this assessment (Parker and Rubenstein, 1981).

Whether general or specific information is used in an RHP comparison can determine the process of RHP assessment in a contest and the withdrawal strategy that results from this assessment. Theory suggests that individuals can respond to general information by assessing their own RHP—a self assessment strategy (Mesterton-Gibbons et al., 1996; Payne and Pagel, 1996, 1997; Payne, 1998). For instance, individuals may persist or withdraw from contests according to the probability of encountering an individual of lower or higher RHP, respectively. More specifically, models that consider the structure of contests suggest that animals can be involved in a war of attrition (WOA), in which they persist up until a personal threshold that is determined by their own RHP and the distribution of RHP in the population (Mesterton-Gibbons et al., 1996). In contrast, access to specific information allows animals to directly compare their own RHP against the RHP of their current opponent and only withdraw if they are certain that they are outmatched. Contests based on this mechanism use a mutual assessment strategy (Parker and Rubenstein, 1981; Hammerstein and Parker, 1982; Enquist and Leimar, 1983; Enquist et al., 1990).

Although animals can benefit from responding to the RHP asymmetry, the information that reflects the asymmetry is inherently uncertain and not completely reliable. Thus, there is always the potential for an individual to make a strategic error in its decision of whether or not to withdraw (Parker and Rubenstein, 1981; Hammerstein and Parker, 1982; Enquist and Leimar, 1983). That is, individuals may persist when they would benefit more from withdrawing or withdraw when it would have been better to persist. These errors can result in unnecessary costs incurred through fruitless persistence and lost opportunities to access a resource, respectively. The potential for these errors to be made has a strong influence on adaptive withdrawal strategies (Crowley, 2000), although it is unclear how withdrawal

strategies change if animals can reduce the chance of error. In this regard, theoretical and empirical evidence has suggested that gathering specific information through a mutual assessment strategy can reduce the risks of making a strategic error and can therefore be adaptive (Enquist and Leimar, 1983). Thus, mutual assessment processes were once thought to predominate in animal contests.

The notion of mutual assessment predominating in nature was once supported by empirical studies, but recent work has brought the validity of these conclusions into question (Taylor et al., 2001; Gammell and Hardy, 2003; Taylor and Elwood, 2003; Briffa and Elwood, 2009). More recent empirical studies suggest that assessment strategy is variable between and within species (e.g., Hsu et al., 2008; Prenter et al., 2008; Kasumovic et al., 2010). Furthermore, the intensified scrutiny of recent studies has uncovered a variety of assessment modes that were not predicted by theory (Arnott and Elwood, 2009a) and there are multiple cases of inconclusive results concerning the assessment strategies being used within a population (Jennings et al., 2005; Morrell et al., 2005; Stuart-Fox, 2006). Therefore, it is clear that a functional understanding of the basis of withdrawal decisions in contests is lacking.

It has been suggested that variation in assessment strategy occurs as the result of a trade-off between the costs and benefits of mutual assessment (Taylor and Elwood, 2003; Prenter et al., 2006; Elias et al., 2008; Arnott and Elwood, 2009a). Specifically, mutual assessment is thought to be beneficial in terms of reduced time and energy demands in contests, but also potentially costly in terms of reliably assessing cues and signals. However, this hypothesis has not been empirically tested or formally examined. We thus developed a model in an effort to initiate a general theory for explaining variation in assessment strategy. As current models of contest behaviour do not consider variation in assessment strategy, we used the argument for partial mutual assessment as the theoretical basis for our model (Prenter et al., 2006). This hypothesis suggests that individuals have reliable information on their own RHP but can gather some degree of information on their opponent's RHP, and thus has elements of both self and mutual assessment. Although this model has yet to receive any formal validation, it does have some empirical support (Kelly, 2006; Smallegange et al., 2007; Elias et al., 2008), which justifies its use as the basis for our model.

7.2 MODEL DESCRIPTION

A summary of the model is given in Figure 18. We consider a population of individuals in which access to a fitness-enhancing resource of value V is determined through direct interactions amongst pairs

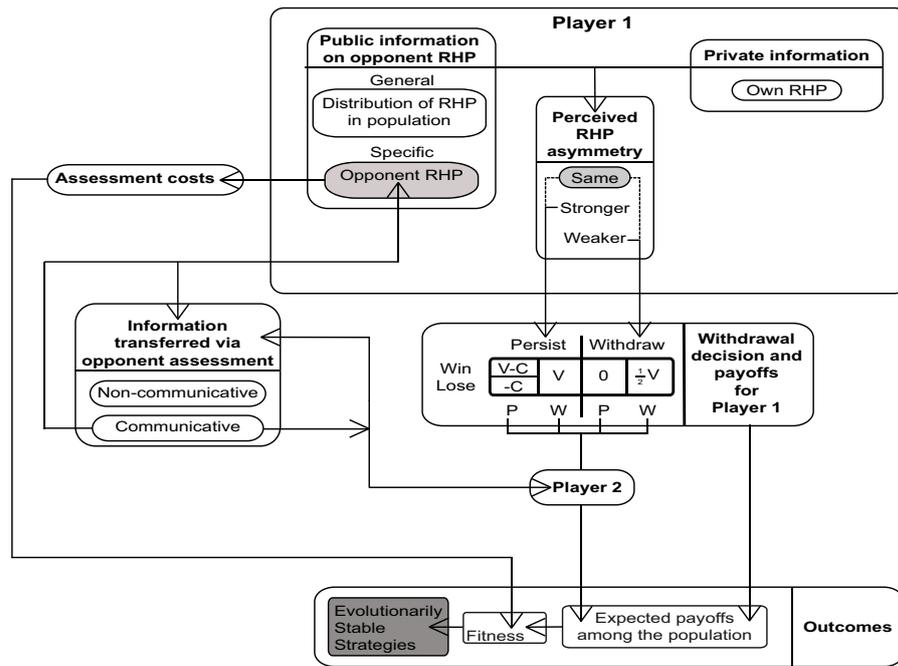


Figure 18: Pictorial representation of the model, showing details of the factors that influence the decision made by Player 1 (Player 2 is symmetrical). Light grey boxes represent the strategic variables that respond to the environment, and the dark grey box represents the focus of our analysis (ESS conditions)

Player 1 decides to persist or withdraw in a contest based on its information concerning the current RHP asymmetry, which is based on private information of its own RHP and public information of Player 2's RHP. In regards to public information, individuals have complete information about the distribution of RHP in the population (general information; Equation 2) but may strategically invest (u_1) in obtaining information on its current opponent (specific information), although this comes at a cost (Γ). Furthermore, the acquisition of specific information may advertently or inadvertently provide Player 2 with information about the RHP asymmetry (similarly, Player 2 may provide Player 1 with information), but only if assessment is communicative (Equation 3, Equation 4). Player 1 will assess whether it is stronger, weaker or equally matched with Player 2, in terms of RHP, on the basis of this information (Equation 7). Because the outcome of contests is perfectly determined by RHP, Player 1 will withdraw if Player 2 is stronger, persist if Player 2 is weaker, and strategically adjust its persistence against a matched opponent (u_2, u_3). The actions of Players 1 and 2 then determine the outcome of the contest over a fitness enhancing resource (V), which is modelled using a hawk-dove game. If both individuals are willing to persist, then they each pay the costs (C) associated with escalation. The expected payoffs of all interactions that take place in the population, including the costs of assessment, then determine the fitness associated with a particular strategy (Appendix A), and an ESS occurs when the strategy adopted by the population can not be invaded by an alternative strategy (Appendix B).

(Players 1 and 2). This resource could represent anything that improves fitness, including food, mating opportunities or an advantageous social position. Within these interactions, individuals use a withdrawal strategy that corresponds to a Hawk-Dove game (Maynard Smith and Parker, 1976), in which they have the option to withdraw from the contest by playing Dove, or persist by playing Hawk. The two individuals are assumed to make their decisions simultaneously, and the result of the interaction determines the fitness consequences for each individual. If both individuals play Hawk, then the interaction escalates: both individuals suffer a fight cost, C , and one individual gains access to the resource. Fight costs can include the time and energy devoted to the contest (Clutton-Brock and Albon, 1979; Hack, 1997b,a; Briffa and Sneddon, 2007), the build-up of metabolic wastes (Briffa and Sneddon, 2007; Copeland et al., 2011), increased predation risk (Jakobsson et al., 1995), physical damage, or the risk of fatality (Enquist and Leimar, 1990; Murray, 1990; Haley, 1994; Payne, 1998; West et al., 2001). We assume that the winner of a contest is perfectly determined by RHP. For simplicity, we assume that individuals can either be weak, W , or strong, S , with strong individuals always winning against weak individuals and evenly matched opponents having an equal chance of winning. If only one individual plays Hawk, then it will gain access to the resource without a fight and if both individuals play Dove, the resource is assumed to be shared or randomly allocated (i.e. payoff = $\frac{1}{2}V$).

We assume that the proportions of individuals in the population having weak and strong RHP are λ and $1 - \lambda$, respectively, with at least some individuals of each type, i.e.,

$$0 < \lambda < 1. \quad (1)$$

Additionally, we assume that individuals have perfect knowledge of their own RHP, but not the RHP of their opponent.

From the perspective of a given individual, the world has four potential RHP combinations, which we have labelled $i = 1 \dots 4$. Namely, WW (weak self, weak opponent; $i = 1$), WS (weak self, strong opponent; $i = 2$), SW (strong self, weak opponent; $i = 3$) and SS (strong self, strong opponent; $i = 4$). If p_i denotes the probability of state i , then

$$p_1 = \lambda^2, \quad p_2 = \lambda(1 - \lambda) = p_3, \quad p_4 = (1 - \lambda)^2. \quad (2)$$

The RHP combination that an individual actually perceives is determined by its strategic investment towards acquiring information about its current opponent (i.e., self or mutual assessment). Because the information in (2) is a facet of the RHP distribution in the population, it is public, and so all individuals are assumed to be initially able to perceive their opponent as weak with probability λ and strong

with probability $1 - \lambda$. However, individuals have the option to improve their information on a specific opponent's RHP through mutual assessment. Individuals strategically decide on how much effort to invest in assessing their opponent; this effort is u_1 for Player 1 and v_1 for Player 2, where $u_1, v_1 \geq 0$. Furthermore, we distinguish between communicative and non-communicative assessment behaviors, as assessment is not necessarily passive or unilateral and can depend on the actions taken by each contestant (Hack, 1997b). Under non-communicative assessment, the behaviors involved in assessing an opponent provide an individual with information, but provide no information to its opponent (e.g., a visual assessment). In contrast, individuals either advertently or inadvertently provide their opponent with information on the RHP asymmetry through performance of assessment behaviors if assessment is communicative (e.g., a tug of war or comparison of signal strength). We establish the degree of communicative assessment by assuming that a given investment towards mutual assessment is only r times as effective at yielding information to the opponent as to the investor (with assessment non-communicative when $r = 0$). Accordingly, let E denote the total effective effort directed at judging the other's RHP correctly. Then for Player 1 we have

$$E = X = u_1 + rv_1 \quad (3)$$

while for Player 2 we have

$$E = Y = ru_1 + v_1. \quad (4)$$

Let $\phi_W(E)$ be the probability that an animal perceives the other contestant correctly if the other animal is weak, and let $\phi_S(E)$ be the probability that an animal perceives the other contestant correctly if the other animal is strong. Then, from above, it is reasonable to assume that

$$\phi_W(0) = \lambda, \quad \phi_S(0) = 1 - \lambda \quad (5)$$

and $\phi_W(\infty) = \phi_S(\infty) = 1$. For the sake of simplicity, we assume that the accuracy of assessing an opponent (independently of opponent RHP) increases with total effort according to

$$\frac{1 - \phi_W(E)}{1 - \phi_W(0)} = \frac{1 - \phi_S(E)}{1 - \phi_S(0)} = e^{-\alpha E}. \quad (6)$$

Here, the probability of making an incorrect perception (given effort towards assessment) relative to the initial probability of being incorrect (i.e., pure self assessment) is determined by an exponential rate parameter, α (Figure 19). Thus, from (5) and (6), the respective probabilities of perceiving a weak or strong opponent correctly increase with total effective effort according to

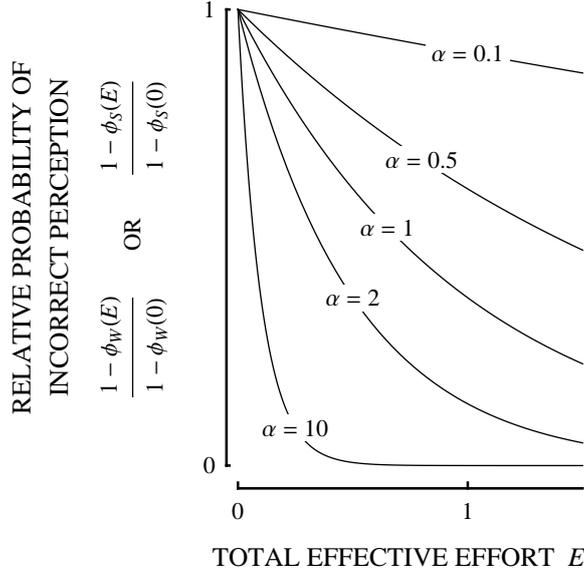


Figure 19: Probability of an incorrect perception relative to the initial probability of an incorrect perception as a function of total effort towards assessing an opponent's RHP, for various values of the parameter α

$$\begin{aligned}\phi_W(E) &= 1 - \{1 - \phi_W(0)\}e^{-\alpha E} = 1 - (1 - \lambda)e^{-\alpha E} \\ \phi_S(E) &= 1 - \{1 - \phi_S(0)\}e^{-\alpha E} = 1 - \lambda e^{-\alpha E}.\end{aligned}\quad (7)$$

The rate parameter α represents the efficacy of assessment (i.e., the capacity for effort invested towards mutual assessment to correctly determine the opponent's RHP). This could reflect the sensory and cognitive abilities of the assessor, the reliability of signalling, or previous experience with the opponent. Additionally, mutual assessment is not free: it incurs a cost Γ per unit of effort u_1 or v_1 . Such assessment costs can arise from a number of sources, although few studies have explicitly considered them. For instance, individuals may need to produce signals that are costly in time or energy in order to receive honest information from their opponent (Dawkins and Guilford, 1991), with the cost of signalling increasing as the information content of the signal increases (Enquist et al., 1990; Hack, 1997b). Additionally, receiving information from an opponent may expose an individual to predation risk (Dawkins and Guilford, 1991) or may involve being damaged by an opponent's attack (Enquist and Leimar, 1983; Payne, 1998). There may also be costs associated with the development of cognitive or perceptive abilities required for making

assessments (Taylor and Elwood, 2003; Prenter et al., 2006; Elias et al., 2008; Arnott and Elwood, 2009a).

For each of the four possible actual states i in the model, there are four possible perceptual states, which we label $j = 1 \dots 4$: *CC* (both animals perceive their opponent's RHP correctly; $j = 1$), *CI* (only Player 1 perceives correctly; $j = 2$), *IC* (only Player 2 perceives correctly; $j = 3$) and *II* (neither animal perceives the other's RHP correctly; $j = 4$).

Each contestant is assumed to respond to the perceived RHP combination by playing Hawk if it perceives *SW* and Dove if it perceives *WS*. Individuals that perceive the RHP combination as *WW* play Hawk with strategic probability u_2 for Player 1 and v_2 for Player 2, hence Dove with probability $1 - u_2$ or $1 - v_2$. Those that perceive *SS* play Hawk with strategic probability u_3 for Player 1 and v_3 for Player 2, hence Dove with probability $1 - u_3$ or $1 - v_3$. This aggression has its limits at either being never, or always, aggressive against a matched opponent (i.e., $0 \leq u_i, v_i \leq 1$ for $i = 2, 3$). Individuals that have an incorrect perception respond to a weak opponent as if it were strong, or to a strong opponent as if it were weak. In other words, an individual that has an incorrect perception of the RHP combination makes a strategic error in terms of its withdrawal strategy.

Thus, each individual's strategy is a 3-dimensional vector, $u = (u_1, u_2, u_3)$ for Player 1, who represents a mutant strategy, and $v = (v_1, v_2, v_3)$ for Player 2, who represents the population. Components of strategy are constrained according to $u_1, v_1 \geq 0$ and $0 \leq u_i, v_i \leq 1$ for $i = 2, 3$; in particular, all are nonnegative numbers.

The resultant fitness to a mutant u -strategist in a population of v -strategists, denoted by $f(u, v)$, is now readily calculated as the expected value—over all possible combinations of actual and perceived RHP—of the payoff to strategy u , minus the costs of assessment. Details of this computation are given in [Appendix A](#).

7.3 ESS ANALYSIS

Population strategy v is an evolutionarily stable strategy or ESS in the sense of Maynard Smith (1982) if it does not pay a potential mutant to adopt any alternative strategy to v ; v is a strong ESS if it is also uniquely the best reply to itself ($f(v, v) > f(u, v)$ for all $u \neq v$), and a weak ESS if there is at least one alternative best reply u (such that $f(u, v) = f(v, v)$), but v is a better reply than u to all such u ($f(v, u) > f(u, u)$). Intuitively, in a population at a strong ESS, any mutant strategy is immediately selected against; whereas, at a weak ESS, a strategy that is an alternative best reply can gain an initial toe-hold, but cannot spread before being selected against. For the sake of simplicity, we assume throughout that each component of strategy

is independent of the other two, so that a potential mutant strategy $u = (u_1, u_2, u_3)$ differs from an ESS $v^* = (v_1^*, v_2^*, v_3^*)$ only in one component of the vector.

Detailed ESS calculations are presented in [Appendix B](#) and can be summarized as follows. First, we distinguish an ESS as Type I or Type II according to whether it involves pure self assessment ($v_1^* = 0$) or some form of mutual assessment ($v_1^* > 0$). Either type of ESS could have up to nine subtypes, because the escalation probability v_2 when perceiving *WW* can be 0, 1 or intermediate; and likewise for the escalation probability v_3 when perceiving *SS*. However, only five of the possible Type-I subtypes and only six of the Type-II subtypes can arise ([Appendix B](#)). We distinguish the Type-I subtypes as IA, IB, IC, ID or IE, as defined in the caption to [Figure 20](#). We distinguish the Type-II subtypes as IIa, IIb, IIc, IIe, IIf or IIg as defined in the caption to [Figure 21](#), choosing lower-case subscripts that link to a corresponding Type-I subtype where one exists; thus we avoid using the label IIc, because IC signifies ($v_1^* = 0$ and) $v_2^* = 0, v_3^* = 1$, whereas no ESS with ($v_1^* > 0$ and) $v_2^* = 0, v_3^* = 1$ exists.

To aid in analysis, we define two dimensionless parameters:

$$\beta = \frac{V}{C}, \quad \gamma = \frac{\Gamma}{\alpha C}. \quad (8)$$

The first parameter, β , which we call relative resource value, measures the value of the resource relative to the cost of escalation. The second parameter, γ , which we call relative assessment cost, measures the effective assessment cost, which is $\frac{\Gamma}{\alpha}$, relative to the cost of escalation, C . To see why Γ/α is the effective cost of assessment, note from (6) that $E = 1/\alpha$ is the amount of effort required to reduce relative perception error to e^{-1} or 37%; and because the cost per unit effort is Γ , the cost of reducing relative error to 37% is $\Gamma \cdot 1/\alpha$. Note that γ may be small—and hence assessment may be cost-effective relative to escalation—either because Γ is small or because α is large (or because C is large). Smaller values of γ reflect more efficient information gain.

7.3.1 *The relative costs of mutual assessment and escalation*

An individual that is behaving optimally can afford to bear only certain costs. It is in the allocation of these costs between mutual assessment and the capacity to escalate that determines whether self or mutual assessment is the ESS for a given set of ecological conditions defined by V, C, λ, α and Γ . Specifically, the assessment strategy used at the ESS is determined by the relative assessment cost, γ , defined by (8). Mutual assessment is evolutionarily stable when the effective cost of mutual assessment is low relative to the cost of escalation, and self assessment is evolutionarily stable when the effective cost of mutual

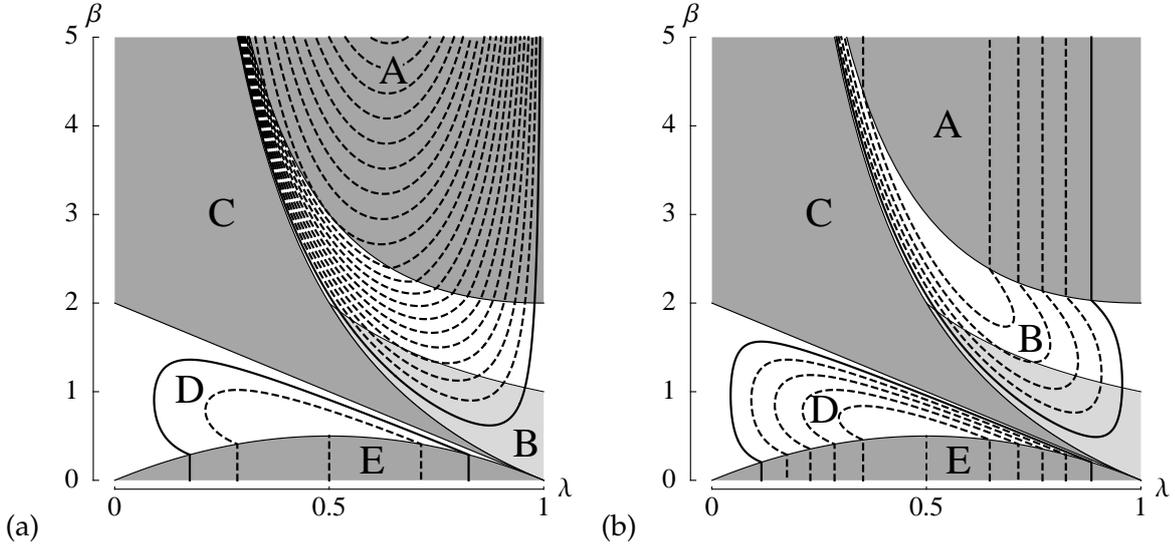


Figure 20: Five regions of the λ - β plane corresponding to five different types of pure self-assessment ESS. The regions are distinguished by their shading. Region K corresponds to a Type-IK ESS, defined below for $K = A, B, C, D, E$ and discussed in detail in [section B.1](#) (as indicated parenthetically)

$$\text{IA: } v_1^* = 0, v_2^* = 1, v_3^* = 1 \quad (\S\text{B.1.1})$$

$$\text{IB: } v_1^* = 0, 0 < v_2^* < 1, v_3^* = 1 \quad (\S\text{B.1.9})$$

$$\text{IC: } v_1^* = 0, v_2^* = 0, v_3^* = 1 \quad (\S\text{B.1.3})$$

$$\text{ID: } v_1^* = 0, v_2^* = 0, 0 < v_3^* < 1 \quad (\S\text{B.1.5})$$

$$\text{IE: } v_1^* = 0, v_2^* = 0, v_3^* = 0 \quad (\S\text{B.1.2})$$

Superimposed are contour maps of the surface $\gamma = \gamma_c(\lambda, \beta, r)$ representing the critical relative cost threshold, for (a) $r = 0$ and (b) $r = 1$. Both arcs of the lowest contour, for height $\gamma = \frac{1}{48}$, are shown solid; all other contours are shown dashed, at equal height increments of $\frac{1}{48}$. For $r = 0$, the diagram shows contours for $\gamma = \frac{1}{48}, \dots, \frac{5}{12}$; for $r = 1$, the upper arc of the $\gamma = \frac{1}{8}$ contour and all higher contours lie above the region covered by the diagram.

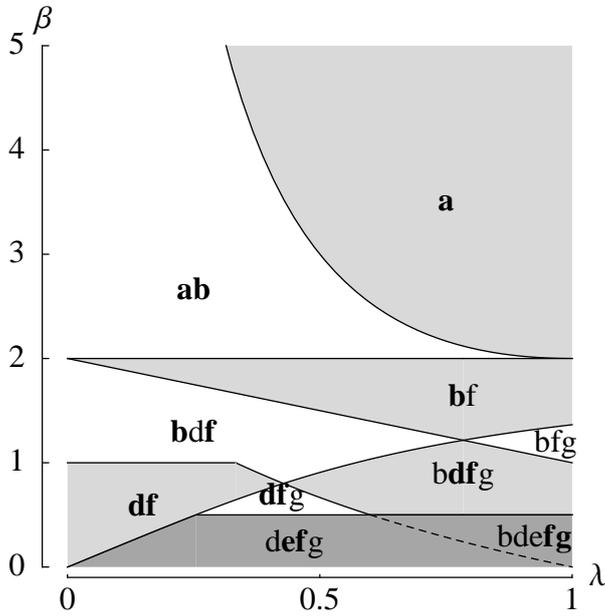


Figure 21: Regions of the λ - β plane corresponding to analytical constraints on the different types of mutual-assessment ESS. The diagram indicates regions from which a Type-IIk ESS, defined below for $k = a, b, d, e, f, g$, has not been excluded analytically, with bold face indicating that the ESS type has been found somewhere in that region (even if only at one extreme). Thus, for example, a Type-IIa ESS may correspond either to the shaded region a or to the unshaded region ab, but only a Type-IIa ESS can correspond to region a; likewise, a Type-IIe ESS can be found only in region e, from which a Type-IIb ESS has been excluded only to the left of the dashed curve

$$\text{IIa: } v_1^* > 0, v_2^* = 1, v_3^* = 1 \quad (\text{\S B.2.1})$$

$$\text{IIb: } v_1^* > 0, 0 < v_2^* < 1, v_3^* = 1 \quad (\text{\S B.2.9})$$

$$\text{IIc: } v_2^* = 0, 0 < v_3^* < 1 \quad (\text{\S B.2.5})$$

$$\text{IId: } v_1^* > 0, v_2^* = 0, v_3^* = 0 \quad (\text{\S B.2.2})$$

$$\text{IIe: } v_1^* > 0, 0 < v_2^* < 1, 0 < v_3^* < 1 \quad (\text{\S B.2.6})$$

$$\text{IIg: } v_1^* > 0, 0 < v_2^* < 1, v_3^* = 0 \quad (\text{\S B.2.8})$$

assessment is relatively high. There is thus a critical threshold that γ must exceed for self assessment at the ESS; otherwise, there is mutual assessment at the ESS. This critical threshold is a function of λ , β and r , which we denote by $\gamma_c(\lambda, \beta, r)$. From [section B.1](#), we obtain

$$\gamma_c(\lambda, \beta, r) = \begin{cases} \frac{1}{2}(1-\lambda)\lambda^2\{(1-r)\beta + 2(1+r)(1-\lambda)\} & \text{if } (\lambda, \beta) \in A \\ \frac{1}{2}(1-\lambda)\{1+r(1-\lambda\beta)\}\{\lambda\beta - 2(1-\lambda)\}/\lambda & \text{if } (\lambda, \beta) \in B \\ 0 & \text{if } (\lambda, \beta) \in C \\ \frac{1}{2}(1+r)\lambda\beta\{1 - \frac{\beta}{2(1-\lambda)}\} & \text{if } (\lambda, \beta) \in D \\ (1+r)\lambda^2(1-\lambda)^2 & \text{if } (\lambda, \beta) \in E \end{cases} \quad (9)$$

where the regions A, B, C, D and E are defined in [section B.1](#); these regions are independent of r , and are distinguished by shading in [Figure 20](#).

The regions A, ..., E correspond to differences in whether the strategic probabilities of withdrawal at the self-assessment ESS (namely, $1 - v_2^*$ and $1 - v_3^*$) are 0, 1 or intermediate, as indicated in [Figure 20](#), where we require both (λ, β) to lie in K and γ to exceed $\gamma_c(\lambda, \beta, r)$ for v^* to be a Type-IK ESS. Because $\gamma_c(\lambda, \beta, r)$ varies continuously (and is nonnegative) over the entirety of the semi-infinite rectangle $0 < \lambda < 1, \beta > 0$ depicted in [Figure 20](#), the equation $\gamma = \gamma_c(\lambda, \beta, r)$ defines a surface. A contour map of this surface has been superimposed on [Figure 20](#) for both $r = 0$ (non-communicative assessment) and $r = 1$. Self assessment is evolutionarily stable whenever γ exceeds the height of the surface.

Thus, the relative resource value β and the frequency λ of weak RHP in the population—through their effect on the critical threshold—ultimately determine whether there is self or mutual assessment at the ESS (as does r , but this dependence is discussed separately below). Generally, mutual assessment must be more cost-effective (i.e., have lower effective cost Γ/α in relation to the costs of escalation C) to occur in region D or E than to occur in region A or B ([Figure 20](#)). Furthermore, as λ approaches 0, regions D and E grow while regions A and B shrink. In contrast, regions D and E shrink and regions A and B grow as λ approaches 1. In this regard, regions D and E characterize a population in which weak individuals never persist and strong individuals sometimes persist. In contrast, regions A and B characterize a population in which strong individuals always persist and weak individuals sometimes persist. In other words, each of the regions in (9) correspond to different strategic probabilities of withdrawal. The contour maps in [Figure 20](#) also indicate that there is a complex relationship between γ_c and β . When $\lambda = \frac{1}{2}$, for example, γ_c is constant for $0 < \beta < \frac{1}{2}$ and $1 < \beta < 2$, but decreases with β for

$\frac{1}{2} < \beta < 1$ and increases with β for $\beta > 2$ (except in the special case $r = 1$). Furthermore, γ_c varies more rapidly when r is low than when r is high. The case $\lambda = \frac{1}{2}$ corresponds to [Figure 22](#) and [Figure 23](#) and is analyzed in detail in [Appendix C](#).

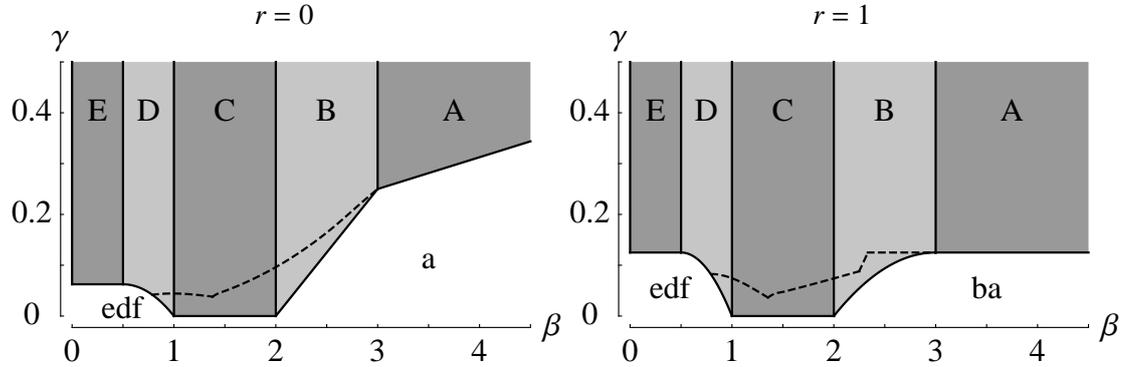


Figure 22: Effect of r on a self-assessment ESS for $\lambda = \frac{1}{2}$. There cannot exist a Type-I ESS in an unshaded region (where $\gamma < \gamma_c$), but there is always a Type-I ESS in a shaded region (where $\gamma > \gamma_c$); in region K, the ESS is Type-IK. In essence, the effect of increasing r from 0 to 1 is to raise the base of region E and to lower the base of region A while maintaining the contiguity of all regions. A Type-II ESS can exist in an unshaded region or below the dashed curve in the shaded regions (corresponding to the shaded regions of [Figure 23](#))

7.3.2 The effect of communication

The potential for mutual assessment to be communicative ($r > 0$) has contrasting effects on the critical relative assessment cost, γ_c ([Figure 20](#)). Specifically, as noted earlier, there are regions in which increasing r increases γ_c , implying that individuals can sustain greater relative costs of mutual assessment when assessment is communicative, compared to when it is non-communicative. Additionally, there are regions in which increasing r decreases γ_c , implying that mutual assessment must be more cost-effective when assessment is communicative than when less communication occurs for it to be adopted. These effects of communication can be appreciated by noticing how the contours shift as r increases from 0 to 1 in [Figure 20](#). In regions D or E and the lower (shaded) portion of region B where $\lambda\beta < 1$, the contours move closer together as r increases, and so $\partial\gamma_c/\partial r > 0$. By contrast, in region A and the upper (unshaded) portion of region B where $\lambda\beta > 1$, the contours move further apart as r increases, and so $\partial\gamma_c/\partial r < 0$. Thus, the greater the extent to which an opponent's effort reduces the uncertainty that an animal's perception is correct, the more that mutual assessment is favored in regions D, E and part

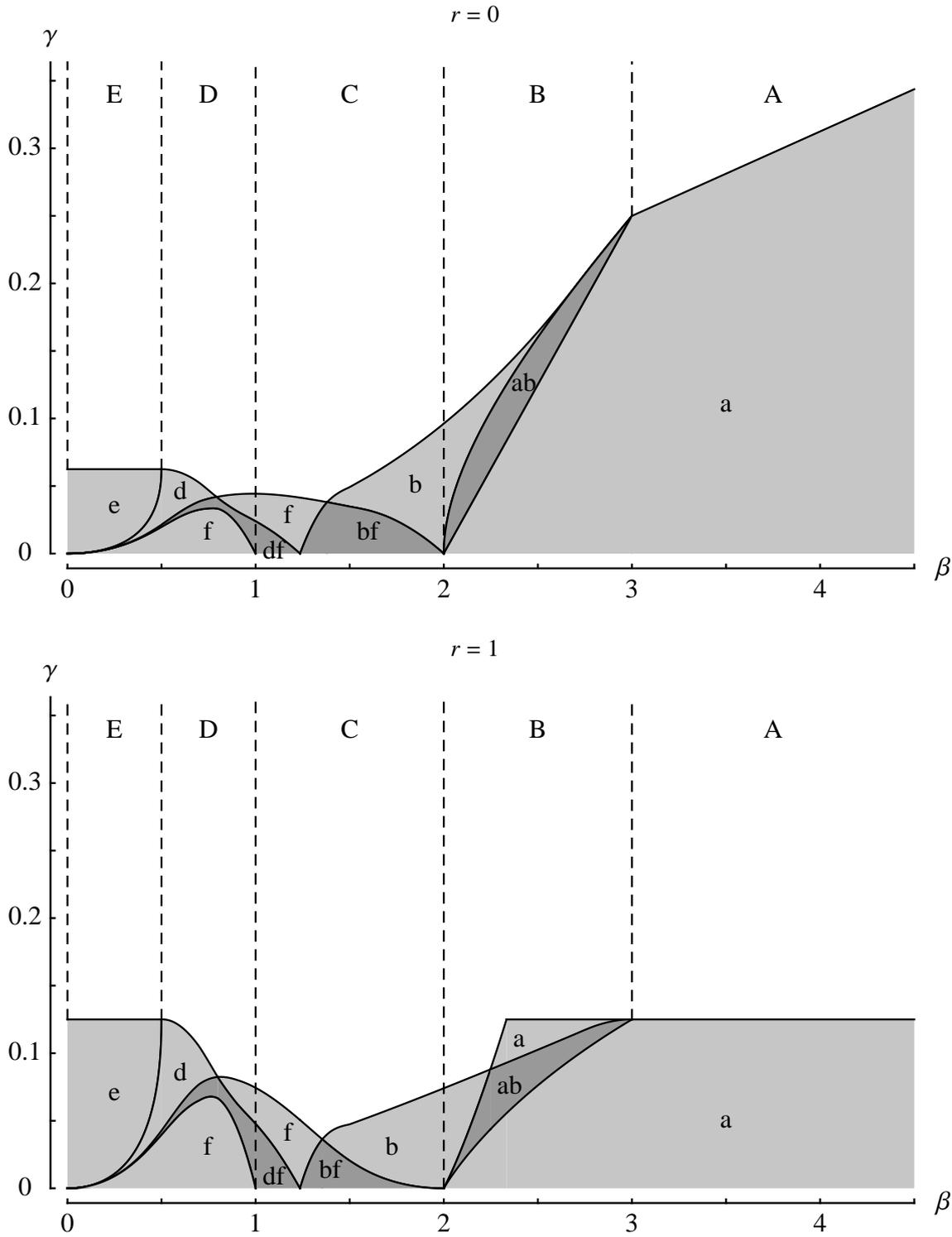


Figure 23: Effect of r on a mutual-assessment ESS for $\lambda = \frac{1}{2}$. There can be a Type-II ESS only in a shaded region; in region k the ESS is Type-II k . Darker shading indicates more than one category of Type-II ESS in that region. For example, at the point $(\beta, \gamma) = (1.4, 0.01)$ for $r = 0$ there is both a Type-II b ESS with $\alpha v_1^* = 0.2257, v_2^* = 0.0603, v_3^* = 1$ and a Type-II f ESS with $\alpha v_1^* = 2.425, v_2^* = 0.685, v_3^* = 0.7196$

of region B (it being easier for γ to be lower than a higher critical threshold), and the more that self assessment is favored in region A and most of region B (it being easier for γ to be higher than a lower critical threshold).

The effect of communicative assessment on investment towards mutual assessment depends on RHP, owing to a difference in the pay-offs of opponents making strategic errors between strong and weak individuals. Specifically, strong individuals benefit when opponents make fewer strategic errors and weak individual benefit when their opponents make more strategic errors (Appendix A, Table 20). The relative benefits of opponent error to weak individuals versus the costs to strong individuals then determine whether increasing r has a positive or a negative effect on γ_c . When the benefits of opponent error to weak individuals are greater, such as when the RHP distribution is skewed towards weak individuals (e.g. $\lambda > 0.5$) and these individuals benefit from persistence against matched opponents (e.g. $v_2^* = 1$), then r will have a negative effect on γ_c (Figure 20). In such cases, individuals can benefit more from hiding information on their own RHP and only investing towards mutual assessment when it is very cost-effective in relation to the costs of escalation. On the other hand, r will have a positive effect on γ_c when the costs of opponent error to strong individuals are greater, such as when escalation is relatively costly compared to resource value (e.g $\beta < 2$). This is equivalent to individuals sharing the costs of mutual assessment through communication, allowing them to invest in mutual assessment even when it is relatively costly in comparison to the cost of escalation.

7.3.3 *Strategic error is necessary for assessment strategy to vary*

Notably, there is a region in which $\gamma_c = 0$ (Figure 20; region C), implying that here self assessment is an ESS regardless of relative cost. In this region, the ESS has the form $v^* = (0,0,1)$; and it is shown in subsection B.2.3 that there cannot be an ESS of the form $v^* = (v_1^*,0,1)$ with $v_1^* > 0$. Thus investment towards mutual assessment provides no benefits, since the optimal withdrawal strategy has no risk of strategic error. The risk of strategic error is absent because the population has adopted a pure withdrawal strategy that depends on RHP, such that weak individuals always withdraw and strong individuals always persist; weak individuals will never escalate contests that cannot be won, and strong individuals will never withdraw when victory is guaranteed. Put simply, it is impossible for mutual assessment to exist as an ESS when using a withdrawal strategy that contains no element of strategic error. However, withdrawal strategies that incorporate strategic error allow for the existence of a mutual as-

assessment ESS. Therefore, strategic error is necessary for there to be variation in assessment strategy.

Table 18: Evolutionarily stable strategies v^* with self ($v_1^* = 0$) or mutual ($v_1^* > 0$) assessment can be classified according to the strategic withdrawal components of the ESS, v_2^* and v_3^* (probabilities of persisting when perceiving WW and SS , respectively). Note that STRONG or WEAK refers to type of ESS, as opposed to RHP type: Mutant strategies are always selected against at a strong ESS, whereas mutant strategies can spread initially before being selected against at a weak ESS. Here \bullet denotes a positive number less than 1

CASE	v_2^*	v_3^*	SELF ASSESSMENT		MUTUAL ASSESSMENT	
a	1	1	IA	STRONG	IIa	STRONG
b	\bullet	1	IB	WEAK	IIb	WEAK
c	0	1	IC	STRONG		NO SUCH ESS
d	0	\bullet	ID	WEAK	IIc	WEAK
e	0	0	IE	STRONG	IId	STRONG
f	\bullet	\bullet	NO SUCH ESS		IIe	WEAK
g	\bullet	0	NO SUCH ESS		IIg	WEAK

7.3.4 Variation in withdrawal strategy and alternative ESS conditions

Analysis of the model also indicates that variation in withdrawal strategy (Table 18) is associated with variation in assessment strategy. Firstly, some withdrawal strategies are dependent on a particular mode of assessment. In particular, unconditional withdrawal or persistence based on perceiving one's opponent to have the same RHP can be evolutionarily stable only under self assessment (Table 18, Case c). Similarly, at the ESS, the probability of persistence in contests perceived as matched can be greater for weak contestants (Table 18, case g) or mixed with withdrawal for both RHP categories (Table 18, case f) only under mutual assessment. Secondly, the mode of assessment determines limits (in terms of β , λ and γ) for a given withdrawal strategy to be part of the ESS. For example, when $\lambda = \frac{1}{2}$, unconditional Hawk (Table 18, Case a) requires $\beta > 3$ with self assessment (Figure 22), but is possible as long as $\beta > 2$ with mutual assessment (Figure 23). There are also regions in which either self or mutual assessment can be evolutionarily stable for the same values for β , λ and γ , which is due to the adoption of alternative withdrawal strategies (Figure 23). For instance, even when $\gamma_c = 0$, mutual assessment can be evolutionarily stable if either weak individuals are more aggressive or strong individuals are less aggressive than under self assessment (Table 18, Cases b, d, f compared to c).

7.4 DISCUSSION

There are two pertinent and simultaneous trade-offs relating to the assessment of opponents during contests. Firstly, all individuals must decide between reducing the risks of strategic error by investing in mutual assessment, or increasing the capacity to persist in contests over resources. Secondly, weaker individuals in a population must decide whether to acquire information about their opponents at the cost of revealing their own inferiority. Theoretically, the selection pressure underlying these trade-offs is the use of withdrawal strategies that, due to incomplete information, carry an inherent risk of responding inappropriately to an opponent but can otherwise increase access to limited resources.

This model also demonstrates that a difference in payoffs between weak and strong individuals can significantly affect the benefits of mutual assessment. Firstly, the group that benefits from gathering information can vary. When contests are costly in relation to the benefits of winning, weak individuals avoid fighting altogether, but strong individuals benefit from some aggression. Thus, mutual assessment is not beneficial to weak individuals, but it can allow strong individuals to avoid costly escalation against matched opponents. In contrast, when contests are relatively inexpensive, all individuals benefit by being aggressive, at least to some extent. However, weak individuals benefit by avoiding contests that they cannot win, and hence benefit from mutual assessment. Strong individuals, on the other hand, can potentially win any fight and gathering information is not beneficial since they are willing to escalate unconditionally. Secondly, the difference between weak and strong fighters can establish a conflict over the quality of information that is transferred when assessment is communicative, which is discussed in detail below. Thirdly, the need for mutual assessment can be avoided if individuals adopt a pure withdrawal strategy according to their RHP, which could imply that conventional solutions to contests can sufficiently reduce the costs associated with both mutual assessment and escalation. However, the use of such a strategy is restricted to particular ecological conditions.

7.4.1 *Variation between self and mutual assessment*

In order for an individual to maximise the resources it can gain from contests, it may need to adopt a withdrawal strategy that inherently carries the risk of making a strategic error. This risk can be reduced by adopting a mutual assessment strategy, but doing so reduces the individual's capacity to bear the costs associated with escalation. That is, although escalation is costly, animals may need to fight to access resources, and effort spent assessing opponents can reduce their abil-

ity to persist in a fight. Thus individuals must compromise between reducing the risk of strategic error and maintaining the ability to engage in escalated interactions. It is the relative costs of these alternatives that determine whether there is self or mutual assessment at the ESS. In other words, the forgone ability to afford involvement in escalated contests is the opportunity cost of mutual assessment. For example, jumping spiders (*Phidippus clarus*) attempting to usurp a territory appear to first assess the RHP of the resident and then switch to a self-assessment based war of attrition if they assess themselves to have the RHP advantage (Kasumovic et al., 2010). This behavior implies that the intruder has reduced its investment towards obtaining specific information in favor of being able to persist in the war of attrition for longer. Our results thus contrast with the hypothesis that variation in assessment strategy is based purely on the trade-off between the costs and benefits of mutual assessment (Taylor and Elwood, 2003; Prenter et al., 2006; Elias et al., 2008; Arnott and Elwood, 2009a). Specifically, although the costs and benefits of mutual assessment are important, it may be the comparison of this ratio to the costs of escalation that determines the stable assessment strategy, rather than the ratio on its own.

Our model predicts that assessment strategy will vary according to the value of contested resources, the costs of escalation, and the cost-effectiveness of assessment. A comparison of assessment strategies used among fig wasp species suggests that assessment strategy varies with the value of resources in a fashion consistent with the predictions of our model (Pereira and Prado, 2005; Moore et al., 2008). In particular, male fig wasps often use self assessment in fights over access to females in species for which females are extremely limited (Enquist and Leimar, 1987; Murray, 1987; Colegrave, 1994). In contrast, mutual assessment appears to be used in species for which a given mating opportunity is less valuable, although the structure of the fig is also likely to be important (Pereira and Prado, 2005; Moore et al., 2008). A shift from self to mutual assessment with decreasing resource value is expected under our model when contests are excessively costly, which conforms to fig wasp contests that carry the risk of serious injury and fatalities. Our model also predicts that assessment strategy can shift from mutual to self assessment with an increase in escalation costs when relative resource value is high and individuals are typically aggressive against matched opponents. This prediction is supported by observations of switching assessment strategies from mutual to self assessment as the contest escalates from pure display to, presumably more costly, physical interactions (Morrell et al., 2005; Elias et al., 2008; Hsu et al., 2008; Kasumovic et al., 2010). Finally, (Elias et al., 2008) showed that mutual assessment appeared to increase in contests between jumping spiders (*P. clarus*) that

had previous experience with one another when compared to the first contest between the same individuals. This result is consistent with our model if experience improves the efficacy, and hence the cost-effectiveness, of mutual assessment.

7.4.2 *The effect of communicative assessment*

The degree to which mutual assessment behavior provides opponents with information may have an important influence on the opportunity costs faced by an individual. Specifically, our model predicts that the transfer of specific information as a result of making an assessment (i.e. communicative assessment) can either increase or decrease the critical threshold that determines assessment strategy (Figures 20, 22, 23). The root of this differential effect comes from our assumptions regarding variation in the RHP of the population and the payoffs of interactions. Specifically, weak individuals receive greater expected payoffs if their opponents make a strategic error, while strong individuals benefit more if their opponents make correct decisions. This assumption is supported by observations of contests in convict cichlids (*Amatitlania nigrofasciata*): opponents that assess an individual to be weak are more likely to escalate than opponents that assess an individual to be strong (Leiser et al., 2004). Thus, weak individuals may suffer, and strong individuals benefit, from sharing information on their RHP with their opponent. Consequently, weaker individuals benefit from hiding information on their own RHP and may thus avoid communicative mutual assessment. On the other hand, stronger individuals benefit from sharing information on their own RHP, and thus communicative assessment discounts their investment towards mutual assessment. In other words, if assessment is communicative, weak individuals face a trade-off between gaining information on opponents and providing opponents with information, while strong individuals do not. This information conflict can then influence the functional significance of self and mutual assessment strategies, assuming that assessment strategy is independent of RHP.

Communication of RHP between contesting individuals has traditionally been considered as a cooperative behavior that allows contestants to resolve a conflict without resorting to excessively costly outcomes (Clutton-Brock and Albon, 1979; Crespi, 1986; Rubenstein and Hack, 1992; Keeley and Grant, 1993; Hurd, 1997). For instance, the sequential assessment model predicts that contestants should fully cooperate on sharing information on RHP asymmetries during contests and that information transfer is independent of RHP (Enquist and Leimar, 1983; Enquist et al., 1990). However, our results suggest that, while individuals may share a common interest in avoiding costly outcomes, there can be conflicts of interest over the quality of infor-

mation being transferred that depend on RHP and the evolution of cooperative mutual assessment will be limited by this conflict. Specifically, weak individuals will attempt to limit information transfer (e.g., by performing fewer, or less informative, communicative behaviors), and attempts by weak individuals to hide information will increase with the value of the contested resource and decrease with the costs of persistence. For example, (Enquist et al., 1990) observed contests in the cichlid *Nannacara anomala* and found that, although both contestants signalled their RHP to their opponent, the smaller contestant of a pair was less willing to perform signals that gave accurate information than the larger contestant. Alternatively, weak individuals may rapidly escalate in order to prevent their opponents from making an accurate assessment of the RHP asymmetry and force them into making a premature withdrawal decision (Just et al., 2007; Svensson et al., 2012). The information conflict hypothesis also predicts that the performance of communicative assessment behaviours will be associated with the absolute RHP of a given individual, rather than the relative RHP of the contestants. Additionally, contests that rely on communicative assessment (e.g., sequential assessment) may be less likely in populations where the RHP distribution is skewed towards weaker individuals.

7.4.3 *Mutual assessment and withdrawal strategies*

From a theoretical standpoint, there are some notable differences between the results of our model and Crowley (2000) that could indicate the influence of obtaining specific information on withdrawal strategies. Specifically, Crowley (2000) shows that the ESS withdrawal strategy is an RHP-dependent pure strategy if individuals have access to only general information, there are only two RHP categories that are equally prevalent in the population, and strong individuals always defeat weak individuals. That is, strong individuals always play Hawk, and weak individuals always play Dove. However, we find that mixed strategies, in which individuals play a mixture of Hawk and Dove, can exist under the same conditions, although this outcome depends on relative resource value. Thus, the option to invest in obtaining specific information may result in the adoption of a mixed ESS for withdrawal strategies even if specific information is not used. Alternatively, this difference may be due to Crowley's (2000) inclusion of an escalation cost asymmetry between winners and losers, or the costs of sharing when both individuals play Dove (although he found the latter to have little effect). The implications of our result is that the potential to invest in obtaining specific information (even if it is not obtained) can disrupt the use of a strategy in which individuals fight if they are above an RHP threshold and withdraw if they are

below, in favor of a strategy in which withdrawal decisions are made on the basis of probability.

7.4.4 *Conclusions and future developments*

The model presented in this paper can be expanded to investigate the influence of other important factors on the evolution of assessment strategies and to test the robustness of its findings. For instance, it will be necessary to explore the implications of continuous variation in RHP among the population and variation in the degree to which RHP determines contest outcome (Crowley, 2000; McNamara and Houston, 2005). Furthermore, both theory and observations show that the costs of contests can vary depending on the assessment strategy being used, the outcome of the contest, and the RHP of the contestants (e.g. the cost of a contest is expected to increase as RHP asymmetry decreases for mutual assessment; losers may pay greater escalation costs; high RHP individuals may inflict, and be able to receive, more costs; (Enquist et al., 1990; Crowley, 2000; Leiser et al., 2004; Hsu et al., 2008)). Similarly, the costs of assessment are likely to vary with RHP asymmetry, with assessment being less costly the greater the RHP asymmetry (Enquist and Leimar, 1983; Enquist et al., 1990), and possibly varying with the absolute RHP of a contestant (Leiser et al., 2004). Thus, the implications of alternative RHP conditions and cost structures must be explored to account for a more accurate representation of nature and to improve our understanding of assessment strategies.

In this paper, we proposed that variation in assessment strategy is the result of a balance between investment towards mutual assessment and the capacity to escalate, but there may be other important limitations on mutual assessment (Whitehouse, 1997; Taylor et al., 2001; Taylor and Elwood, 2003; Prenter et al., 2006; Elias et al., 2008; Arnott and Elwood, 2009a). For instance, there may be constraints to information processing—from cognitive abilities, available information and sensory acuity—that limit mutual assessment in some species (Taylor and Elwood, 2003; Prenter et al., 2006; Elias et al., 2008; Arnott and Elwood, 2009a). Alternatively, investment towards mutual assessment may reduce an individual's RHP, or individuals may have to initially gather experience in contests before being able to make an accurate assessment (Arnott and Elwood, 2009a). There is even the potential for no role assessment (neither self nor mutual) to occur in contests, such as if individuals fight indiscriminately (Colegrave, 1994; Cook and Bean, 2006; Moore et al., 2008) or are able to adjust their withdrawal strategy to experience (Whitehouse, 1997). Furthermore, most contest models, including this one, assume that individuals compare information on their own RHP to public information

on opponent RHP. However, some animals appear to compete in a way that suggests private information is ignored and withdrawal decisions are made entirely on the basis of specific information without the comparative process of mutual assessment (Wise and Jaeger, 1998; Rillich et al., 2007; Prenter et al., 2008; Arnott and Elwood, 2009a). Thus, future theoretical developments may need to consider the use of general and specific information independently of a comparison with private information. Overall, it is clear that we must consider a wide range of processes that extend beyond the scope and capabilities of this model in order to understand assessment strategies.

Despite the broad scope concerning assessment strategies, our model supports an important role of strategic error at the heart of contest behaviour through its influence on withdrawal strategies (Parker and Rubenstein, 1981), aggressiveness (Just et al., 2007) and opponent assessment (Enquist and Leimar, 1983; Just et al., 2007, ; this study). Furthermore, asymmetries in the payoffs of sharing information between contestants may lead to conflicts over sharing information, which could have important implications for any model that considers the use of public information. Together, these factors may serve as central components of future models that attempt to provide a general explanation of variation in assessment strategies.

Part IV

SYNTHESIS

SYNTHESIS

8.1 SPATIO-TEMPORAL SCALING RELATIONSHIPS

Animals face varying levels of uncertainty when making decisions. The level of uncertainty that an animal must deal with stems from heterogeneity in its spatial environment, and variation in environmental conditions over time (Schmidt et al., 2010). However, spatial heterogeneity and temporal variability can be correlated with one another, such that the degree of uncertainty present in a given situation (due to temporal variation) can be dependent on the spatial scale at which the information is gathered (Wiens, 1989; Costanza and Maxwell, 1994). In particular, at small spatial scales the environment may be predictable over short time-scales, and at large spatial scales the environment may be predictable over long time-scales (Figure 24). In other words, the smaller the area being considered, the less likely its current state can be predicted on the basis of older information, and the more relevant recent information becomes. In contrast, as the spatial extent being considered increases, the more relevant older information becomes and the less relevant recent information becomes. With regards to sampling, a relationship between spatial and temporal scales would imply that the value of prior information (in terms of its potential to predict current conditions) would be dependent upon the spatial scale at which an individual is making a decision. Thus, decreases in the value of prior information at smaller spatial scales will result in there being greater benefits for updating information through sampling.

Part I dealt with the case of breeding site selection in the terrestrial toadlet, *P. bibronii*. Breeding site selection is an excellent system in which to explore the relationship between spatio-temporal scale and sampling, as decisions are made over multiple spatial scales and behavioural responses to uncertainty are somewhat understood (Switzer, 1993; Schmidt et al., 2010; Piper, 2011). Accordingly, we found that the information used to select breeding sites by male *P. bibronii* was dependent on spatial scale (chapter 2). Translocating males to an alternative suitable breeding patch resulted in the males returning to their patch of origin, demonstrating a high degree of site-fidelity at the patch scale. However, within patches, site-fidelity was rare and males chose their nest-sites partly according to the current social conditions (chapter 3). Male *P. bibronii* thus show a tendency

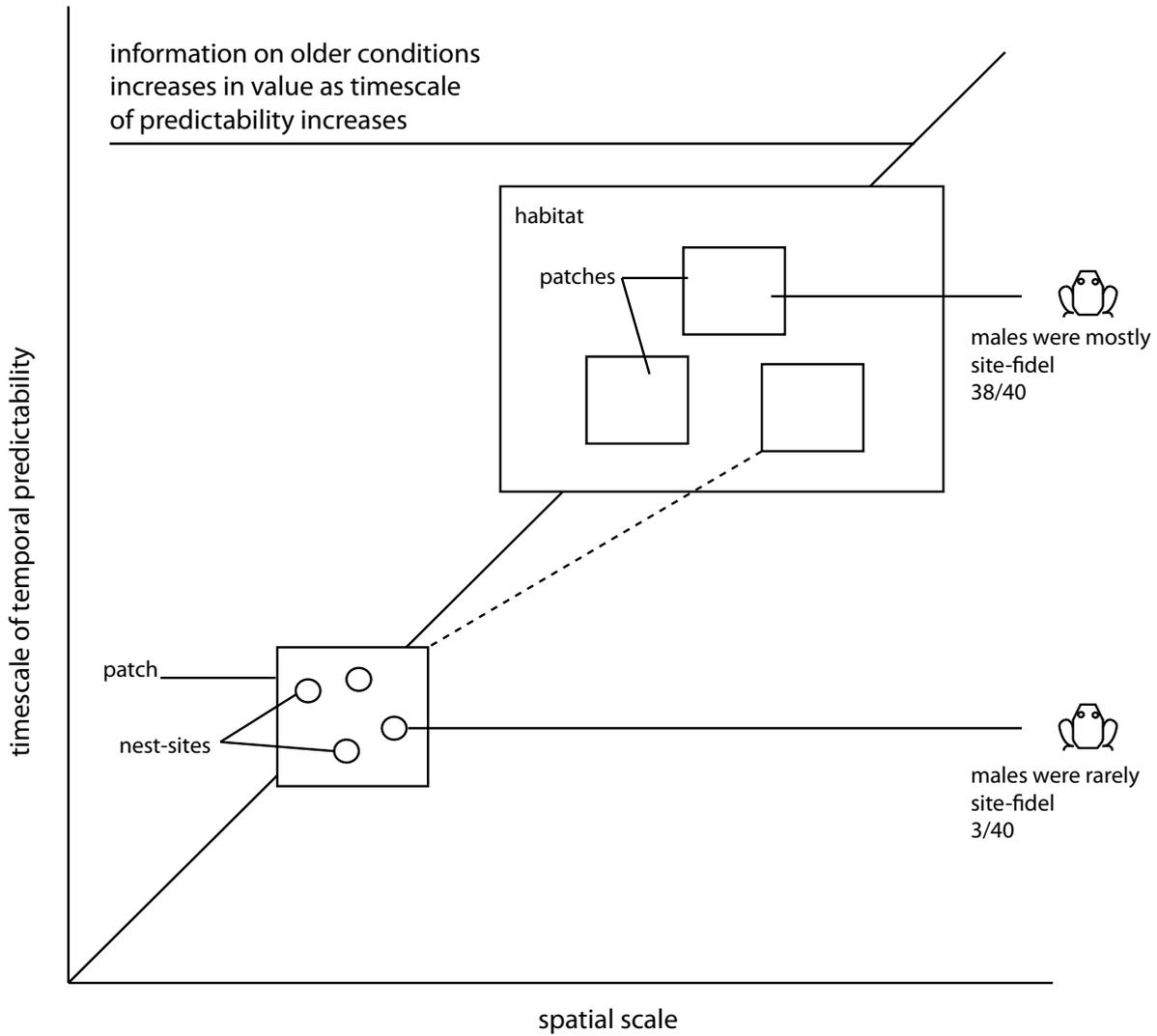


Figure 24: The value of choosing a nest-site based on sampled information is scale dependent in *Pseudophryne bibronii*, as determined from changes in the expression of site-fidelity ([chapter 2](#))

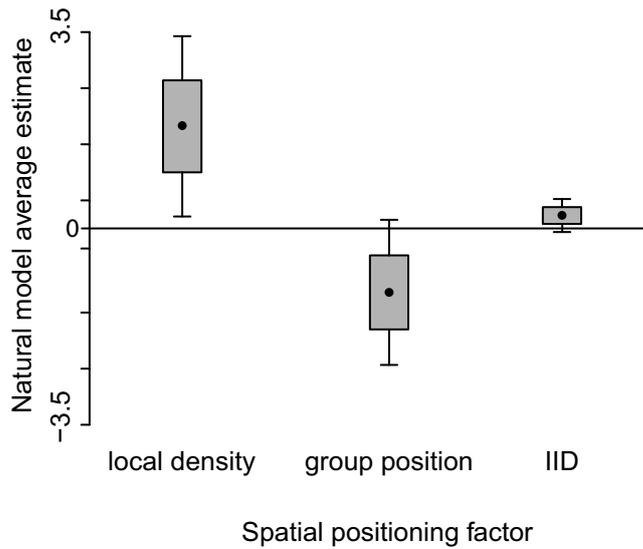


Figure 25: Natural model average estimates for the effect of spatial positioning cues on the likelihood of abandoning a nest-site in *Pseudophryne bibronii* (chapter 3). Dots give the location of the estimate for each factor, boxes provide the location of the standard error and whiskers give the upper and lower 95% confidence intervals. Local density had a significant effect on nest-site choice, whilst group position and IID may have a tendency to affect nest-site choice. These results suggest that male *P. bibronii* sample some aspects of their social environment in order to improve their fitness with regards to nest-site choice –however, we were unable to determine what the benefits of responding to this information were

to vary their investment towards sampling at different spatial scales when choosing a breeding site.

The variation in the use of sampled information at different spatial scales in *P. bibronii* supports the predicted relationship between spatial scale and environmental predictability. Specifically, male *P. bibronii* may benefit by being site-fidel to relatively predictable habitat patches, and update previously held information when choosing a nest-site within the patch (Figure 24). Males may be site-fidel at the patch scale because previously gathered information allows a suitable patch to be chosen whilst avoiding the costs of sampling (chapter 2). According to the expected relationship between spatio-temporal scale and environmental uncertainty, this information will only be relevant for predicting the quality of a particularly sized area, since the environmental patterns that influence reproductive success at smaller spatial scales may be occurring at smaller time-scales. Correspondingly, males appeared to relax their use of site-fidelity when choosing a nest-site within a patch. Instead, males gathered information about the local spatial arrangement of their competitors and chose nest-sites partly according to this information (chapter 3; Figure 25). The decrease in the use of site-fidelity at smaller spatial scales conforms with models that consistently predict that the benefits of site-fidelity decrease as the environment becomes less predictable (e.g. Switzer, 1993). In summary, I conclude that if the quality of patches varies predictably over breeding seasons and the quality of nest-sites within the patch do not, then male *P. bibronii* may benefit by responding to prior information when choosing a habitat patch and updating information when choosing a nest-site within the patch (Figure 24). The existence of a relationship between spatio-temporal scale and environmental uncertainty could have significant consequences for decisions that are made over multiple spatial and temporal scales, such as foraging, habitat selection and predator avoidance because individuals will have to use information differently as the spatial scale of their decisions changes.

There is an alternative to this explanation, however. Males may have actually gathered information about novel patches and decided that they were unsuitable breeding sites. It is unlikely that they made this decision on non-social factors, such as soil quality for example, since novel sites were being utilised by other males prior to the experiment and in previous years. Instead, males may use other males as a cue for breeding site quality and, since they were deposited in empty patches, assessed the site to be poor quality. However, males still returned to their original patch, despite also being empty. Additionally, control males did not choose to settle in another patch, despite being returned to the study site after re-settlement had begun in other patches. Thus, if males are using the presence of other males as a cue

for site quality, the value of this information may be lower than the value of previous breeding experience.

Identifying and understanding patterns and processes of information use that relate to spatial and temporal scale is a critical component for developing a theory for the ecology of information use (Schmidt et al., 2010). As such, we require additional studies that test whether individuals adjust the information that they sample according to a positive relationship between spatial scale and the time-scale of temporal predictability. Because of the expected generality of such a process, such studies should not only focus on sampling the social environment, but all aspects of information gathering and processing. These studies should not be taken lightly, as adaptive information use is critically determined by the evolutionary value of information gathered at different points in time (Stephens, 1989, 1991; Mangel, 1990). For instance, the value of information depends on the rate at which the information degrades (which according to this relationship, is dependent on spatial scale) and the rate at which individuals forget previously gathered information (Dall and Cuthill, 1997). Forgetting is thought to be an adaptive quality, as it can reduce the accumulation of sampling errors (e.g. Luttbeg and Warner, 1999). Thus, the functional significance of forgetting may also depend on spatial scale. However, our current understanding of how landscape processes influence information use is lacking, and identification of general processes would make a substantial development toward a consistent framework.

8.2 THE INTERACTIVE EFFECT OF LANDMARKS ON SAMPLING THE SOCIAL ENVIRONMENT

Despite commonly being nothing more than an inanimate feature of the landscape, the presence of a landmark can ultimately determine whether individuals benefit from sampling their social environment. Interestingly, the literature review (chapter 4) indicates that landmarks can influence the payoffs associated with sampling in a variety of ways, depending on the process that results in its adoption for a territorial boundary (Figure 26).

Firstly, landmarks can impose costs on sampling the world beyond territorial boundaries when they have a constraining effect (Figure 26 a, b). Secondly, landmarks can improve the efficiency of sampling when individuals are uncertain about the social consequences of using different areas (Stamps and Krishnan, 1999; Sih and Mateo, 2001). In such cases, the clear boundaries hypothesis (Figure 26 c, d) posits that landmarks facilitate spatial associations made between social interactions and the landscape, thereby improving the efficiency of sampling information on the consequences of using a particular space

(Eason et al., 1999; Gosling and Roberts, 2001; St. Louis et al., 2004; Smith, 2011).

The experiment on landmark effects in cichlids did not allow me to determine whether individuals could make a learned association between landmarks and agonistic interactions, as assumed by the clear boundaries hypothesis. This was because there were no consistent and significant differences in space use between fish that were exposed to a resident and those that had a solitary exposure (chapter 5). Generally, these results suggest that convict cichlids are unable to form a reliable spatial association between a landmark and agonistic interactions in a short time-frame. However, the results may also suggest that variation in the cues used to form spatial associations can affect the reliability of spatial associations, especially when cues come into conflict with what an individual has already learned. If this is the case, then it would imply that the uncertainty inherent in spatial associations, even those made on the basis of landmarks, can affect an individual's assessment of the social environment. For instance, if an individual associates a landmark with a dangerous conspecific, and the landmark moves, then the animal's information on the conspecific will be disrupted. The consequences of such a disruption could take a variety of forms, including increased investment towards sampling in order to update the reliability of assessment, or inefficient use of space in response to an inaccurate assessment. In any case, the results of this study indicate that the use of landmarks for clear boundaries may be more complex than a case of classical spatial conditioning between a landmark and boundary fights. Instead, the use of landmarks for clear boundaries may be dependent on the use of multiple spatial cues, the ecology and personal history of individuals, and, importantly, the accurate assessment of the likelihood and consequences of territorial encounters.

Finally, according to the landmarks-as-convention hypothesis (Mesterton-Gibbons and Adams, 2003), landmarks can remove the need for individuals to sample their opponents by providing a conventional solution to an uncertainty problem. Assuming that competing neighbours must establish a boundary between their respective territories and that reducing uncertainty about an opponent's competitive ability is sufficiently costly, then landmarks may provide a cost-effective solution that removes the need for residents to sample information on their territorial neighbours (Figure 26 e, f).

In any case, it is clear that the presence of landmarks can have a significant influence on how individuals use information present in their social environment, and that variation in the use of this information can have significant consequences for an individual and for territorial populations (chapter 4). Thus, further development of a theory for the ecology of information use would require a serious considera-

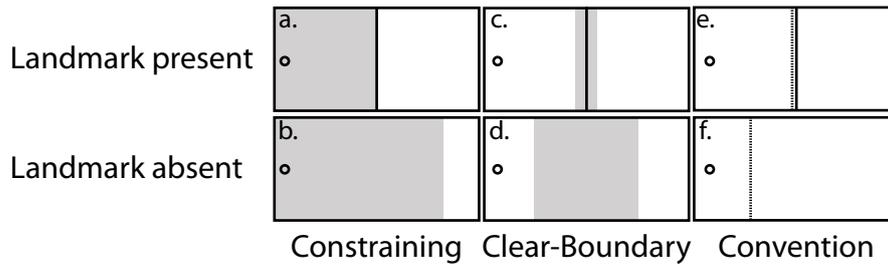


Figure 26: The effect of a landmark (solid vertical line) on an individual's (circle) sampling behaviour depends on the mechanism by which the landmark is adopted for a boundary (chapter 4). When the landmark is constraining, it can limit the area in which an individual is able to effectively sample from, represented by the shaded region in a and b. A clear-boundary landmark improves the accuracy of estimating the location of the boundary (represented by the shaded regions in c and d) by providing a spatial marker for sampling social interactions. A conventional landmark allows the boundary location (dotted lines in e and f) to be established without the costs that are incurred when the landmark is absent; specifically the energetic investment towards sampling and the risk of having a small territory, as in f

tion of how landmarks interact with social behaviour, as interactions between the landscape, individual decision making and population level patterns are an integral component of this theory. However, the review presented in chapter 4 has made it clear that a functional understanding of the adoption of landmarked boundaries is far from complete, and, furthermore, that the population level consequences of this behaviour are not well understood at all.

8.3 VARIATION IN INFORMATION VALUE AND ITS CONSEQUENCES

The value of information can vary for different individuals within a population, and this may have important consequences when individuals are attempting to obtain information from one another (Jablonka, 2002; Bonnie and Earley, 2007; Seppanen et al., 2007; Valone, 2007). Additionally, an individual's actions, including the decision to sample or provide information, can depend on the actions taken by other members of the population (Maynard Smith, 1974). Consequently, the value of information to a given individual can depend on how its conspecifics are utilising information. Thus the evolution of behaviours that involve sampling the social environment can be strongly tied to conflicts over information transfer within a population.

This concept is readily apparent in chapter 7, in which the introduction of an asymmetry in fighting ability (and hence the expected payoffs associated with interaction) leads to processes that skew the value of information within a population (Figure 27). For

instance, weak individuals can benefit from sampling to avoid fights with strong individuals that escalate unconditionally, whilst strong individuals receive no benefits from sampling (the lightly shaded region in [Figure 27](#)). Furthermore, the model demonstrates that variation in other environmental factors can result in the skew of information value changing from benefitting one class of individuals to another. For example, when contests are costly in relation to the benefits of winning, strong individuals benefit from sampling their opponents but weak individuals do not (the dark shaded region in [Figure 27](#)). Thus, the relative value of contested resources and the cost of fighting can affect whether weak or strong individuals in the population can benefit from sampling. The outcome of these processes is variability in the benefits of sampling, such that sampling can be selected for in some individuals, but selected against (or not at all) in other individuals. The model also demonstrated that, because of this variation in the value of information, linking sampling with information transfer can lead to conflicts over the quality of information that is being transferred, and hence the value of sampling. In our model, this conflict was manifested as a sampling trade-off that was present in weak, but not strong individuals. Analysis indicated that this conflict can have substantial effects on the evolution of sampling within a population (arrows in [Figure 27](#)).

8.4 THE VALUE OF CONVENTIONS

Whilst variation in traits that influence the outcome of interactions between individuals can lead to variation in the benefits of sampling, as discussed above, it can also result in the adoption of behaviours that remove the selective pressure to sample. In particular, it can be beneficial for individuals to adopt a strategic convention in certain circumstances, which allow the costs associated with sampling to be avoided.

The value of conventions is theoretically supported by [chapter 4](#) and [chapter 7](#) of this thesis. Firstly, the landmarks-as-convention hypothesis demonstrates that arbitrary conventions can remove the need for individuals to sample their territorial neighbours ([chapter 4](#)). Additionally, the model presented in [chapter 7](#) shows that the need to sample opponents during contests can be completely avoided when strong individuals are always willing to escalate and weak individuals never fight (unshaded region in [Figure 27](#)). However, the stability of these conventions requires the costs of disregarding the convention to be sufficiently high in comparison to its benefits. In both cases however, it is clear that the selection pressure for sampling can be reduced through a convention. Thus, social conventions may be an important

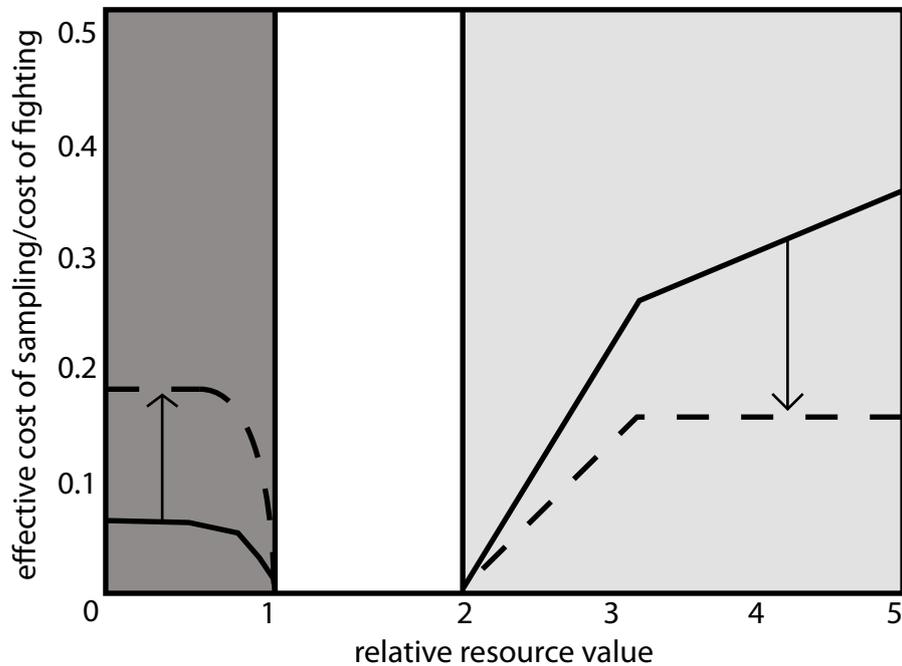


Figure 27: Whether sampling is adaptive in contests (mutual assessment) or not (self assessment), depends on the effective cost of sampling in relation to the cost of fighting (relative costs) and the value of the contested resource in relation to the cost of fighting (relative resource value). The solid black lines in this figure represent the critical relative costs threshold, above which self assessment is an ESS, otherwise mutual assessment (sampling) is the ESS (chapter 7). This figure represents the case for a population comprised of weak and strong fighters, that are equally distributed (i.e. 50% chance that a given opponent could be either). In the dark shaded region, strong fighters benefit from sampling, whilst weak fighters benefit from sampling in the lightly shaded region. Social conventions are possible in the region where no shading, or critical relative costs threshold, is present. Arrows show the change in relative costs threshold to the dashed lines when sampling also provides opponents with information. Note that the threshold increases in the dark shaded region, and decreases in the lightly shaded region

adaptation that allows individuals to behave efficiently without having to sample the social environment.

In terms of developing the theory information use, the value of conventions represents an under-appreciated escape from the selective pressure to sample for new information. Furthermore, the evolution of conventions demonstrates the importance of how interactions within the social environment can affect the manner in which information is used. Thus, further developments of the theory may need to consider if there are evolutionary alternatives to sampling that can result from social interactions; this effectively implies that models of information use may need to be based on game-theoretic (Maynard Smith, 1974) and/or self-consistent principles (e.g. Kokko et al., 2006; Kokko and Lopez-Sepulcre, 2007) in order to properly consider the evolutionary outcomes of information problems present in nature.

8.5 BEHAVIOURAL FLEXIBILITY AND SAMPLING THE SOCIAL ENVIRONMENT

Uncertainty in the environment drives selection for the use of strategies that allow an individual to adjust to a broader range of environmental conditions (behavioural flexibility). In particular, selection for behavioural flexibility increases with the increasing likelihood of alternative environmental conditions and the costs of a sub-optimal response to these alternatives (Gould, 1974; Stephens, 1989; Dall and Cuthill, 1997; Luttbeg and Warner, 1999). Furthermore, the more generalised an individual becomes (i.e. as the flexibility of an individual increases), the greater the value of information that corresponds with alternative environmental conditions (Stephens, 1989; Mangel, 1990) and thus, the greater the benefits of sampling information relating to these conditions (Dall et al., 2005). This is because individuals that are tracking variation in a wider range of environmental conditions are better able to optimise their behaviour when conditions change.

Our results conform to these predictions. In particular, toadlets appeared to gather information about a persistent intruder in order to benefit from calling behaviour that is adjusted to the perceived threat of the intruder (chapter 6; Figure 28). Theory suggests that such behaviour is adaptive when the consequences of interacting with an intruder are highly variable but can be predicted based on the intruder's behaviour (Temeles, 1994). That is, individuals can benefit from responding to threatening and non-threatening intruders in different ways, and individuals that invest in differentiating between different types of intruders can adopt more effective strategies than those that give the same response to all intruders. Additionally, the toadlets appeared to vary their use of sampling strategies in response to the perceived level of environmental uncertainty as spatial scale

varied (chapter 2; Figure 24). The change in behaviour reflected the predicted increase in sampling benefits as the level of uncertainty increases (Figure 24).

Despite this support, the results of analysing the theoretical model for assessment strategies in contests (chapter 7) imply that the value of information can depend on more than the level of behavioural flexibility. In particular, the ability to respond to valuable information may drive selection for strategies that can provide a more efficient generalised response that requires no new information, which may in turn reduce the value of gathering new information (Figure 29). In other words, there may be an eco-evolutionary feedback loop (Kokko et al., 2006; Kokko and Lopez-Sepulcre, 2007) between behavioural flexibility and the value of information that is driven by the payoffs of sampling for new information.

The evidence comes from a comparison between a model that allows individuals to improve information (chapter 7) and one that includes the same level of uncertainty but no opportunity to reduce it, formulated by Crowley (2000). In particular, we found that individuals can benefit by using both Hawk and Dove strategies, but Crowley (2000) showed that individuals benefit by specialising in either Hawk or Dove behaviour depending on their fighting ability. The principal difference between the two models is that ours considers the potential to reduce uncertainty about the outcome via sampling. Thus, the model presented in chapter 7 suggests that behavioural flexibility can be influenced by variation in the value of information. In other words, in a world where individuals are unable to improve their information on RHP asymmetries, there exists a 'best average response' (Stephens, 1989) to all contests that involves an RHP dependent pure Hawk or pure Dove strategy. If, however, individuals are able to sample their opponents, then individuals with more complete information will behave differently and disrupt the stability of the best average response. Consequent competition between individuals that update information and those that don't results in the 'best average response' evolving to include a greater degree of flexibility. This then diminishes the value of sampling for new information because the best average response covers a broader range of potential outcomes in the contest, and it involves none of the costs associated with sampling (Figure 27). However, it remains to be seen whether such feedback mechanisms occur beyond the social environment. That is, the possibility for feedback between the value of information and behavioural flexibility may require competition between different sampling strategies within the social environment.

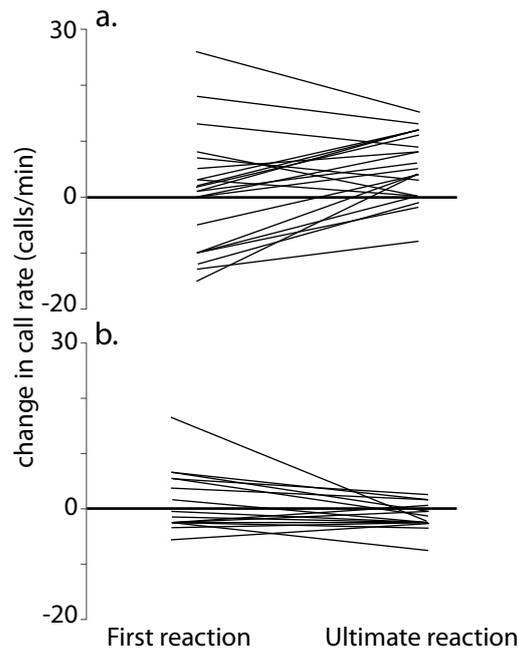


Figure 28: The change in advertisement (a) and aggressive (b) call rates during exposure to a simulated intruder compared to baseline call rates for the first and last bout period in each male of the playback experiment (chapter 6). Note that the change in call rate is highly varied in the first reaction, but are more convergent by the ultimate reaction. Note also that the gradient of the slope is correlated with the magnitude of the first reaction (i.e. the further an initial reaction was from zero, the steeper its gradient). These results suggest that males were adjusting their calling behaviour to an appropriate level with respect to the simulated intruder

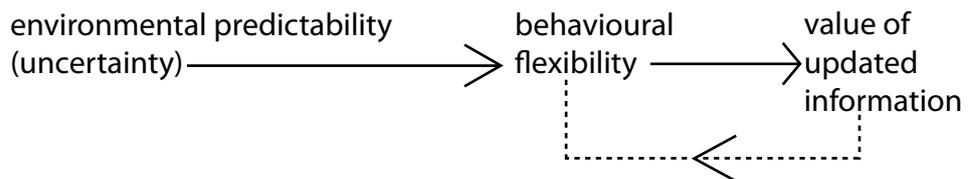


Figure 29: The current model for predicting the value of updated information suggests that it depends on behavioural flexibility. However, analysis of a theoretical model on sampling in contest behaviour (chapter 7) implies that changes in the value of information feed back on behavioural flexibility. Specifically, this occurs because behavioural responses that use no additional information become more generalised when some individuals are able to exploit valuable information by sampling it

8.6 THE COSTS OF SAMPLING

Although animals can benefit from strategies that involve sampling for updated information, these strategies can come at a cost (Dawkins and Guilford, 1991; Luttbegg and Warner, 1999; Jablonka, 2002; Laland, 2004). However, our understanding of these costs, and their ecological and evolutionary implications, remains limited. Generally, investment towards strategies that involve sampling are expected to trade-off against strategies that maximise growth, survival or reproduction (Dall and Cuthill, 1997; Dall et al., 2005). For instance, foragers that sample alternative foraging sites too frequently can miss opportunities for foraging in productive sites (Krebs et al., 1978; Stephens, 1987; Lea et al., 2012). Similarly, chapter 7 identified that individuals that sample their opponents during a contest are less able to invest in fighting and may consequently lose resources to individuals that are more aggressive with less information. Furthermore, sampling can also be costly if it provides opponents with advantageous information. Thus, the costs of sampling in contests appear to be strongly dependent on how other individuals in the population are using information. This implies that the costs of sampling in contests are perhaps similar to sampling in a group of foragers that experience producer-scrounger dynamics, in the sense that the value of sampling is conditional on what others in the population are doing (Dubois et al., 2012).

Investment towards sampling one set of information can also trade-off against sampling other, potentially unrelated, information sources because information processing resources are finite and must be strategically allocated according to expected fitness returns (Dall and Cuthill, 1997). For instance, investment towards sampling opponents in contests may translate to a reduced capacity to track environmental changes relating to foraging or reproduction. The need to sample in a specific context can be reduced by the use of a general best average response, as discussed above (8.4, 8.5), but individuals that use updated information may have an adaptive advantage. Thus, to understand the extent to which sampling a specific set of information is costly in terms of reduced attention to other sources of information, we must determine the extent to which individuals that use sampled information have an advantage over those that use a more generalised pattern of behaviour. The model presented in chapter 7 represents the first steps towards understanding the nature of this competition during contests. Specifically, it indicates that individuals that use sampled information have a selective advantage over those that use generalised responses in a range of circumstances, and that the benefits of sampling depend on interactions between an individual's fighting ability, the value of contested resources, the distribution of fighting abilities within the

population, information transfer between contestants, the efficacy of sampling and the intrinsic cost of sampling.

8.7 CONCLUSIONS

The use of information by organisms as a unifying concept in ecology and evolution is gradually growing, but the need to develop a thorough and consistent framework for generalising results remains. The current framework highlights variation in the fitness value of information and distinguishes between previously held information and updated information. This distinction makes it clear that the benefits associated with updating information do not always outweigh the costs. However, the factors that influence whether it is beneficial to sample information or not are not yet fully understood. This is especially the case in regards to the consequences of sampling from the social environment, as the multitude of conflicting and convergent evolutionary interests of individuals within a population add an extra level of complexity to sampling behaviour.

The aim of this thesis was to explore the costs and benefits of sampling in three distinct contexts and identify general patterns relating to sampling the social environment and to sampling in general. Correspondingly, this thesis has highlighted two social processes that could influence the evolution and ecology of sampling conspecifics: intra-population variation in the value of information, and the value of social conventions that reduce the need to sample. Additionally, my studies on landmarks imply that information transfer between individuals in a population can be influenced by non-social aspects of the environment. Furthermore, the results of this thesis provide supporting evidence for the importance of three important concepts that describe variation in sampling in a more general sense: the relationship between spatio-temporal scale and information value, the value of behavioural flexibility in unpredictable environments, and the existence of trade-offs between sampling and other fitness-enhancing behaviours. As a result of these studies, it is clear that further developments for the ecology of information use will require greater empirical support for the processes that link information use with the phenomena attached to landscapes, such as variation in the value of information at different spatial scales and features such as landmarks. Furthermore, social interactions have an important influence on the value of information that may be necessary to consider in cases where the evolution of conventions or eco-evolutionary feedback is possible.

APPENDIX

CALCULATION OF FITNESS IN CONTESTS

Let $q_{ij}(X, Y)$ denote the probability that the perceptual combination is j when the actual RHP combination is i and the total effective effort expended on mutual assessment is X for Player 1 but Y for Player 2, according to (3) and (4). Then the resultant 4×4 matrix is $Q(X, Y)$ defined by Table 19.

Let a_{ij} be the payoff to Player 1 from an interaction with Player 2 when the RHP combination is i and perceived as j . Then the 4×4 matrix A is calculated as follows. First suppose that both individuals are weak, and that each correctly perceives the other as weak. Then Player 1 escalates with probability u_2 and is nonaggressive with probability $1 - u_2$. Because the corresponding probabilities for Player 2 are v_2 and $1 - v_2$, the payoff to Player 1 in this instance is $a_{11} = \{\frac{1}{2}V - C\} \cdot u_2v_2 + V \cdot u_2(1 - v_2) + 0 \cdot (1 - u_2)v_2 + \frac{1}{2}V \cdot (1 - u_2)(1 - v_2) = \frac{1}{2}V\{1 - v_2 + u_2\} - Cu_2v_2$. If instead Player 1 correctly perceives Player 2 as weak but Player 2 misperceives Player 1 as strong, then because a strong animal is guaranteed to win a fight, Player 2 does not escalate; and so the payoff to Player 1 is V if it escalates and $\frac{1}{2}V$ if it is nonaggressive, i.e., $a_{12} = V \cdot u_2 + \frac{1}{2}V \cdot (1 - u_2) = \frac{1}{2}V\{1 + u_2\}$. Similarly, $a_{13} = 0 \cdot v_2 + \frac{1}{2}V(1 - v_2)$ and $a_{14} = \frac{1}{2}V$.

Next suppose that Player 1 is weak but Player 2 is strong, so that if there is a fight, then Player 2 is guaranteed to win. However, there will be no fight if both perceive correctly: Player 2 will obtain the resource without cost to either contestant, and so $a_{21} = 0$. If, on the other hand, both perceive incorrectly, that is, Player 1 perceives Player 2 as weak while Player 2 perceives Player 1 as strong, then Player 1 will escalate with probability u_2 while Player 2 escalates with probability v_3 , and so $a_{24} = -C \cdot u_2v_3 + V \cdot u_2(1 - v_3) + 0 \cdot (1 - u_2)v_3 + \frac{1}{2}V \cdot (1 - u_2)(1 - v_3) = \frac{1}{2}V(1 + u_2)(1 - v_3) - Cu_2v_3$. Similarly, $a_{22} = 0 \cdot v_3 + \frac{1}{2}V \cdot (1 - v_3)$ and $a_{23} = -C \cdot u_2 + 0 \cdot (1 - u_2)$.

Next suppose that Player 1 is strong but Player 2 is weak, so that Player 1 is guaranteed to win any fight. There will be no fight if both perceive correctly: Player 1 will obtain the resource without cost, and so $a_{31} = V$. If, on the other hand, both perceive incorrectly, that is, Player 1 perceives Player 2 as strong while Player 2 perceives Player 1 as weak, then Player 1 will escalate with probability u_3 while Player 2 escalates with probability v_2 , and so $a_{34} = \{V - C\} \cdot u_3v_2 + V \cdot u_3(1 - v_2) + 0 \cdot (1 - u_3)v_2 + \frac{1}{2}V \cdot (1 - u_3)(1 - v_2) = \frac{1}{2}V\{(1 - v_2 + (1 + v_2)u_3)\} - Cu_3v_2$. Similarly, $a_{32} = \{V - C\} \cdot v_2 + V \cdot (1 - v_2) = V - Cv_2$ and $a_{33} = V \cdot u_3 + \frac{1}{2}V(1 - u_3) = \frac{1}{2}V(1 + u_3)$.

Table 19: The matrix $Q(X, Y)$, which yields the probabilities associated with all 16 possible combinations of actual and perceptual states for an interactions between two individuals

STATE	RHP		PROB(CC)	PROB(CI)	PROB(IC)	PROB(II)
	1	2				
i	1	2	q_{i1}	q_{i2}	q_{i3}	q_{i4}
1	W	W	$\phi_W(X)\phi_W(Y)$	$\phi_W(X)\{1 - \phi_W(Y)\}$	$\{1 - \phi_W(X)\}\phi_W(Y)$	$\{1 - \phi_W(X)\}\{1 - \phi_W(Y)\}$
2	W	S	$\phi_S(X)\phi_W(Y)$	$\phi_S(X)\{1 - \phi_W(Y)\}$	$\{1 - \phi_S(X)\}\phi_W(Y)$	$\{1 - \phi_S(X)\}\{1 - \phi_W(Y)\}$
3	S	W	$\phi_W(X)\phi_S(Y)$	$\phi_W(X)\{1 - \phi_S(Y)\}$	$\{1 - \phi_W(X)\}\phi_S(Y)$	$\{1 - \phi_W(X)\}\{1 - \phi_S(Y)\}$
4	S	S	$\phi_S(X)\phi_S(Y)$	$\phi_S(X)\{1 - \phi_S(Y)\}$	$\{1 - \phi_S(X)\}\phi_S(Y)$	$\{1 - \phi_S(X)\}\{1 - \phi_S(Y)\}$

Table 20: The matrix A , which yields the payoffs associated with all 16 possible combinations of actual and perceptual states for an interaction between two individuals

STATE	RHP	CC	CI	IC	II
i	$\mathcal{P}_1 \quad \mathcal{P}_2$	$j=1$	$j=2$	$j=3$	$j=4$
1	W	$\frac{1}{2}V\{1 - v_2 + u_2\} - Cu_2v_2$	$\frac{1}{2}V\{1 + u_2\}$	$\frac{1}{2}V\{1 - v_2\}$	$\frac{1}{2}V$
2	W	0	$\frac{1}{2}V\{1 - v_3\}$	$-Cu_2$	$\frac{1}{2}V(1 + u_2)(1 - v_3) - Cu_2v_3$
3	S	V	$V - Cv_2$	$\frac{1}{2}V(1 + u_3)$	$\frac{1}{2}V\{(1 - v_2 + (1 + v_2)u_3) - Cu_3v_2\}$
4	S	$\frac{1}{2}V\{1 - v_3 + u_3\} - Cu_3v_3$	$\{\frac{1}{2}V - C\}u_3$	$V\{1 - \frac{1}{2}v_3\} - Cv_3$	$\frac{1}{2}V - C$

Finally, suppose that both individuals are strong, and that each correctly perceives the other as strong. Then Player 1 escalates with probability u_3 while Player 2 escalates with probability v_3 , and so $a_{41} = \{\frac{1}{2}V - C\} \cdot u_3v_3 + V \cdot u_3(1 - v_3) + 0 \cdot (1 - u_3)v_3 + \frac{1}{2}V \cdot (1 - u_3)(1 - v_3) = \frac{1}{2}V\{1 - v_3 + u_3\} - Cu_3v_3$. Similarly, $a_{42} = \{\frac{1}{2}V - C\}u_3 + 0 \cdot (1 - u_3)$, $a_{43} = \{\frac{1}{2}V - C\}v_3 + V \cdot (1 - v_3)$ and—because a fight is inevitable if both misperceive— $a_{44} = \frac{1}{2}V - C$. We thus obtain the 4×4 contest payoff matrix A presented in Table 20, where \mathcal{P}_i is used as a shorthand for Player i . These payoffs exclude the cost of assessment.

However, the total fitness to a u -strategist in a population of v -strategists includes the cost of assessment. We obtain

$$f(u, v) = \sum_{i=1}^4 \sum_{j=1}^4 a_{ij} p_i q_{ij} (u_1 + rv_1, ru_1 + v_1) - \Gamma u_1, \tag{10}$$

where p_i is defined by (2), q_{ij} is defined by Table 19 and a_{ij} is defined by Table 20; note that a_{ij} may depend on u_2, u_3, v_2 or v_3 . After simplification, (10) reduces to

$$f(u, v) = \left\{ \frac{1}{2}\beta B_1(u, v) - B_2(u, v) - e^{-(1+r)(u_1+v_1)\alpha} B_4(u, v) - \gamma u_1 \right\} C \tag{11}$$

where $B_1 \dots B_3$ are defined by Table 21.

Table 21: Definition of terms used to yield an explicit expression for fitness

k	$B_k(u, v)$
1	$1 + (1 - \lambda)^2(u_3 - v_3) + \lambda^2(u_2 - v_2) + (1 - \lambda)\lambda^2\{e^{-(ru_1+v_1)\alpha}v_2 - e^{-(u_1+rv_1)\alpha}u_2\}$ $+ (1 - \lambda)^2\lambda^2e^{-(1+r)(u_1+v_1)\alpha}\{u_2(1 - v_3) - v_2(1 - u_3)\}$
2	$(1 - \lambda)^2\{u_3 + \lambda(1 - u_3)e^{-(u_1+rv_1)\alpha}\{v_3 + \lambda(1 - v_3)e^{-(ru_1+v_1)\alpha}\}$ $+ \lambda^2u_2v_2\{1 - (1 - \lambda)e^{-(u_1+rv_1)\alpha}\}\{1 - (1 - \lambda)e^{-(ru_1+v_1)\alpha}\}$
3	$\lambda^2(1 - \lambda)(v_2\{e^{(u_1+rv_1)\alpha} - (1 - \lambda)(1 - u_3)\} + u_2\{e^{(ru_1+v_1)\alpha} - (1 - \lambda)(1 - v_3)\})$

ESS CALCULATIONS

Here we use $u = (u_1, u_2, u_3)$ to denote the strategy of a focal individual who is a potential mutant, $v = (u_1, u_2, u_3)$ to denote a population strategy and $v^* = (v_1^*, v_2^*, v_3^*)$ to denote a population strategy that is a candidate for ESS. A necessary condition for $0 < v_i^* < 1$ at such an ESS is

$$\left. \frac{\partial f}{\partial u_i} \right|_{u=v=v^*} = 0. \quad (12)$$

Correspondingly, a necessary condition for $v_i^* = 0$ at such an ESS is

$$\left. \frac{\partial f}{\partial u_i} \right|_{u=v=v^*} \leq 0, \quad (13)$$

and a necessary condition for $v_i^* = 1$ at such an ESS is

$$\left. \frac{\partial f}{\partial u_i} \right|_{u=v=v^*} \geq 0. \quad (14)$$

Because $f(u, v)$ is linear in both u_2 and u_3 , there must be alternative best replies when (12) is satisfied with $0 < v_i^* < 1$ for $i = 2$ or $i = 3$, and so v^* can be a strong ESS only if it is a boundary ESS: either $v_2^* = 0$ or $v_2^* = 1$ and either $v_3^* = 0$ or $v_3^* = 1$. Such a v^* is indeed a strong ESS if (13) or (14) is satisfied with strict inequality for both $i = 2$ and $i = 3$, and either (13) is satisfied with strict inequality (for $v_1^* = 0$), or $\partial^2 f / \partial u_1^2 |_{u=v=v^*} < 0$ (for $v_1^* > 0$). Otherwise v^* can only be a weak ESS, and it must be verified directly that $f(v^*, u) > f(u, u)$ when $u \neq v^*$ for alternative best replies u with $f(u, v^*) = f(v^*, v^*)$.

Because we may have $v_i^* = 0$ or $0 < v_i^* < 1$ for $i = 1, \dots, 3$ and $v_i^* = 1$ for $i = 2, 3$ at the ESS, there exist up to $3^2 \times 2 = 18$ possible forms that a candidate ESS can take. We consider each in turn, starting with $v_i^* = 0$ in §B.1 and continuing with $v_i^* > 0$ in §B.2.

B.1 SELF-ASSESSMENT ESS CONDITIONS

To obtain conditions for a (pure) self-assessment ESS, we first set $v_1^* = 0$. Then, from (11) in conjunction with Table 21, we have

$$\begin{aligned} \left. \frac{\partial f}{\partial u_1} \right|_{u=v=v^*} &= \frac{1}{2}\lambda^2(1-\lambda)(1-r)\alpha v_2^*V - (1+r)\alpha(1-\lambda)\lambda\{(1-\lambda)^2v_3^{*2} \\ &\quad - \lambda(1-v_2^*)\{1-\lambda(1-v_2^*)\} - (1-\lambda)v_3^*\{1-2\lambda(1-v_2^*)\}\}C - \Gamma, \end{aligned} \quad (15)$$

$$\left. \frac{\partial f}{\partial u_2} \right|_{u=v=v^*} = \lambda^2\left\{\frac{1}{2}\{(1-v_3^*)(1-\lambda)^2 + \lambda\}V - \{(1-\lambda)\{(1-\lambda)v_3^* + \lambda\} + \lambda^2v_2^*\}C\right\} \quad (16)$$

and

$$\left. \frac{\partial f}{\partial u_3} \right|_{u=v=v^*} = (1-\lambda)^2\left\{\frac{1}{2}(1+\lambda^2v_2^*)V - \{(1-\lambda)\{(1-\lambda)v_3^* + \lambda\} + \lambda^2v_2^*\}C\right\}. \quad (17)$$

We now consider each of nine possibilities for $v_1^* = 0$ in turn.

B.1.1 Type IA ESS

with $v_1^* = 0$, $v_2^* = 1$, $v_3^* = 1$

From (13) with $i = 1$, (14) with $i = 2, 3$ and (15)–(17), we require the inequalities

$$(1-\lambda)\lambda^2\{(1-r)\beta + 2(1+r)(1-\lambda)\} \leq 2\gamma \quad (18a)$$

$$\lambda\beta \geq 2(1-\lambda + \lambda^2) \quad (18b)$$

and $(1+\lambda^2)\beta \geq 2(1-\lambda + \lambda^2)$, which (18b) implies, to hold simultaneously. We will refer to such an ESS as Type IA. From (18b), it corresponds to the shaded region in the upper right of Figure 20. When (18) holds with strict inequality, v^* is a strong ESS.

B.1.2 Type IE ESS

with $v_1^* = 0$, $v_2^* = 0$, $v_3^* = 0$

From (13) with $i = 1, 2, 3$, (15), (17) and (16) we require

$$(1+r)(1-\lambda)^2\lambda^2 \leq \gamma \quad (19a)$$

$$\beta \leq 2\lambda(1-\lambda) \quad (19b)$$

and $(1-\lambda + \lambda^2)\beta \leq 2\lambda(1-\lambda)$, which (19b) implies, to hold simultaneously. We will refer to such an ESS as Type IE. From (19a), it cor-

responds to the lowest shaded region of [Figure 20](#). When (19) holds with strict inequality, v^* is a strong ESS.

B.1.3 Type IC ESS

with $v_1^* = 0, v_2^* = 0, v_3^* = 1$

Here (15) reduces to $-\Gamma$, which is always negative. So from (13) with $i = 2$, (14) with $i = 3$ and (16)-(17) we require

$$2(1 - \lambda) \leq \beta \leq \frac{2(1 - \lambda)}{\lambda}. \quad (20)$$

We will refer to such an ESS as Type IC; it corresponds to the central shaded region of [Figure 20](#). When (20) holds with strict inequality, v^* is a strong ESS.

B.1.4 No Type I ESS with $v_1^* = 0, v_2^* = 1, v_3^* = 0$

From (13) with $i = 1, 3$, (14) with $i = 2$ and (15)-(17) we require both $(1 - \lambda + \lambda^2)\beta \geq 2\lambda$ and $(1 + \lambda^2)\beta \leq 2\lambda$, which is impossible, because $(1 - \lambda + \lambda^2)V < (1 + \lambda^2)V$ for $\lambda > 0$. Hence this case does not arise.

B.1.5 Type ID ESS

with $v_1^* = 0, v_2^* = 0, 0 < v_3^* < 1$

From (13) with $i = 1$, (12) with $i = 3$, (15) and (17) we require

$$(1 + r)\lambda\beta \left\{ 1 - \frac{\beta}{2(1 - \lambda)} \right\} \leq 2\gamma \quad (21)$$

and

$$v_3^* = \frac{\beta - 2\lambda(1 - \lambda)}{2(1 - \lambda)^2} \quad (22)$$

with

$$2\lambda(1 - \lambda) < \beta < 2(1 - \lambda). \quad (23)$$

(and (16) reduces to $-\frac{1}{4}\lambda^2\beta V$, so that (13) holds with strict inequality for $i = 2$). We will refer to such an ESS as Type ID; it corresponds to the lower unshaded region of [Figure 20](#). Even if (21) holds with strict inequality, v^* is only a weak ESS because there are always alternative best replies. That is, with $u = (v_1^*, v_2^*, u_3)$, we have $f(u, v^*) = f(v^*, v^*)$, but $f(v^*, u) - f(u, u) = \left\{ \frac{1}{2}(\beta - 2\lambda(1 - \lambda) - 2(1 - \lambda)^2u_3) \right\} > 0$ for all $u_3 \neq v_3^*$.

B.1.6 No Type I ESS for case *f*

with $v_1^* = 0, 0 < v_2^* < 1, 0 < v_3^* < 1$

This case cannot arise, because (12) would have to hold with $i = 2$ and $i = 3$, implying $v_2^* = -1/\lambda^2 < 0$ and $v_3^* = (1 - \lambda + \lambda^2)/(1 - \lambda)^2 > 1$.

B.1.7 No Type I ESS with $v_1^* = 0, v_2^* = 1, 0 < v_3^* < 1$

This case cannot arise because it requires $2(1 - \lambda)^2 v_3^* = (1 + \lambda^2)\beta - 2\lambda$, by (12) with $i = 3$ and (17). Hence $\partial f / \partial u_2|_{u=v=v^*} = -\frac{1}{2}\lambda^2(\lambda + \{(1 - \lambda)^2 + \lambda\}v_3^*)V = -\frac{1}{4}\lambda^2(1 + \lambda^2)\beta V < 0$ by (16), and so (14) fails to hold for $i = 2$.

B.1.8 No Type I ESS for case *g*

with $v_1^* = 0, 0 < v_2^* < 1, v_3^* = 0$

This case cannot arise because it requires $2\lambda^2 v_2^* = (1 - \lambda + \lambda^2)\beta - 2\lambda(1 - \lambda)$, by (12) with $i = 2$ and (16). Hence $\partial f / \partial u_3|_{u=v=v^*} = \frac{1}{2}\lambda(1 - \lambda)^2(1 - \lambda + \lambda v_2^*)V = \frac{1}{4}(1 - \lambda)^2(1 - \lambda + \lambda^2)\beta V > 0$ by (17), and so (13) fails to hold for $i = 3$.

B.1.9 Type IB ESS

with $v_1^* = 0, 0 < v_2^* < 1, v_3^* = 1$

From (12) with $i = 2$ and (16) we require

$$v_2^* = \frac{\lambda\beta - 2(1 - \lambda)}{2\lambda^2} \quad (24)$$

with

$$\frac{2(1 - \lambda)}{\lambda} < \beta < \frac{2(1 - \lambda + \lambda^2)}{\lambda} \quad (25)$$

and (14) holds with $i = 3$ because $\partial f / \partial u_3|_{u=v=v^*} = \frac{1}{2}(1 - \lambda)^2(1 - \lambda + \lambda^2 v_2^*)V = \frac{1}{4}(1 - \lambda)^2 \lambda \beta V > 0$ by (17). From (13) with $i = 1$ and (15), we also require

$$(1 - \lambda)\lambda\{1 + (3 - 2\lambda)r\}\beta \leq 2(1 + r)(1 - \lambda)^2 + 2\lambda\gamma + r(1 - \lambda)\lambda^2\beta^2 \quad (26)$$

We will refer to such an ESS as Type IB; it corresponds to the upper unshaded region of Figure 20. Even if (26) holds with strict inequality, v^* is only a weak ESS because there are always alternative best replies. That is, with $u = (v_1^*, u_2, v_2^*)$, we have $f(u, v^*) = f(v^*, v^*)$, but $f(v^*, u) - f(u, u) = \{\frac{1}{2}(\lambda\beta - 2(1 - \lambda) - 2\lambda^2 u_2)\} > 0$ for all $u_2 \neq v_2^*$.

Of the nine cases so far considered, we have now excluded four possibilities, namely, $v_1^* = 0, v_2^* = 1, v_3^* = 0$ (§B.1.4), $v_1^* = 0, 0 < v_2^* < 1, 0 < v_3^* < 1$ (§B.1.6), $v_1^* = 0, v_2^* = 1, 0 < v_3^* < 1$ (§B.1.7) and $v_1^* = 0, 0 < v_2^* < 1, v_3^* = 0$ (§B.1.8). In each of the other five cases,

$$v_2^* \leq v_3^*. \quad (27)$$

Let γ_K denote the critical value that γ must exceed for v^* to be a Type-IK ESS. Then, from (18a), (26), §B.1.3, (21) and (19a), $\gamma_A \dots \gamma_E$ are defined by

$$\gamma_A = \frac{1}{2}(1-\lambda)\lambda^2\{(1-r)\beta + 2(1+r)(1-\lambda)\} \quad (28a)$$

$$\gamma_B = \frac{1}{2}(1-\lambda)\{1+r(1-\lambda\beta)\}\{\lambda\beta - 2(1-\lambda)\}/\lambda \quad (28b)$$

$$\gamma_C = 0 \quad (28c)$$

$$\gamma_D = \frac{1}{2}(1+r)\lambda\beta\left\{1 - \frac{\beta}{2(1-\lambda)}\right\} \quad (28d)$$

$$\gamma_E = (1+r)\lambda^2(1-\lambda)^2 \quad (28e)$$

and yield the critical threshold (9). Note that each of (28a), (28b) and (28d) is positive inside the region of Figure 20 where it is relevant; for example, (25) implies $2(1-\lambda) < \lambda\beta < 2(1-\lambda\{1-\lambda\}) < 2 \leq 1+1/r$ for (28b). Note also that $\gamma_A \geq \gamma_E$ for any value of r .

B.2 MUTUAL-ASSESSMENT ESS CONDITIONS

For mutual assessment at the ESS we require $v_1^* > 0$. Hence, from (11) and (12) with $i = 1$, we require

$$v_1^* = \frac{1}{(1+r)\alpha} \ln(\zeta) \quad (29)$$

where ζ must not only satisfy the polynomial equation

$$2\gamma\zeta^2 - \lambda(1-\lambda)\{2(1+r)\{\lambda v_2^*(1-v_2^*) + (1-\lambda)v_3^*(1-v_3^*)\} + (1-r)\lambda\beta v_2^*\}\zeta - 2(1+r)(1-\lambda)^2\lambda^2(1-v_2^*-v_3^*)^2 = 0 \quad (30)$$

but also must exceed 1. For boundary values of v_2^* and v_3^* (which are independent of ζ), this is a quadratic equation with precisely one positive root (except in the case where $v_2^* = 0$ and $v_3^* = 1$, which cannot arise—see §B.2.3); and $\zeta > 1$ becomes

$$(1-r)\lambda^2(1-\lambda)\beta v_2^* + 2(1+r)\lambda(1-\lambda)\{v_3^* + \lambda(1-v_2^*-v_3^*)\}\{1-v_3^* - \lambda(1-v_2^*-v_3^*)\} > 2\gamma. \quad (31)$$

From (11) we obtain

$$\begin{aligned} \frac{2\zeta^2}{\lambda^2 C} \frac{\partial f}{\partial u_2} \Big|_{u=v=v^*} &= (\beta - 2v_2^*)\zeta^2 - (1 - \lambda)(\beta - 4v_2^* + 2)\zeta \\ &\quad + \{(\beta + 2)(1 - v_3^*) - 2v_2^*\}(1 - \lambda)^2 \end{aligned} \quad (32)$$

and

$$\begin{aligned} \frac{2\zeta^2}{(1 - \lambda)^2 C} \frac{\partial f}{\partial u_3} \Big|_{u=v=v^*} &= (\beta - 2v_3^*)\zeta^2 - 2\lambda(1 - 2v_3^*)\zeta \\ &\quad + \{(\beta - 2)v_2^* + 2(1 - v_3^*)\}\lambda^2 \end{aligned} \quad (33)$$

where ζ is defined by (30); also

$$\begin{aligned} \frac{2\zeta^2}{C} \frac{\partial^2 f}{\partial u_1^2} \Big|_{u=v=v^*} &= -\alpha\lambda(1 - \lambda) \left\{ 2(1 + r)^2\lambda(1 - \lambda)(1 - v_2^* - v_3^*)^2 + \right. \\ &\quad \left. + \{(1 - r^2)\lambda\beta v_2^* + 2(1 + r^2)\{(1 - \lambda)(1 - v_3^*)v_3^* + \lambda(1 - v_2^*)v_2^*\}\}\zeta \right\}, \end{aligned} \quad (34)$$

so that $\partial^2 f / \partial u_1^2|_{u=v=v^*}$ is always negative.

We now consider each of the nine possibilities with $v_1^* > 0$ in turn.

B.2.1 Type IIa ESS

with $v_1^* > 0$, $v_2^* = 1$, $v_3^* = 1$

Here, from (30), ζ is the only positive root of the quadratic equation

$$2\gamma\zeta^2 - \lambda^2(1 - \lambda)(1 - r)\beta\zeta - 2(1 + r)(1 - \lambda)^2\lambda^2 = 0, \quad (35)$$

and $\zeta > 1$ requires

$$\lambda^2(1 - \lambda)\{(1 - r)\beta + 2(1 + r)(1 - \lambda)\} \geq 2\gamma \quad (36)$$

or $\gamma < \gamma_A$, by (31) and (28). From (14) with $i = 2$ and (32), we require in addition that

$$(\beta - 2)(\zeta - 1 + \lambda)\zeta \geq 2(1 - \lambda)^2 \quad (37)$$

where ζ is defined by (35), and hence in particular that $\beta > 2$, corresponding to the uppermost shaded and unshaded regions of Figure 21. Then, from (33), (14) holds with strict inequality for $i = 3$ because $\beta > 2$ implies $(\beta - 2)(\zeta^2 + \lambda^2) + 2\lambda\zeta > 0$. We will refer to such an ESS as Type IIa. If (37) holds with strict inequality, then v^* is a strong ESS.

B.2.2 Type IIe ESS

with $v_1^* > 0$, $v_2^* = 0$, $v_3^* = 0$

Here, from (31), we require

$$(1+r)\lambda^2(1-\lambda)^2 > \gamma \quad (38)$$

or $\gamma < \gamma_E$, in which case

$$\zeta = \lambda(1-\lambda)\sqrt{(1+r)/\gamma} \quad (39)$$

by (30). From (14) with $i = 2, 3$ and (32)-(33), we require in addition that

$$\beta\zeta^2 - (1-\lambda)(\beta+2)\zeta - (\beta+2)(1-\lambda)^2 \leq 0 \quad (40a)$$

$$(\beta\zeta - 2\lambda)\zeta + 2\lambda^2 \leq 0, \quad (40b)$$

the second of which implies the first. Note that because $\zeta > 1$, (40b) implies $\beta < 2\lambda$. Furthermore, (40b) implies $\beta \leq 2\lambda(\zeta - \lambda)/\zeta^2$. But $2\lambda(\zeta - \lambda)$ has an absolute maximum of $\frac{1}{2}\zeta^2$ for $\lambda = \frac{1}{2}\zeta$, and so it also follows that $\beta \leq \frac{1}{2}$, which restricts this case to the dark shaded region of Figure 21¹. We will refer to such an ESS as Type IIe. If (40) holds with strict inequality, then v^* is a strong ESS.

B.2.3 No Type II ESS for case c

with $v_1^* > 0$, $v_2^* = 0$, $v_3^* = 1$

Here (31) reduces to $0 > 2\gamma$, which is impossible. Hence this case does not arise.

B.2.4 No Type II ESS with $v_1^* > 0$, $v_2^* = 1$, $v_3^* = 0$

Here, from (31), we require

$$\lambda^2(1-\lambda)(1-r)\beta > 2\gamma, \quad (41)$$

in which case ζ is the only positive root of (30) or

$$\zeta = \frac{\lambda^2(1-\lambda)(1-r)\beta}{2\gamma}. \quad (42)$$

¹ The left-hand boundary of this region is actually an arc of the curve $\lambda\beta^3 + 4(\beta - 2\lambda) = 0$, as opposed to the line $\beta = 2\lambda$; however, the curve and the line are virtually indistinguishable for $\lambda \leq \frac{1}{4}$ (with the line lying ever so slightly above the curve).

From (14) with $i = 2$, (13) with $i = 3$ and (32)–(33) we require in addition that

$$(\beta - 2)\zeta^2 - (1 - \lambda)(\beta - 2)\zeta + \beta(1 - \lambda)^2 \geq 0 \quad (43a)$$

$$\beta\zeta^2 - 2\lambda\zeta + \beta\lambda^2 \leq 0. \quad (43b)$$

and hence, on multiplying the first of these inequalities by -1 before adding them, that $\beta\zeta(1 - \lambda) + \beta(2\lambda - 1) + 2\zeta(\zeta - 1) \leq 0$. However, this inequality can never hold because $\zeta > 1$, and so the left-hand must exceed $\beta(1 - \lambda) + \beta(2\lambda - 1) + 2\zeta(\zeta - 1) = \beta\lambda + 2\zeta(\zeta - 1)$, which is positive. So this case does not arise.

B.2.5 Type IId ESS

with $v_1^* > 0$, $v_2^* = 0$, $0 < v_3^* < 1$

Here, with $v_2^* = 0$, (12) must hold for $i = 1, 3$ and (13) must hold for $i = 2$. Thus, with $v_2^* = 0$, the right-hand side of (33) must equal zero, yielding

$$v_3^* = \frac{\beta\zeta^2 - 2\lambda\zeta + 2\lambda^2}{2(\zeta - \lambda)^2}; \quad (44)$$

(30) must hold, which yields the cubic equation

$$(1 + r)\beta\lambda(1 - \lambda)^2\{(\beta - 2)\zeta + 2\lambda\}\zeta + 4\gamma(\zeta - \lambda)^3 = 0 \quad (45)$$

for ζ , on substituting (44) into (30); and from (32), $\partial f / \partial u_2|_{u=v^*} \leq 0$ requires

$$2\beta(\zeta - 1)\{\zeta(\zeta - \lambda) + \lambda(1 - \lambda)\} \leq (1 - \lambda)\{\beta^2(1 - \lambda)\zeta + 4(\zeta - 1)(\zeta - \lambda)\}. \quad (46)$$

Note that (45) implies $(\beta - 2)\zeta + 2\lambda < 0$ (because $\zeta > \lambda$), hence $\beta < 2$ and $\zeta > 2\lambda / (2 - \beta)$. Also, the left-hand side of (45) must be less than the right-hand side evaluated for $\beta = 2$, or

$$\beta < \frac{2(1 - \lambda)}{\zeta - 1} \left\{ \frac{(\zeta - \lambda)^2 + \lambda(1 - \lambda)}{\zeta(\zeta - \lambda) + \lambda(1 - \lambda)} \right\}. \quad (47)$$

The term in squiggly brackets cannot exceed 1. Hence if $\zeta \geq 2$, then $\beta < 2(1 - \lambda)$; and if $1 < \zeta < 2$, then $2 > 2\lambda / (2 - \beta)$ implies $\beta < 2 - \lambda$. Either way, $\beta < 2 - \lambda$. We will refer to such an ESS as Type IId. For example, with $r = 0$, $\lambda = 0.5$, $\beta = 0.7$ and $\gamma = 0.04$ we obtain $\alpha v_1^* = \ln(1.2613) = 0.232$, $v_2^* = 0$ and $v_3^* = 0.304$.

Even if (46) holds with strict inequality, v^* is only a weak ESS because there are always alternative best replies. That is, with $u = (v_1^*, v_2^*, u_3)$ we have $f(u, v^*) = f(v^*, v^*)$ but $f(v^*, u) - f(u, u) > 0$ for all $u_2 \neq v_2^*$. This condition is hard to establish analytically, but it

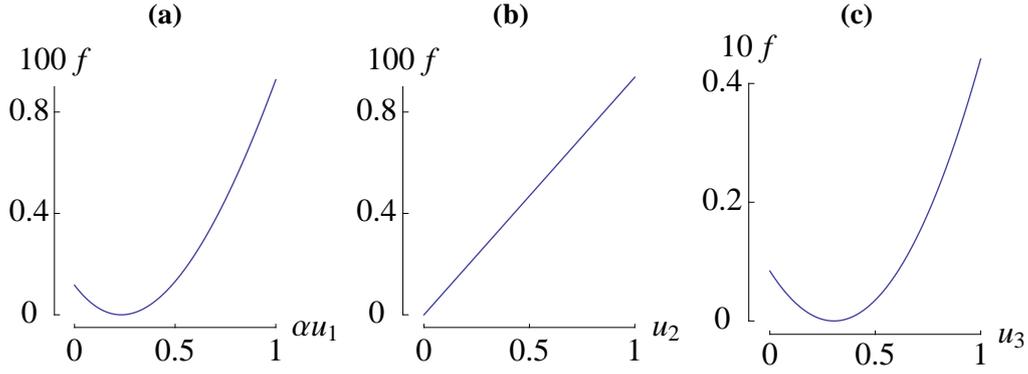


Figure 30: Verification of sufficiency conditions for a Type-II ESS with $r = 0$, $\lambda = 0.5$, $\beta = 0.7$, $\gamma = 0.04$ and hence $\alpha v_1^* = 0.232$, $v_2^* = 0$, $v_3^* = 0.304$. (a) With $u = (u_1, v_2^*, v_3^*)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$. (b) With $u = (v_1^*, u_2, v_3^*)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$. (c) With $u = (v_1^*, v_2^*, u_3)$, $f(v^*, v^*) = f(u, v^*)$ for all u but $f(v^*, u) - f(u, u)$ is positive for all $u \neq v^*$

is easy to verify numerically in any specific case. For example, it is verified by [Figure 30](#) for the example given above.

B.2.6 Type IIf ESS

with $v_1^* > 0$, $0 < v_2^* < 1$, $0 < v_3^* < 1$

Here (12) must hold for $i = 2$ and $i = 3$ as well as for $i = 1$. If $\beta \geq 2$, then the expression on the right-hand side of (33) must at least equal $2(1 - v_3^*)(\zeta - \lambda)^2 + 2\zeta\lambda$ and hence be positive, a contradiction; hence $\beta < 2$. With v_1^* satisfying (29), setting the right-hand sides of (32)–(33) both equal to zero yields a pair of simultaneous linear equations for v_2^* and v_3^* , which are readily solved. The resultant expressions for v_2^* and v_3^* are quotients of fourth-order polynomials in ζ , which also depend on β , γ , λ and r ; they are both negative if $\beta = 0$, indicating that this case does not arise for small positive values of β , but in practice its minimum feasible value can be found only by numerical means. Substituting the expressions for v_2^* and v_3^* into (30) yields a ninth-order polynomial equation for ζ that is far too cumbersome to present. Nevertheless, it is readily solved by numerical means for any given values of r , λ , β and γ . For example, with $r = 0$, $\lambda = 0.2$, $\beta = 0.7$ and $\gamma = 0.01$ there are two solutions greater than 1, but only the larger one corresponds to a positive value of v_2^* . We then obtain $\alpha v_1^* = \ln(3.824) = 1.34$, $v_2^* = 0.171$ and $v_3^* = 0.334$. Note that $v_3^* > v_2^*$.

We will refer to such an ESS as Type IIf. A Type-IIf ESS is always a weak ESS, because there are always alternative best replies. That is, with $u = (v_1^*, u_2, v_3^*)$ or $u = (v_1^*, v_2^*, u_3)$, we have $f(u, v^*) = f(v^*, v^*)$,

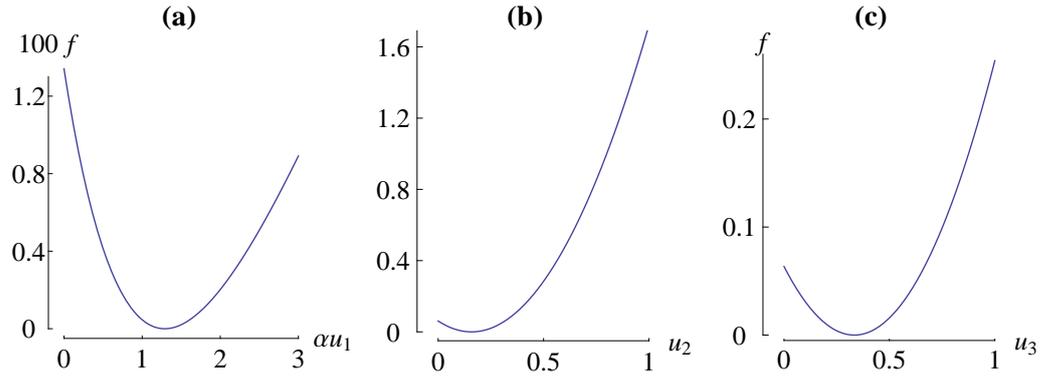


Figure 31: Verification of sufficiency conditions for a Type-II ESS with $r = 0$, $\lambda = 0.2$, $\beta = 0.7$, $\gamma = 0.01$ and hence $\alpha v_1^* = 1.34$, $v_2^* = 0.171$, $v_3^* = 0.334$. (a) With $u = (u_1, v_2^*, v_3^*)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$. (b) With $u = (v_1^*, u_2, v_3^*)$, $f(v^*, v^*) = f(u, v^*)$ for all u but $f(v^*, u) - f(u, u)$ is positive for all $u \neq v^*$. (c) With $u = (v_1^*, v_2^*, u_3)$, $f(v^*, v^*) = f(u, v^*)$ for all u but $f(v^*, u) - f(u, u)$ is positive for all $u \neq v^*$

but $f(v^*, u) - f(u, u) > 0$ for all $u_2 \neq v_2^*$ or all $u_3 \neq v_3^*$, respectively. These conditions are verified by Figure 30 for the example given above.

B.2.7 No Type II ESS with $v_1^* > 0$, $v_2^* = 1$, $0 < v_3^* < 1$

Here, with $v_2^* = 1$, (12) must hold for $i = 1, 3$ and (14) must hold for $i = 2$. Thus, with $v_2^* = 1$, the right-hand side of (33) must equal zero, yielding

$$v_3^* = \frac{\beta\zeta^2 - 2\lambda\zeta + \beta\lambda^2}{2(\zeta - \lambda)^2}; \tag{48}$$

(30) must hold, which yields the quintic equation

$$4\gamma\zeta^2(\zeta - \lambda)^3 + \lambda(1 - \lambda)\left\{(1 + r)(1 - \lambda)\{4\lambda\zeta^3 + \beta^2(\zeta^2 + \lambda^2)^2\} - 2\beta\zeta\{(1 + r)(\zeta + \lambda)(\zeta^2 + \lambda^2) - 2\lambda(r\zeta^3 + \lambda^3 + \lambda\zeta\{(2 - r)\zeta + (2r - 1)\lambda\})\}\right\} = 0 \tag{49}$$

for ζ , on substituting (48) into (30); and the right-hand side of (32) must not be negative, requiring

$$2(\beta - 2)\zeta(\zeta - 1)\{\zeta(\zeta - \lambda) + \lambda(1 - \lambda)\} \geq \beta^2(1 - \lambda)^2\{\zeta^2 + \lambda^2\} \tag{50}$$

and hence in particular $\beta > 2$. From (48), however, $v_3^* < 1$ requires $(\beta - 2)(\zeta^2 + \lambda^2) + 2\lambda\zeta < 0$, and this contradiction ensures that this case cannot arise.

B.2.8 Type IIg ESS

with $v_1^* > 0$, $0 < v_2^* < 1$, $v_3^* = 0$

Here, with $v_3^* = 0$, (12) must hold for $i = 1, 2$ and (13) must hold for $i = 3$. Thus, with $v_3^* = 0$, the right-hand side of (32) must equal zero, yielding

$$v_2^* = \frac{\beta\{\zeta(\zeta - 1 + \lambda) + (1 - \lambda)^2\} - 2(1 - \lambda)(\zeta - 1 + \lambda)}{2(\zeta - 1 + \lambda)^2}; \quad (51)$$

(30) must hold, which yields the quintic equation

$$\begin{aligned} &4\gamma\zeta^2(\zeta - 1 + \lambda)^3 + \lambda^2(1 - \lambda)\left\{\beta^2\{\zeta(\zeta - 1 + \lambda) + (1 - \lambda)^2\}\right. \\ &\quad \left.\{2r\zeta(\zeta - 1 + \lambda) + (1 + r)(1 - \lambda)^2\}\right. \\ &\quad \left.- 2\beta\zeta(\zeta - 1 + \lambda)\{r\zeta^2 + (1 - \lambda)^2 + (\zeta - 1 + \lambda)^2\}\right\} = 0 \end{aligned} \quad (52)$$

for ζ , on substituting (51) into (30); and the right-hand side of (33) must not be positive, requiring

$$\lambda^2\beta^2\{\zeta(\zeta - 1 + \lambda) + (1 - \lambda)^2\} + 2\beta\zeta^2(\zeta - 1)(\zeta - 1 + 2\lambda) \leq 4\lambda\zeta(\zeta - 1)(\zeta - 1 + \lambda). \quad (53)$$

Because the second term on the left-hand side must be strictly smaller than the right-hand side when the coefficient 2 in the last factor is replaced by 1, it is readily seen that $\beta\zeta < 2\lambda$. Because the first term on the left-hand side must be strictly smaller than the right-hand side, we also have $\lambda\beta^2 < 4(\zeta - 1)$. Combining these inequalities, we find that the point (λ, β) must lie below the curve $\lambda\beta^3 + 4(\beta - 2\lambda) = 0$, as indicated in Figure 21. Numerical experiment indicates that the above conditions can be satisfied if both γ is sufficiently small and λ is sufficiently large; for example, with $r = 1$, $\lambda = 0.8$, $\beta = 0.2$ and $\gamma = 0.01$ we obtain $av_1^* = \ln(2.518) = 0.4617$, $v_2^* = 0.02309$ and $v_3^* = 0$.

We will refer to such an ESS as Type IIg. A Type-IIg ESS is always a weak ESS, because there are always alternative best replies. That is, with $u = (v_1^*, u_2, v_3^*)$, we have $f(u, v^*) = f(v^*, v^*)$, but $f(v^*, u) - f(u, u) > 0$ for all $u_2 \neq v_2^*$. This condition is verified by Figure 32 for the example given above.

This is the only type of ESS for which $v_2^* > v_3^*$. Note that this case does not arise when $\lambda = \frac{1}{2}$ (Appendix C).

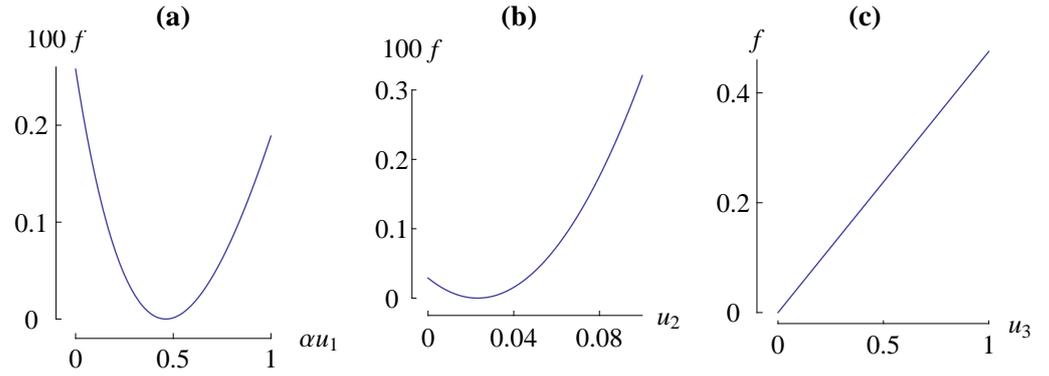


Figure 32: Verification of sufficiency conditions for a Type-IIg ESS with $r = 1$, $\lambda = 0.8$, $\beta = 0.2$, $\gamma = 0.01$ and hence $av_1^* = 0.4617$, $v_2^* = 0.02309$, $v_3^* = 0$. (a) With $u = (u_1, v_2^*, v_3^*)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$. (b) With $u = (v_1^*, u_2, v_3^*)$, $f(v^*, v^*) = f(u, v^*)$ for all u but $f(v^*, u) - f(u, u)$ is positive for all $u \neq v^*$. (c) With $u = (v_1^*, v_2^*, u_3)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$

B.2.9 Type IIb ESS

with $v_1^* > 0$, $0 < v_2^* < 1$, $v_3^* = 1$

Here, with $v_3^* = 1$, (12) must hold for $i = 1, 2$ and (14) must hold for $i = 3$. Thus, with $v_3^* = 1$, the right-hand side of (32) must equal zero, yielding

$$v_2^* = \frac{\zeta\{\beta(\zeta - 1 + \lambda) - 2(1 - \lambda)\}}{2(\zeta - 1 + \lambda)^2}. \tag{54}$$

For $v_2^* < 1$ we require

$$\beta < \frac{2\{\zeta(\zeta - 1 + \lambda) + (1 - \lambda)^2\}}{\zeta(\zeta - 1 + \lambda)}; \tag{55}$$

and because the right-hand side of (55) decreases with ζ , it cannot exceed its value as $\zeta \rightarrow 1$. We deduce that

$$\beta < \frac{2(1 - \lambda + \lambda^2)}{\lambda}. \tag{56}$$

Also, (30) must hold, which yields the cubic equation

$$(1 - \lambda)\lambda^2\{2(1 - \lambda) - \beta(\zeta - 1 + \lambda)\}\{(1 + r)\zeta - r\beta(\zeta - 1 + \lambda)\} + 2\gamma(\zeta - 1 + \lambda)^3 = 0 \tag{57}$$

for ζ , on substituting (54) into (30); and the right-hand side of (33) must not be negative, requiring

$$\beta^2\lambda^2(\zeta - 1 + \lambda) + 2\beta\zeta(\zeta - 1)(\zeta - 1 + 2\lambda) \geq 4(\zeta - 1)\{\zeta(\zeta - 1 + \lambda) + \lambda(1 - \lambda)\} \tag{58}$$

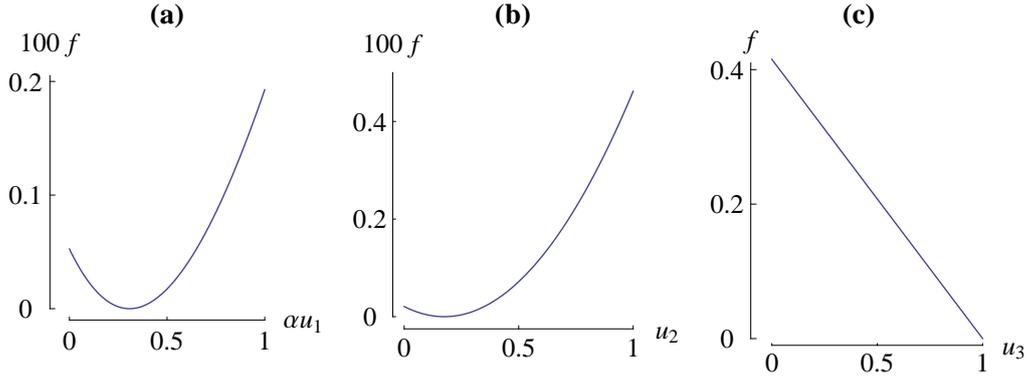


Figure 33: Verification of sufficiency conditions for a Type-IIb ESS with $r = 0$, $\lambda = 0.2$, $\beta = 3$, $\gamma = 0.01$ and hence $\alpha v_1^* = 0.3077$, $v_2^* = 0.1751$, $v_3^* = 1$. (a) With $u = (u_1, v_2^*, v_3^*)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$. (b) With $u = (v_1^*, u_2, v_3^*)$, $f(v^*, v^*) = f(u, v^*)$ for all u but $f(v^*, u) - f(u, u)$ is positive for all $u \neq v^*$. (c) With $u = (v_1^*, v_2^*, u_3)$, $f(v^*, v^*) - f(u, v^*)$ is positive for all $u \neq v^*$

and hence that

$$\beta > \min \left\{ 1, \frac{2(1-\lambda)}{1+\lambda} \right\}. \quad (59)$$

For suppose that $\beta \leq 1$. Then the difference between the left- and right-hand sides of (58) cannot exceed $2\zeta^2(2-\zeta) - (1-\lambda)(1+5\lambda)\zeta - \zeta + \lambda(1-\lambda)(4-\lambda)$, which is negative if $\zeta \geq 2$ (because the last term is strictly less than 1); and if $1 < \zeta < 2$, then $v_2^* > 0$ requires $(1+\lambda)\beta > 2(1-\lambda)$.

We will refer to such an ESS as Type IIb. For example, with $r = 0$, $\lambda = 0.2$, $\beta = 3$ and $\gamma = 0.01$ we obtain $\alpha v_1^* = \ln(1.3603) = 0.3077$, $v_2^* = 0.1751$ and $v_3^* = 1$. A Type-IIb ESS is a weak ESS because there are always alternative best replies. That is, with $u = (v_1^*, u_2, v_3^*)$ we have $f(u, v^*) = f(v^*, v^*)$ but $f(v^*, u) - f(u, u) > 0$ for all $u_2 \neq v_2^*$. This condition is verified by Figure 33 for the example given above.

Of the nine cases so considered in this section, we have now excluded three possibilities, namely, $v_1^* > 0$, $v_2^* = 0$, $v_3^* = 1$ (§B.2.3), $v_1^* > 0$, $v_2^* = 1$, $v_3^* = 0$ (§B.2.4) and $v_1^* > 0$, $v_2^* = 1$, $0 < v_3^* < 1$ (§B.2.7). Constraints on the remaining six possibilities for a Type-II ESS are summarized by Figure 21.

THE CASE OF THE MAXIMUM-VARIANCE POPULATION

The results of §B.2 are quite complicated, and thus arguably somewhat at odds with our overall goal of using a minimal model to clarify central issues. Accordingly, we specialize to $\lambda = \frac{1}{2}$, which simplifies matters considerably. Now contestants are equally likely to be matched or unmatched, and so variance of opponents is at a maximum.

The critical values defined by (28) now depend only on β and r , and so for any fixed r we can clearly identify all five categories of Type-I ESS in a β - γ plane. The result is shown for $r = 0$ and $r = 1$ in Figure 22, where there is always a Type-IK ESS in shaded region K. For intermediate values of r , the corresponding regions are intermediate in the sense that increasing r from 0 to 1 raises the base of region E and lowers the base of region A while maintaining the contiguity of all regions. In the unshaded regions, only a Type-II ESS can arise. Above the dashed curves in the shaded regions, only a Type-I ESS can arise. Below the dashed curves in the shaded regions, however, a Type-II ESS can arise alongside the Type-I ESS for that region. Thus the ESS is not in general unique.

To appreciate this point, we first consider a Type-IIa ESS. From §B.2.1, a Type-IIa ESS arises only if $\beta > 2$. From (35), for $\lambda = \frac{1}{2}$ the ESS arises with

$$\zeta = \frac{(1-r)\beta + \sqrt{(1-r)^2\beta^2 + 64(1+r)\gamma}}{32\gamma} \quad (60)$$

whenever (36)–(37) are satisfied with strict inequality. From (36), we require the point (β, γ) in Figure 22 to lie below the line with equation $\gamma = \frac{1}{16}\{1+r+(1-r)\beta\}$; and from (37), we require $(\beta-2)\zeta(2\zeta-1) > 1$, which must hold for $\beta > 3$ but for $2 < \beta < 3$ requires

$$\gamma < \frac{1}{16}\left\{(\beta-2)\{1+(1+\beta)r\} + |1-(\beta-1)r|\sqrt{(\beta-2)(\beta+6)}}\right\} \quad (61)$$

as well as $\gamma < \frac{1}{16}\{1+r+(1-r)\beta\}$ to hold. In Figure 23, (61) demarcates the left-hand boundary of the darker shaded region marked ab. In the lighter shaded region to the right, the ESS is uniquely Type IIa. Comparing with Figure 22, we see that the region in which a Type-IIa ESS arises does not intersect region A, but it overlaps the lowest part of region B, as indicated by the dashed lines.

Next we consider a Type-IIe ESS. From §B.2.2, a Type-IIe ESS arises only if $\beta \leq \frac{1}{2}$. The ESS arises if (39) satisfies (38) and (40b) with strict inequality, that is, if

$$\frac{(1+r)\beta^2}{8(1-\beta) + \sqrt{1-2\beta}} < \gamma < \frac{1+r}{16}. \tag{62}$$

The corresponding region is shaded in Figure 23.

For $\lambda = \frac{1}{2}$ a Type-IIg ESS (§B.2.8) does not exist. To see this, we note that the second term on the left-hand side of (53) must be strictly smaller than the right-hand side. For $\lambda = \frac{1}{2}$, the difference reduces to $\zeta(\zeta - 1)(2\beta\zeta^2 - 2\zeta + 1)$, which must be negative, and so $2\beta\zeta^2 - 2\zeta + 1 < 0$. But then the numerator of (51), which reduces to $\frac{1}{2}(2\beta\zeta^2 - 2\zeta + 1) + \frac{1}{4}(1 - 2\zeta)\beta$, is also negative, contradicting $v_2^* > 0$.

It is straightforward to see that, for $\lambda = \frac{1}{2}$, a Type-IIb ESS (§B.2.9) can exist only if $1 < \beta < 3$. We infer $\beta < 3$ from (56). To show that $\beta > 1$, suppose that it is possible to have $\beta \leq 1$. Then, because the left-hand side of (58) increases with β , the inequality can hold only if it holds for $\beta = 1$, that is, if $\frac{7}{8} - \frac{11}{4}\zeta + 4\zeta^2 - 2\zeta^3 \geq 0$, which requires $\zeta \leq 1.12208$. From (54), $v_2^* > 0$ requires $\zeta > \frac{1}{2} + 1/\beta \geq 1.5$, and from this contradiction we infer that $\beta \leq 1$ is false. But 1 is not the greatest lower bound for β . A more refined argument, based on the discussion that follows, shows that a Type-IIb ESS exists only if $\sqrt{5} - 1 < \beta < 3$ (regardless of the value of r).

A Type-IIb ESS will actually exist for $\sqrt{5} - 1 < \beta < 3$, however, only if γ lies in a suitable range; outside this range, the ESS is of a different type. To obtain upper and lower bounds on γ , we first rewrite (57) for $\lambda = \frac{1}{2}$ as

$$\gamma = \frac{\{\beta(2\zeta - 1) - 2\}\{2(1+r)\zeta - r\beta(2\zeta - 1)\}}{8(2\zeta - 1)^3}. \tag{63}$$

Note that the right-hand side of this equation is always positive when $\zeta > \frac{1}{2} + 1/\beta$ (required by $v_2^* > 0$) if $\beta \leq 1 + 1/r$, but is negative when $\zeta > r\beta/\{2(r\beta - r - 1)\} > \frac{1}{2} + 1/\beta$ if $\beta > 1 + 1/r$, which can only happen if $r > \frac{1}{2}$ (because $\beta < 3$). A Type-IIb ESS cannot exist for any value of γ that either exceeds the maximum of the right-hand side of (63) or fails to exceed its minimum, which can be shown to require $\gamma > \max\{0, \frac{1}{2}(\frac{1}{2}\beta - 1)\}$ if $r = 0$ but to require $\gamma > \max\{0, \frac{1}{16}(\beta - 2)(\beta + 2 - \sqrt{(\beta - 2)(\beta + 6)})\}$ if $r = 1$; however, the corresponding expression for intermediate values of r is too unwieldy to be useful, even though it is straightforward to find analytically. Moreover, any attempt to locate the upper bound analytically likewise leads to excessively unwieldy algebra that is scarcely conducive to clarity. Instead, therefore, we have found the upper limit of γ 's range by numerical optimization and presented the results in

Figure 23. Note that this optimization is constrained (possible values of ζ must satisfy $\zeta > 1$, $0 < v_2^* < 1$ and $\partial f / \partial u_3|_{u^*=v^*} > 0$).

A similar analysis applies to a Type-IIId ESS, which (for $\lambda = \frac{1}{2}$) can exist only if $\beta < \frac{3}{2}$ (§B.2.5), and to a Type-IIIf ESS, which can exist only if $\beta < 2$ (§B.2.6). To obtain upper and lower bounds for a Type-IIId ESS, we first rewrite (45) as

$$\gamma = \frac{(1+r)\beta\zeta\{(2-\beta)\zeta-1\}}{4(2\zeta-1)^3} \quad (64)$$

and then optimize it numerically, as described above, to yield the results for $r = 0$ and $r = 1$ that are plotted in **Figure 23**. Likewise for Type IIIf, although we refrain from presenting the corresponding analogue of (64); as noted in §B.2.5, it is excessively unwieldy.

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