Social networks and individual behaviour variation in wild crickets

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: …………………………………………………………..

Abstract

Individuals engage in competitive and cooperative interactions with conspecifics. Furthermore, within any population of interacting individuals there are typically consistent differences among-individuals in behavioural traits. Understanding the importance of both these types of individual-specific behaviours allows us to understand why populations are structured as they are, why individuals show apparently limited behavioural flexibility, and how these elements link to population-level properties. I used extensive video camera monitoring of a population of wild field crickets (*Gryllus campestris*) to study the interactions and behaviours of uniquely identified individuals. I studied the shyness, activity and exploration of individuals of this population across contexts: from young to old and between captivity and the wild. This allowed me to confirm that individuals were relatively consistent across their adult lifetimes for all three traits, but only consistent between captivity and the wild for activity and exploration. I then found that high activity levels were positively related to high mating rates and short lifespans. Crucially, lifetime mating success was not related to activity level, indicating that the trade-off between lifespan and mating success was sufficient to allow variation in activity level to persist across generations. I also found that cricket social network structure is stable across generations despite the complete turnover of individuals every year. This social network structure influences sexual selection, with some male crickets heavily involved in networks of both pre- and post-copulatory competition, yet males are unable to use pre-copulatory competition to avoid post-copulatory competition. Additionally, positive assortment by mating rate between males and females may reduce the fitness of males with high mating rates, as they face stronger sperm competition. Finally, I used actor-based models to determine the factors predicting cricket social network structure and to test and reject the social-niche hypothesis for the maintenance of among-individual variation in behaviour. I also demonstrated that little else is needed in a stochastically changing network aside from positive assortment by mating rate to simulate a population with a similar skew in mating success to the one observed in the real cricket population. These results give insights into the importance of trade-offs and stochasticity in maintaining the extensive variation in the natural world.

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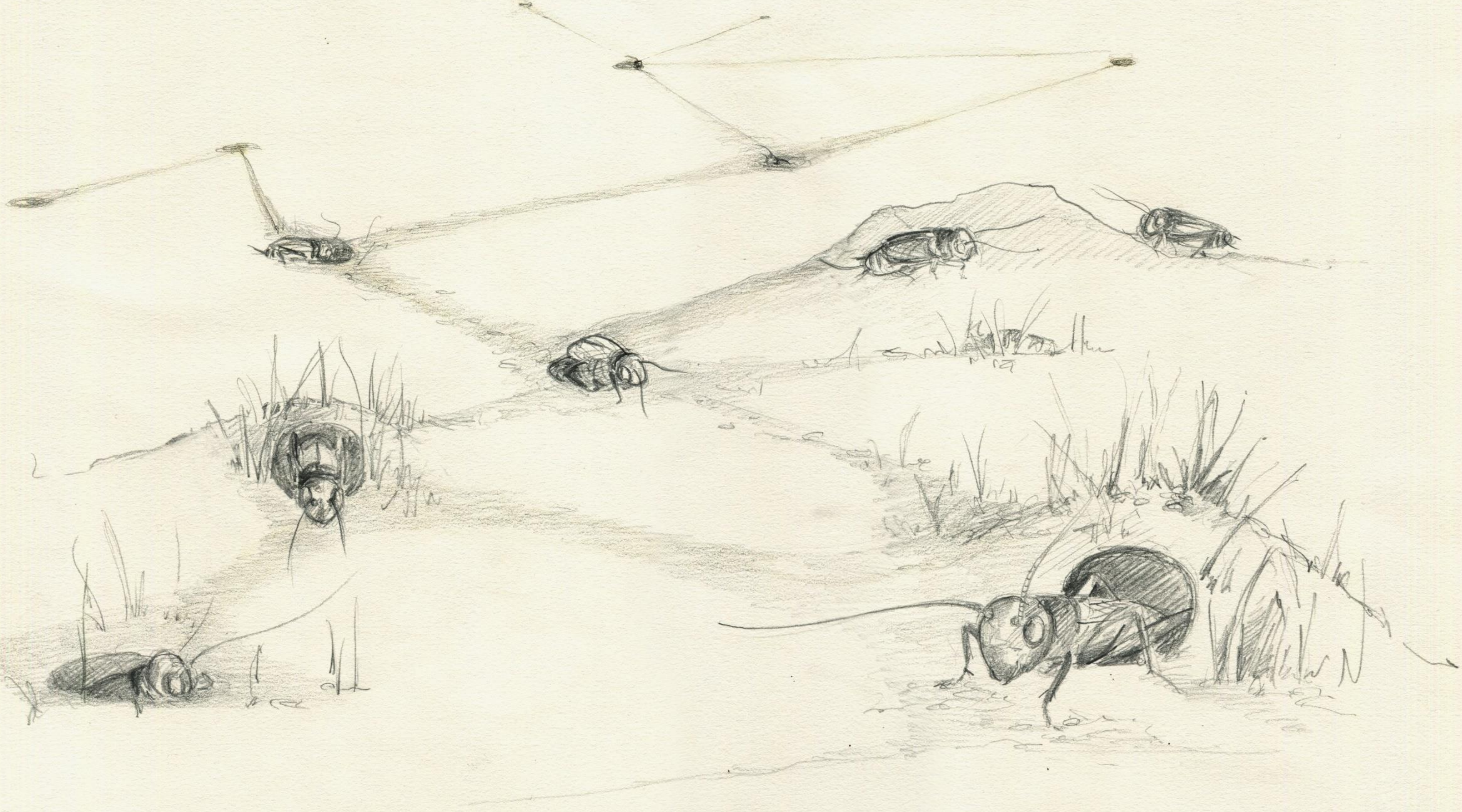

Drawing of crickets by Emma Wood (ewood-art.co.uk)

“Let us strive, on the contrary, within the measure of our capacity, to force a gleam of light from the vast unknown; let us examine and question and, here and there, wrest a few shreds of truth. We shall sink under the task; in the present ill-ordered state of society, we shall end, perhaps, in the workhouse. Let us go ahead for all that; our consolation shall be that we have increased by one atom the general mass of knowledge, the incomparable treasure of mankind.”

- Jean-Henri Fabre, The Life of the Fly (translated by Alexander Teixeira de Mattos)

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1. General introduction

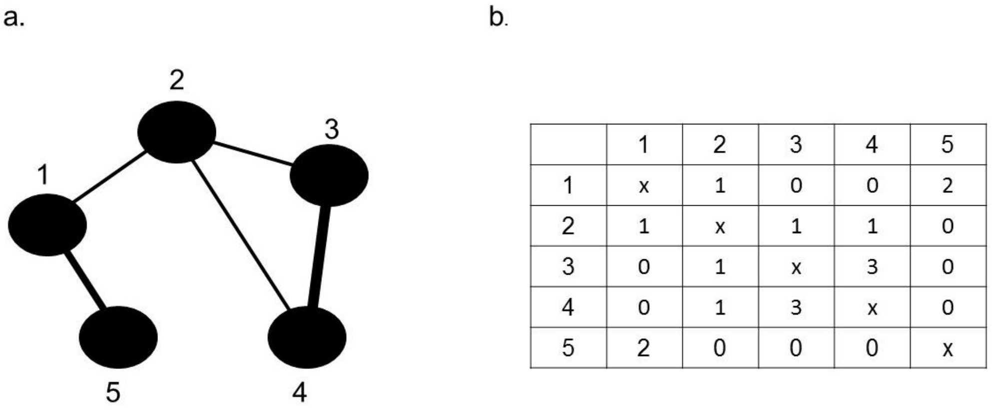
Background

Individuals in a social world

Natural selection has shaped animals to be adapted to their environment. Individuals of all species will engage in competitive interactions with conspecifics for access to mates or resources, and sexual species need cooperative interactions with the opposite sex to mate. These interactions represent an individual's social environment. How this social environment is shaped and creates selective pressures that influence behaviour and fitness is of interest to various fields within biology, from behavioural ecologists to quantitative geneticists (Sih *et al.* 2009; Bijma 2014).

An excellent set of methods to quantify this social environment comes from the field of Social Network Analysis (SNA). In SNA, each individual under consideration is designated as a point or "node", and social interactions or associations between individuals are demarcated by links or "edges" between them (Fig. 1.1a). This network can also be represented as a square matrix, with zeroes in cells indicating that the individuals of that row and column did not interact, and a non-zero term indicating that they did interact and the strength of that interaction (Fig. 1.1b). Note that this is a symmetrical (undirected) network, in that individuals are associating or interacting, rather than one individual directing social behaviour at another. This then means that the matrix is symmetrical about the diagonal.

Originating from sociology, with links to the mathematical and physical sciences, SNA is a burgeoning field in its own right. A vast array of techniques have been developed in SNA, providing a large tool-kit for those interested in animal behaviour to examine the role of the social environment in ecological and evolutionary processes (Croft *et al.* 2008; Krause *et al.* 2014).



	1	2	3	4	5
1	x	1	0	0	2
2	1	x	1	1	0
3	0	1	x	3	0
4	0	1	3	x	0
5	2	0	0	0	x

Figure 1.1. Two different ways of representing a social network: a. shows individuals represented as nodes, with edges drawn between them if they interacted. The thickness of the line corresponds to the strength of that interaction. In b. the same network is represented in matrix form. Note how this matrix is symmetrical about the diagonal, as this network is undirected in that nodes share a connection rather than each sends a connection to the other node.

Primary interests in social network studies include identifying the processes at the level of the individual that predict population-level properties such as network structure (Edelman & McDonald 2014; Ilany *et al.* 2015; Cantor *et al.* 2015; Aplin *et al.* 2015a), and how differences among-individuals in social network metrics such as “degree” (the number of unique connections an individual possesses) or “betweenness” (the importance of the individual for connecting different parts of the network) relate to other traits of those individuals (Croft *et al.* 2009; Formica *et al.* 2011), and what implications these have for fitness (Formica *et al.* 2012; Royle *et al.* 2012; Wey *et al.* 2013).

This focus on individual behaviours and among-individual differences has been a significant research area in behavioural ecology in the last two decades (Desrochers 1992; Wilson 1998; Coleman & Wilson 1998). That there are consistent differences across contexts among-individuals of the same population in behaviours such as activity, risk-taking or sociality (i.e. they display “personality”; Dall *et al.* 2004), is now widely acknowledged (Sih *et al.* 2004a,b; Réale *et al.* 2007). Such variation is ubiquitous (Bell *et al.* 2009), linked to fitness (Smith & Blumstein 2008) and implies various ecological and evolutionary consequences (Wolf & Weissing 2012). Understanding why individuals display such personality, when one might expect behaviour to either be flexible or to converge around adaptive peaks, is now a major focus in evolutionary biology (Mangel & Stamps 2001; Stamps 2007; Dingemanse & Wolf 2010; Wolf & Weissing 2010; Sih *et al.* 2014b).

Studying individuals in the wild

To measure such variation, individuals need to be repeatedly assayed for a behaviour to determine the relative contributions of among- and within-individual variation to the total variation in behaviour. As individuals may change their associates from one moment to the next, repeated measures of the social environment are also required to reliably determine key associates of an individual. This makes the effective identification and regular monitoring of individuals key for both approaches. Observing the free choice of social interactions typically needs to occur in the wild, as otherwise individual movement and hence social interaction choice will be artificially constrained. That studies on any individual-level behaviours need to be conducted in the most natural setting possible has been suggested for a variety of reasons. Individuals may respond to stimuli with unnatural responses when tested in the laboratory (Niemelä & Dingemanse 2014), they may follow unnatural development pathways if they are raised in the laboratory (Archard & Braithwaite 2010), and if populations are maintained in captivity they may evolve so that their behaviours no longer match those expressed by their wild relatives (McDougall *et al.* 2006). This then creates the need for studies on individuals in the wild, where individuals are closely monitored and their traits recorded over their lifetimes, for multiple generations (Clutton-Brock & Sheldon 2010). With advances in marking and tracking technology and reductions in cost, such individual-orientated studies in the wild are becoming more common-place. They do however typically take place on mammals and birds, perhaps as these animal are larger and more recognisable to humans, facilitating their marking and tracking. However, this is problematic if our conclusions about individual variation in behaviours and social interactions in the wild are based on studies on taxa that represent less than 1% of animal life (Kralj-Fišer & Schuett 2014).

This is in contrast to the huge amount of research in evolutionary biology that uses captive invertebrates and fish as study systems. This research is incredibly valuable and has greatly enhanced our understanding of the variation in the natural world. The challenge then is to transplant such study systems into the wild, combining their ease of manipulation, short generation times and variety of behaviours with the ability to tag and monitor individuals over their lifetimes.

WildCrickets

These considerations motivated this thesis. I worked on the WildCrickets project (www.wildcrickets.org) to investigate individual behaviours and social interactions of a wild invertebrate. This project uses a large network of video cameras to record the entire adult lives of a population of the field cricket *Gryllus campestris* (Rodríguez-Muñoz *et al.* 2010, 2011; Bretman *et al.* 2011). *G. campestris* emerge as adults in the spring having spent the winter in burrows they dig themselves as nymphs. A combination of cameras placed over burrows and direct observation for non-video monitored burrows allows the exact emergence date of most individuals to be recorded. Adults are tagged, and once sexually mature, males start to sing by rubbing their wings together to attract mates. Individuals of both sexes move among burrows in search of potential mates (Rost & Honegger 1987; Hissmann 1990), with both sexes benefitting from promiscuity (Rodríguez-Muñoz *et al.* 2010). If a male or a female encounters a member of the same sex at a burrow, typically the pair will fight, with the loser evicted from the burrow (Alexander 1961). Individuals require access to a burrow to shelter from predators and to mate. If they encounter a member of the opposite sex at a burrow, the male will call to the female and present his abdomen to her, to encourage her to mate (Veen *et al.* 2012). The female may then mount him, and he will attempt to attach a spermatophore to her genital opening which then pumps sperm into the female over the following 30 minutes or so. A pair may immediately separate after this, or stay together for several days, generally mating repeatedly. These interactions with members of the same and opposite sex mean that successfully negotiating the social environment is crucial for the fitness of *G. campestris*, even though they are not overtly “social” i.e. they do not feed, move or reproduce in groups. It also means that the vast majority of behaviours relevant to fitness occur at the burrow. Therefore, the network of cameras positioned over the cricket burrows are effective for monitoring the behaviour of individual crickets over their adult lifetimes.

The WildCrickets system therefore presents an ideal opportunity to study the individual behaviours and social interactions of an invertebrate in the wild. Much research into these areas in the wild has focused on mammals and birds, so this system will test whether the theories generated on vertebrates have wider relevance. Furthermore, aspects of field-cricket biology, such as their short adult lifespans and short generation times, allow me to investigate new questions that may not be feasible in organisms that have adult lifespans longer than a typical PhD project, post-doctoral position or research grant.

Thesis structure

My thesis follows two related arms of exploration, which I then link back together in the final chapters:

Cricket “personality”

First, I investigate among-individual variation in a range of behavioural traits in *G. campestris*. Chapter two explores how individuals change their levels of shyness, activity and exploration with age, whether individuals get more different from each other they age, or if the whole population changes in concert. This would have implications for the degree of among-individual variation present in the population if some crickets increased their activity levels with age while some others decreased. I also investigate whether correlations between traits exist among- and/or within-individuals, as correlations at the population level could be created by either relationship.

In chapter three I determine whether tests of shyness, activity and exploration in the laboratory and/or environmental conditions can predict equivalent behaviours in the wild. That captive behavioural assays predict analogous behaviours in the wild is often assumed, but very rarely demonstrated conclusively.

Chapter four investigates whether the among-individual variation in activity fits into a life-history syndrome. This is a common prediction, but robust empirical tests of the key trade-offs supposed by this model are lacking. I also quantify how much of the overall variation in behaviour this long-term consistency accounts for, alongside short-term consistency and within-individual change. Splitting variation in behaviour in this way and then comparing them in the same units (% of variance explained) is not yet a common approach, but allows us to directly compare the contribution of different sources of variation, and so their relative importance, and to evaluate theories that attempt to account for different kinds of variation.

Cricket social networks

The second arm of my thesis explores elements of the social network structure of the population of crickets. In chapter five I investigate questions in sexual selection, such as whether pre-and post-copulatory competition are linked at the individual and dyadic level, using techniques from SNA. I also determine whether the structure of the mating network is likely to increase or decrease the variance in reproductive success due to assortment by promiscuity.

The topic of chapter six is whether the social network structure of the cricket population is stable over evolutionary time. I use data I have collected along with data from earlier years of the WildCrickets project to construct exponential random graph models of the cricket social network in six years, spanning eight generations. I then determine whether these network models can predict the networks in alternative years, and what other difference between the years relate to the difference in predictive ability.

Chapter seven is a methods chapter, introducing Stochastic Actor-Orientated Models (SAOMs) in the R package “RSiena”. This technique can be used to investigate dynamic change in network structure, alongside changes in other traits, while incorporating various covariates. These models were developed in sociology, yet have huge, but as yet unrealised, potential in behavioural ecology. I describe the models, provide examples, and make recommendations on when a SAOM is, and is not, appropriate. Online supporting information for this chapter gives a walk-through, R code and data, for readers to try applying a SAOM themselves.

Chapter eight builds on the previous chapter, using SAOMs to conduct dynamic analyses of both the fighting and mating networks of *G. campestris.* This chapter also serves to link together the two arms of the thesis; I model both changes in social network structure and changes in individual activity level. I determine whether fighting behaviour is related to activity level, and concurrently model the development of the fighting and mating networks, including testing for relationships between the two. This allows us to understand the social network structure of the population and to account for the strong skew in mating success observed in *G. campestris*, which is common to many animal populations.

I close with a general discussion in chapter 9. I discuss the findings of multiple chapters when they relate to the same questions, and suggest approaches that would extend our understanding of both variation in individual behaviour and variation in social interactions among populations.

The particular rationale and methodology is provided within each chapter. Each is designed to stand alone, having been either published, submitted for publication or in preparation for submission. As such, there is some necessary repetition of background information and methodology. I hope this is not overly tedious. Chapters that have been published or submitted will have subsequently received minor edits to better fit into the thesis, and chapters will refer to each other, either in published form or by chapter number, when relevant. I use “we” in all chapters except the general introduction and discussion, as each chapter was produced while working with my supervisors Tom Tregenza and Rolando Rodríguez-Muñoz. In the case of chapters having been published or in review, the full citation, including other co-authors, is given at the start of the chapter. The address for authors is: “Centre for Ecology and Conservation, University of Exeter, Penryn, Cornwall, TR109FE, UK” unless otherwise stated.

2. Dynamics of among-individual behavioural variation over adult lifespan in a wild insect

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Abstract

Investigating patterns of among and within-individual trait variation in populations is essential to understanding how selection shapes phenotypes. Behaviour is often the most flexible aspect of the phenotype, and to understand how it is affected by selection, we need to examine how consistent individuals are. However, it is not well understood whether among-individual differences tend to remain consistent over lifetimes, or whether the behaviour of individuals relative to one another varies over time. We examined the dynamics of four behavioural traits (tendency to leave a refuge, shyness, activity and exploration) in a wild population of field crickets (*Gryllus campestris*). We tagged individuals and then temporarily removed them from their natural environment and tested them under laboratory conditions. All four traits showed among-individual variance in mean levels of expression across the adult lifespan, but no substantial differences in how expression changed with age. There were mixed results for how among-individual variation changed with age, indicating no clear pattern. Our findings reveal seldom examined changes in the means and variances of traits over the adult lifetime of wild individuals. Such changes will have important implications for the relationship between behavioural traits, life-histories and fitness and the consequences of selection on wild individuals.

Key words: animal personality, behavioural reaction norms, Gryllus, plasticity, wild crickets.

Introduction

Explaining variation in wild populations is crucial to the study of evolution. Evolutionary and ecological studies have often considered behavioural variation among individuals in a single population to be noise surrounding adaptive peaks (Wilson 1998). However, recent studies have emphasized that such among-individual behavioural variation is persistent and likely to be adaptive (Wilson 1998; Dall *et al.* 2004; Smith & Blumstein 2008; Bell *et al.* 2009). Consistent among-individual behavioural variation has classically been studied in traits such as boldness-shyness, exploration, aggressiveness or activity. These traits, often referred to as "personality traits" are thought to reflect underlying tendencies and hence are expected to influence other behaviours across contexts in a consistent way (Réale *et al.* 2007). However, an individual's phenotype has the potential to exhibit plasticity over its lifetime (Nussey *et al.* 2007). Therefore, adaptive explanations for the maintenance of consistent behavioural variation among individuals must deal with potential age-related behavioural variation within individuals (Dingemanse & Réale 2005; Schuett *et al.* 2010; Kight *et al.* 2013).

Two key aspects of behavioural consistency are among-individual differences (i.e., the extent to which an individual is reliably different from other individuals), and the absolute variation (or lack of variation) in a trait over time within individuals, also known as repeatability and stability (Nussey *et al.* 2007; David *et al.* 2012). Few studies have examined how these variance components change over time. Human behaviour is known to become more consistent with age, with reinforcement of behaviour suggested as a key mechanism (Roberts & Del Vecchio 2000), but studies on non-morphological or life-history traits in wild animals are less common (see Wilson *et al.* 2008 and Brommer 2013b for reviews). Work on *Drosophila* has indicated that additive genetic variance in fecundity follows a U-shaped curve, with lowest variance at intermediate ages (Tatar *et al.* 1996), while mortality shows the opposite pattern (Promislow *et al.* 1996). Furthermore, heritability in laying date of wild mute swans (*Cygnus olor)* also followed a U-shaped pattern (Charmantier *et al.* 2006), with highest heritability at the oldest ages. Dingemanse *et al.* (2012) measured exploratory behaviour over time in great tits (*Parus major*) and found that, in four separate populations, among-individual variance was higher in repeated tests compared to an initial test. They did not however model whether variance changes continually with individual age, which would allow us to assess whether a continual increase or the U-shaped pattern exists as found in the above studies.

A meta-analysis by Bell *et al.* (2009) on the repeatability of behaviour found that juveniles are more consistent than adults. However, there was no comparison for different stages of the adult life, yet as this is when reproduction takes place it is when the heritability of traits is relevant. Repeatability is related to heritability (but does not necessarily set the upper limit; Dohm 2002) and so influences the expected response to selection. If repeatability estimates do differ depending on the age of the organism, then measurements at one point in time may not adequately reflect the true repeatability of that trait. This could lead to over- or under-estimates for response to selection and rate of evolutionary change (Charmantier *et al.* 2006). What is required are repeated estimates of variance components over the adult lifetime of individuals. Furthermore, recent reviews have highlighted how individuals within a population may not all respond to environmental change or aging in the same way (Nussey *et al.* 2007; Dingemanse *et al.* 2010). If individuals change with age differently, their level of behaviour relative to others can differ depending on the age they are measured at (Kluen & Brommer 2013; Brommer 2013c). The study of relationships between the trait and other behavioural or life-history traits that are more stable over time is common (Dingemanse *et al.* 2004; Brown *et al.* 2005; Minderman *et al.* 2009; Amy *et al.* 2010; Cole & Quinn 2012; Patrick *et al.* 2012; Adriaenssens & Johnsson 2013; Aplin *et al.* 2013; Bouwhuis *et al.* 2014). However, if correlations or rank orders of behaviours change over time, then detecting such associations will entirely depend on when measures are taken, and could give wildly different results (Kluen & Brommer 2013). For instance, Wolf *et al.* (2007a) predict that individuals with high future reproductive fitness will take fewer risks, while Sih & Luttbeg (2010) predict that risk taking and reproductive success are in fact positively related. Teasing these hypotheses apart without traits that have rank-order stability over the reproductive lifetime of individuals is difficult, yet crucial if we are to understand the evolution of animal personalities.

Measurement over the adult lifespan requires the individual to be identified when it becomes adult, and followed continually afterwards. This is hard to do in wild animals (but see: Martin & Réale 2008; Réale *et al.* 2009; Dingemanse *et al.* 2012; Aplin *et al.* 2013), hence studies looking at behavioural change over lifetimes have tended to use animals raised in captivity (Sinn *et al.* 2008; Herde & Eccard 2013). However, accidental selection by breeding populations of study organisms in captivity could lead to unnatural decreases or increases in among-individual variation, or mean levels of behaviour quite different from that expressed in the wild (McDougall *et al.* 2006; Archard & Braithwaite 2010). Even those animals that are offspring of wild parents may show unusual developmental trajectories due to captivity conditions (Archard & Braithwaite 2010). Therefore, studies on wild populations are crucial.

The paucity of repeated measures on wild animals' behaviour is especially true for invertebrates, which are often difficult to study in the wild because of their small size (but see Briffa & Greenaway 2011; Pinter-Wollman *et al.* 2012). However, insects such as field crickets are good candidates for the study of behaviour in wild animals, due to their regular use of particular burrows which serve as refuges from predation (Rodríguez-Muñoz *et al.* 2011). This makes it possible to tag individuals and locate them in the environment by monitoring their burrows (Rost & Honegger 1987; Hissmann 1990; Rodríguez-Muñoz *et al.* 2010, 2011). Moreover, various field cricket species have been extensively used in behavioural studies conducted in the laboratory (Hedrick 2000; Hedrick & Kortet 2006, 2011; Niemelä *et al.* 2012b,a).

Here we study the behaviour of a population of the European field cricket *G. campestris* in the wild. We captured all the members of an isolated population, tagged them, and released them back into the field. At the same time we assayed their behaviour for four traits. Subsequently, we regularly recaptured and re-tested them, to examine how the repeatability of those traits changed over time and if behaviour of individuals in relation to each other varies over their adult lifetime. We also investigated correlations among behaviours at both the among- and within-individual level. Separating phenotypic correlations into these two components is essential to avoid erroneous conclusions about correlations, as among-individual correlations can mask within-individual correlations (David *et al.* 2014). Furthermore, it allows us to determine whether there is potential for correlated plasticity of traits (Dingemanse & Dochtermann 2013; Brommer 2013a), which suggests that traits form "evolutionary characters" (Araya-Ajoy & Dingemanse 2014).

We predict that patterns of among-individual variance will follow similar patterns to that previously observed in behavioural traits and so increase with age (Roberts & Del Vecchio 2000; Dingemanse *et al.* 2012) and this to be reflected in estimates of repeatability. We then predict that individuals will be stable over their lifetime in their ranking relative to each other (Brommer 2013b). Finally, a meta-analysis suggests that the direction of correlations is typically weakly positive (Garamszegi *et al.* 2012) so we refrain from making any strong predictions regarding the correlations, especially as few studies have split phenotypic correlations into both among- and within-individual correlations.

Methods

Study subjects

The study was carried out at the “WildCrickets” project field site in Northern Spain (Rodríguez-Muñoz *et al* 2010; Bretman et al 2011). In this univoltine species, nymphs and adults spend most of their lives in or around burrows that they individually dig in the ground and defend from other conspecifics. At our study site, eggs hatch from May to July and nymphs remain active until October-November when they start diapause as late instars. They become active again between late January and March, when they start to forage and undergo one or two more nymphal moultings before they moult into adults in April-May. Once they become sexually mature, the males will sing to attract females, and both sexes will start moving frequently among burrows in search of mates. Males and females will share a burrow, but within-sexes there are fights for possession of burrows and no co-habiting (Rodríguez-Muñoz *et al.* 2011). We collected data during April-June when adults are active, in 2013 and 2014. Data from each year are pooled and differences modelled using year as a fixed effect (see Statistical analysis below). Using a network of video cameras (120 in 2013 and 133 in 2014) and regular direct observations for non-video monitored burrows, we were able to determine the occupation of burrows by nymphs, and the adults’ emergence dates. We began trapping and testing newly-emerged adults three days after their emergence date (3.76 ± 3.33, mean ± SD). Trapping typically ran from 08:00 – 16:00 GMT. We fixed a vinyl tag with cyanoacrylate glue with a unique alpha-numeric code to the pronotum of individuals. This method is the outcome of many years of testing; only 1-4% of crickets per year need to be re-tagged due to losing their original tag. We used a trap designed by Luke Meadows (https://crickettrapping.wordpress.com/). This is very effective at catching any cricket that attempts to emerge from the burrow, reducing the effect of trap-shy or trap-happy individuals (Biro & Dingemanse 2009; Carter *et al.* 2012b). Once caught, we placed the crickets in individual 150 ml plastic containers then transferred them to the cricket processing area in a building 30m away from the centre of the meadow. Traps were checked every 15 minutes to ensure crickets did not languish in the trap. Once a cricket was caught, to prevent other animals (including other crickets) from taking over the burrow, the trap was left blocking the entrance while the cricket was being tested. We tested crickets on the day they were caught, placing them in controlled temperature room at 20.12 ± 0.82 °C (mean ± SD) for video observation. The total time a cricket was in captivity was 90-120 minutes, with an additional 40 mins at first capture for the tagging procedure. After testing and tagging, crickets were returned to the burrow they were caught from. Subsequent to the first capture, we re-caught and re-tested each individual cricket at time intervals of around ten days, starting from the date of the first post-emergence test and continuing until the individual was no longer observed alive.

Experimental Set-up

We conducted tests in 16 open-topped plastic boxes 290 x 201 x 212 mm, with a piece of A4 paper lining the bottom. The paper was replaced between consecutive tests and the boxes wiped first with soapy water and then ethanol to remove any pheromones released by previous crickets. We monitored each box from above with a fixed camera, connected to a computer in the adjacent cricket processing area. We used software designed for CCTV surveillance (iCatcher, www.icode.co.uk/iCatcher), which has been extensively customised by the developer to facilitate its use in biological studies. We tracked and recorded the movements of each cricket during the tests. This allowed up to 16 crickets to be tested simultaneously. Before the start of the test, we placed the focal crickets in opaque cylindrical tubes (80 x 20mm), with detachable lids at either end. We placed each sealed tube on its side into one of the boxes against the centre of one end of the box, with the head of the cricket facing towards the centre of the box. Once we had placed all crickets in position, we removed the lids at the same end as the crickets' heads and left the room. We recorded the exact time of lid removal for each focal cricket, but within a test these differed by less than one minute. Tests ran for 30 minutes.

After a 30 minute test we returned crickets to their 150ml plastic containers and left them in an isolated room for another 30 minutes. We then repeated the test described above, placing crickets into boxes irrespective of the box they had previously been tested in. After these two tests, we weighed and tagged newly emerged adults (see Rodríguez-Muñoz *et al.* 2010 for details). We released tagged adults by returning them to the burrow from which they had been collected, ensuring that they re-entered the burrow. Total handling time was similar (within 30 minutes) for all crickets being tested as we could test one set of individuals during the 30 minutes isolation period of another set. Unless otherwise stated, for all analyses we only used the first of the two tests carried out for each day the cricket was captured. We also ran analyses for the less conservative approach of using the second trial to measure traits that required a cricket to leave the tube when the cricket failed to emerge on the first trial, and found qualitatively similar results (not shown).

Adult male crickets start singing (a shrill sound made by rubbing the fore-wings together to attract mates) a few days post-emergence, indicating that they are sexually active. This could alter the perceived environment for crickets in neighbouring boxes. To prevent bias resulting from occasional singing by one or more of the adult males being tested, we played a recording of four male crickets singing throughout tests that involved sexually active adult crickets. This recording was made in the same meadow at a similar temperature to the experimental conditions. This procedure standardised the auditory environment to one in which song from ≥4 males was always present.

Data collection

We examined four behaviours. First, tendency to leave the tube, with whether or not the cricket left the tube at all in the 30 minutes as a binary response variable. Second, position on the boldness-shyness continuum was measured as "shyness" and defined as the latency between the start of the test and the time when the cricket's head emerged from the tube (Hedrick 2000; Hedrick and Kortet 2006; 2011; Niemelä et al 2012a, b). This measure is strongly correlated with the time until the entire body leaves the tube (Hedrick & Kortet 2006) and the time until a cricket becomes active inside the tube (Niemelä *et al.* 2012b). The third behaviour was activity: general tendency to move around (Réale *et al.* 2007; Tremmel & Muller 2012). Using iCatcher, we set eight unique virtual trip wires across the box in a lattice, four vertical and four horizontal, with each wire covering half the length or width of the box, giving the appearance of a three by three square grid. Once the cricket's head emerged from the tube, iCatcher counted the number of times the cricket crossed any wire after it had emerged from the tube. An individual's activity score was the number of trip wires it crossed per second it spent outside of the tube. We used an offset of the log of the number of seconds the cricket was outside the tube, allowing us to use the raw number of tripwires the cricket crossed as a response, and so a Poisson distribution error structure. Finally, we quantified exploratory behaviour (Réale *et al.* 2010). This was the number of unique trip wires a cricket crossed in the first minute after it had left the tube. This represents the crickets' tendency to visit different areas of the box rather than repeatedly being active in one corner.

These four traits were chosen as having the potential to be to ecologically-relevant to our study population. Both sexes build and spend a lot of time at burrows, which are used as a refuge from predators, while also moving among other burrows in the field to find potential mates. Therefore, our measures of tendency to leave the tube and shyness closely mimic the behaviour crickets express in the field when leaving their burrows, while activity and exploration reflect general movement among burrows and willingness to visit new burrows respectively.

Statistical analyses

We conducted all analyses in R ver. 3.0.2 (R Core Team 2013), using the package MCMCglmm (Hadfield 2010a). First we constructed random regression (RR) models (also known as random slope models) for each trait (Nussey *et al.* 2007; Dingemanse *et al.* 2010). RRs model each trait as being linearly predicted by age for each individual, as in Edenbrow & Croft (2011). We only consider a linear relationship, as the estimation of high-order polynomials requires a larger number of measures per individual than we could collect. We fitted an intercept and slope of a regression line for each individual, so we can estimate the among-individual variation in these intercepts and slopes as well as estimate the intercept-slope correlation (Nussey *et al.* 2007; Dingemanse *et al.* 2010). RRs fit individual functions of continuous covariates (in our case, age) as random effects (Henderson 1982) and have been extensively used to investigate ontogeny (e.g. estimating individual growth curves; Wilson *et al.* 2005). Following Martin *et al.* (2011), we retained individuals that only recorded traits scores on one trial, as although they cannot contribute to estimates of variance among slopes they can contribute to estimates of variance among intercepts. When the covariate has been centred, significant among-individual variation in the intercepts of the RRs indicates that individuals consistently differ in the trait at the mean value of the covariate. Significant among-individual variation in slopes indicates that individuals change with age differently. A significant intercept-slope interaction indicates that an individual’s mean trait level is related to the way the trait changes with age. Furthermore, RRs can be used to estimate the change in among-individual variance over time (Brommer 2013c). This gives an estimate of the continuous change in among-individual variance over time, which we plot for each trait.

We also wished to get point estimates for both among-individual and residual variance across the adult lifespan of our individuals. As described above, each time we captured the crickets they were tested twice, and for this analysis this second test is also used. Therefore, we can calculate point estimates for the repeatability of cricket behaviour for the first capture and each subsequent recapture. To avoid confounding effects from the possibility that individuals that die at a young age are over-represented at early ages and may also differ systematically from longer lived individuals, we only included crickets that at some point were re-caught at 30 days old or older. To estimate the among-individual and residual variance for each capture, an interaction between ID and capture number (1-4) was included in the among-individual and residual covariance structure of the mixed model, giving separate estimates for among-individual and residual variance for each of the captures. There were in fact four crickets who were captured a fifth time. However, this is not a great enough number to estimate the variance components with any confidence, so these tests (but not the other test for these crickets) were excluded. We calculated repeatability for non-Gaussian data following Nakagawa & Schielzeth (2010), using their definition of repeatability as the proportion of variance that is reproducible across repeated measures of an individual. We calculate repeatability scores from the posterior distributions of among-individual and residual variances, and provide the mode and the 95% credible intervals (CRIs) of the resulting distributions.

To determine whether shyness, activity and exploration were correlated with one another, we built a multivariate mixed-effect model. We could not include tendency to leave the tube in this model as all three traits required a cricket to leave the tube. We set the relationship between shyness and the offset (log of the number of seconds outside of the tube) for activity as -1 (as they are the inverse of each other) and the relationship between the offset and exploration as 0. We extracted the among-individual and residual variances and covariances for the traits, allowing us to calculate the among- and within-individual correlations (Hadfield 2010a; Dingemanse & Dochtermann 2013; Brommer 2013a). Correlations are calculated by dividing the covariance of the traits in question by the square root of the product of their variances and judged important if the 95% CRIs do not cross zero. The fixed effects in each model were sex (males as the contrast), age (number of days from emergence date), laboratory temperature (°C), mass at first capture (grams) and year (a two-level factor, 2013 or 2014, with 2014 as the contrast). Age, mass and temperature were all mean centred. We also included the test number as a fixed effect, to allow us to estimate and control for any habituation effects. Finally, we also included the maximum age at which that cricket was ever tested at as a fixed effect, also mean centred. This allowed us to model the effect of selective disappearance, and so measure both within-individual change with age and among-individual difference between ages (van de Pol & Verhulst 2006). In the multivariate model the fixed effects were modelled to have separate effects on each response variable. The posterior distributions modes (PDMs) and the CRIs for random and fixed effects from each model are given in the Tables 2.1-4. The effect of a factor is modelled as a frequency distribution of effect strengths. The importance of among-individual variance in intercepts and slopes and residual variance is judged by the distance from zero and the spread of the 95% CRIs. If the variance is truly 0 the CRIs will have zero coverage (Higgins & Thompson 2002), so narrow CRIs near 0 indicate a lack of variance in that component. Importance of the fixed effects and covariances is judged by whether the 95% CRIs overlap zero. Tendency to leave the tube was modelled with an ordinal error structure, a logit link function and additive errors. The residual variance cannot be estimated simultaneously with the among-individual variance in a model with a binary response as it is wholly described by the mean, so we fixed it to one (Hadfield 2010b). Shyness and activity were modelled with a Poisson distribution, a log-link function and additive errors, exploration with a Gaussian distribution and additive errors. As the tendency to cross zero trip wires is modelled in the analyses for activity, those scores are removed for the analyses of exploration. This allows us to fit a Gaussian distribution; without removing the zeros the distribution is not amenable to analysis. Models were assessed for appropriate mixing and smooth posterior distributions of effects. Priors were made less informative and number of iterations increased until satisfactory model plots were obtained.

Interpreting results

Each of the effects is modelled as a distribution of the likely influence of that effect, defined by a mode (PDM) and its lower and upper 95% credible intervals (LCRI & UCRI respectively). Fixed effects are judged significant if the estimates of the CRIs do not cross zero, while MCMCglmm also provides the pMCMC score, useful to assess “significance” in analogy with studies using a frequentist framework. Random effects are measures of variance and so (except in unusual circumstances; Smith & Murray 1984) are always above zero. Therefore, their importance is judged by the spread for the CRIs and comparison with the residual variance. Model selection cannot be based on information criteria as the deviance information criterion (DIC) calculated by MCMCglmm is not “focused” appropriately for non-Gaussian data (Hadfield 2012) nor can models be compared with F or Likelihood ratio tests as the effects do not have effect sizes. Instead we constructed the model with all terms of interest, and interpreted the effect of each variable in the maximal model (following convention e.g. Sardell *et al.* 2012).

Results

Among and within-individual change with age, and change in among-individual variance with age

In total we performed 2474 assays over 582 individuals. Of these, 1248 came from the first test of a recapture, and were used in the RR to model the tendency for a cricket to leave the tube. This is slightly more than half the total number of tests as some crickets were not tested twice at a recapture due to time constraints. Results from this model are presented in Table 2.1. In summary, there was substantial among-individual variance in intercepts, but not in slopes, and the intercept-slope correlation was not significant. Crickets were more likely to leave the tube as they aged and when it was warmer. Males showed a non-significant tendency to be less likely to leave the tube. There was no evidence for selective disappearance, so crickets with longer adult lifespans did not have a different tendency to leave the tube to crickets with short adult lifespans. Mass did not influence tendency to leave the tube. Crickets showed no evidence of habituation as the effect of test substantially overlapped zero, and crickets were equally likely to leave the tube in each year.

The among-individual change with age (= within-indiviual change with age (fixed effect of age) + effect of selective disappearance (fixed effect of maximum age); van de Pol and Verhulst 2006) was of the same sign as the within-individual change with age. This indicates that an individual was more likely to leave the tube as it aged and older adults are more likely to leave the tube than younger adults. This correspondence in sign between the among-individual change and the within-individual change was found for all the traits we examined.

Table 2.1: The tendency of the crickets to leave the tube. Given are the posterior distribution modes (PDMs) and the 95% credible intervals (CRIs). V_A refers to among-individual variance. In models with a binary response when estimating the among-individual variance the residual variance is entirely defined by the mean (Hadfield 2010b), and so it is not given. Fixed effect names are underlined, those that have 95% CRIs that do not cross zero are also in bold.

Component	***PDM***	***Lower 95% CRI***	***Upper 95% CRI***	***pMCMC***
V_A in Intercepts	0.680	0.304	1.353	NA
V_A in Slopes	0.002	< 0.001	0.006	NA

Intercept - slope covariance	0.009	-0.022	0.032	NA
Intercept - slope correlation	0.058	-0.344	0.922	NA
Model intercept	1.066	0.484	1.798	NA
Age	**0.060**	**0.024**	**0.093**	**0.001**
Mass	-0.007	-0.933	1.124	0.863
Temperature	**0.433**	**0.296**	**0.651**	**< 0.001**
Sex	-0.219	-0.566	0.015	0.077
Test	-0.095	-0.313	0.106	0.386
Maximum age	-0.007	-0.019	0.003	0.176
Year	-0.180	-0.471	0.158	0.318

In 61% of the above assays crickets left the tube. These measures were used for the RRs for shyness and activity. Of these 763 assays, a cricket crossed zero trip wires in one minute 22% of the time, leaving 596 measures for the RR of exploration. The results from these RRs are presented in Table 2.2.

Table 2.2. Results of random regression models for shyness, activity and exploration. The relative importance of among-individual variance (V_A) in intercepts and slopes, and residual individual variance is judged by the distance of the posterior distribution mode (PDM) from 0 and the spread of the 95% credible intervals (CRIs). Effects that have 95% CRIs that do not cross zero are in bold. Fixed effects are underlined.

Trait	***Component***	***PDM***	***Lower 95% CRI***	***Upper 95% CRI***	***pMCMC***
Shyness	V_A in Intercepts	0.125	0.030	0.238	NA
	V_A in Slopes	0.003	0.003	0.004	NA
	Intercept-slope covariance	-0.001	-0.006	0.004	NA
	Intercept-slope correlation	-0.044	-0.280	0.144	NA
	Model intercept	5.570	5.227	5.936	**NA**
	Age	**-0.018**	**-0.041**	**-0.003**	**0.021**
	Mass	-0.227	-0.862	0.411	0.479
	Temperature	**-0.162**	**-0.263**	**-0.052**	**0.004**
	Sex	-0.187	-0.341	0.0127	0.074
	Test	0.054	-0.083	0.159	0.558
	Maximum age	0.003	-0.005	0.009	0.651
	Year	**-0.360**	**-0.565**	**-0.090**	**0.01**
	Residual variance	1.010	0.843	1.152	NA

Activity	V_A in Intercepts	0.891	0.523	1.308	NA
	V_A in Slopes	0.003	0.002	0.005	NA
	Intercept-slope covariance	**-0.040**	**-0.060**	**-0.022**	NA
	Intercept-slope correlation	**-0.769**	**-0.869**	**-0.575**	NA
	Model intercept	-3.362	-3.815	-2.883	NA
	Age	**0.060**	**0.037**	**0.084**	**< 0.001**
	Mass	0.377	-0.493	1.485	0.316
	Temperature	**0.286**	0.245	0.559	**< 0.001**
	Sex	-0.197	-0.494	0.065	0.139
	Test	-0.095	-0.237	0.061	0.290
	Maximum age	**-0.016**	**-0.028**	**-0.004**	**0.011**
	Year	0.177	-0.191	0.461	0.418
	Residual variance	0.480	0.367	0.615	NA
Exploration	V_A in Intercepts	0.517	0.047	1.165	NA
	V_A in Slopes	0.006	0.004	0.008	NA
	Intercept-slope covariance	-0.012	-0.038	0.004	NA
	Intercept slope correlation	-0.228	-0.514	0.058	NA
	Model intercept	3.927	3.171	4.593	NA
	Age	0.019	-0.018	0.052	0.375
	Mass	0.565	-0.898	1.773	0.533
	Temperature	**0.483**	**0.227**	**0.671**	**< 0.001**
	Sex	-0.062	-0.433	0.344	0.814
	Test	-0.090	-0.321	0.130	0.484
	Maximum age	0.004	-0.013	0.019	0.734
	Year	**0.684**	**0.172**	**1.104**	**0.007**
	Residual variance	3.570	2.858	4.222	NA

For shyness (Fig. 2.1), there was among-individual variance in intercepts, so individuals showed consistent differences in shyness, but there was again little among-individual variance in slopes and no intercept-slope correlation. Crickets left the tube faster when older, at higher temperatures, and in 2014. Males showed a non-significant tendency to be shyer than females. Again there was no evidence of habituation, selective disappearance or mass.

There was among-individual variance in intercepts for activity (Fig. 2.2), but little in slopes, and there was a significant, negative intercept-slope correlation. Crickets were more active when older and at hotter temperatures, and short-lived crickets were more active than long-lived crickets. Otherwise there was no effect of sex, mass, year or habituation.

For exploration (Fig. 2.3), there was among-individual variance in intercepts, little in slopes, and no intercept-slope correlation. Exploration increased with temperature, and was higher in 2014 than in 2013. Males showed a non-significant tendency to be less exploratory. Otherwise there was no effect of selective disappearance, mass, or habituation.

All traits showed a similar pattern in the change of the among-individual variance with age. There was a small decrease in among-individual variance from the youngest to the mean age, then a large increase through to old age. This appears to be a mixture of a steady increase and a U-shaped curve (Fig. 2.4).

Differences in variance estimates across recaptures

Across tests 1-4 there were 318, 339, 310 and 150 measures from crickets that survived to be tested at greater than 30 days old, including both tests from each capture. Average ages at each recapture were 4.2, 21, 32 and 40 days for tests 1-4. For crickets that left the tube, and so were included in the analyses for shyness and activity, there were 135, 247, 242 and 133 measures for tests 1-4. The average ages over tests 1-4 for this subset was 4.9, 21, 32 and 41. There were 99, 210, 200 and 123 measures of a non-zero exploration score across tests 1-4. Average ages in this subset was 5.2, 21, 32 and 41.

Estimates of among-individual and residual variance, along with repeatability estimates for each of the four traits is presented in Table 2.3. Tendency to leave the tube showed repeatability between 0.36 and 0.5, with no clear pattern across captures. Shyness only had a repeatability above zero (based on the lower 95% CRIs) once, for crickets in the third capture (0.29). Activity showed an initial medium level of repeatability (0.383) with a very consistent and low level of repeatability for the remaining three tests (all just under 0.1).

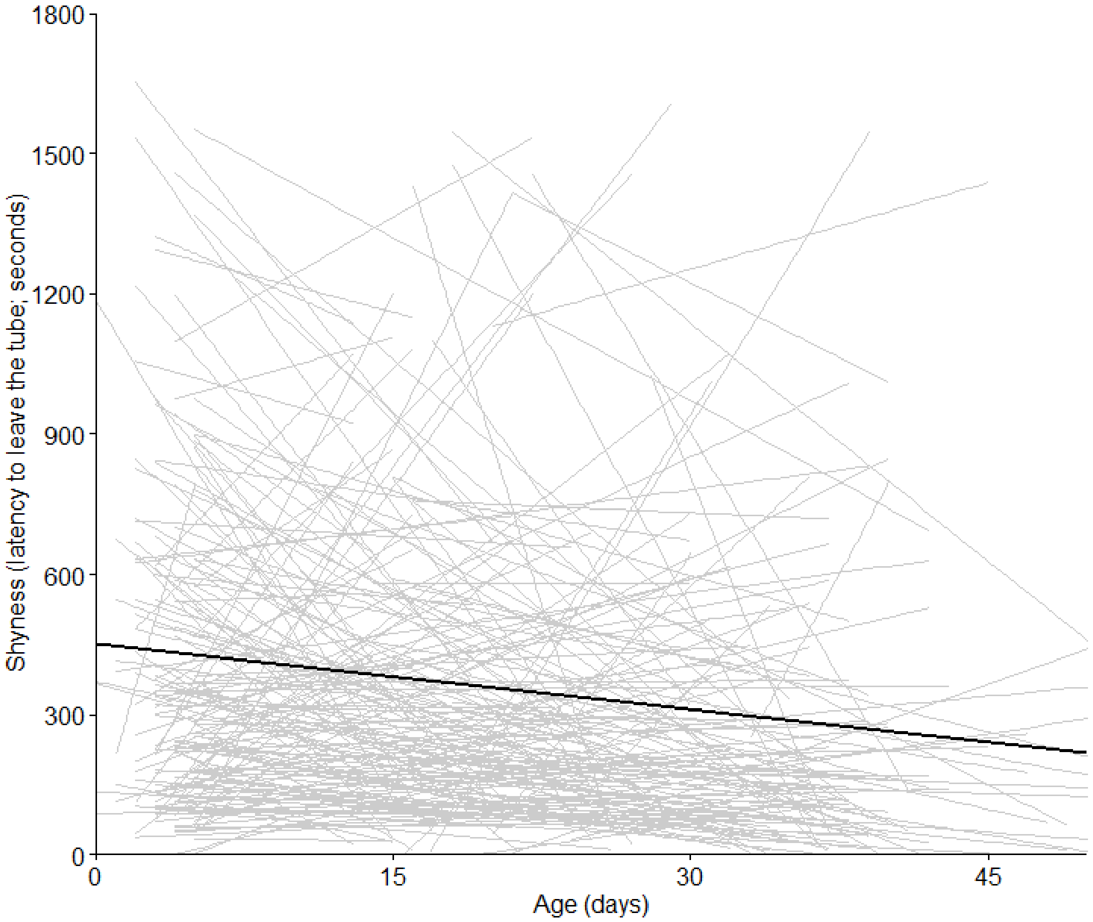

Figure 2.1. Individual plots of shyness change with age, with a linear trend line through each individual’s data points in grey and a population line in black. Shyness showed an important degree of among-individual variation in intercepts, but not in slopes and there was no intercept-slope correlation (r = -0.044). The fixed effect of age was negative, so individuals decreased their shyness with age (see Table 2.2 for full results).

Apart from the 3rd test these were significantly lower than the repeatability at test one. At no capture did crickets show non-zero repeatability for exploration. Fixed effects were included in the models but are not shown as the confidence of the estimate will be inflated by including both test for a given capture.

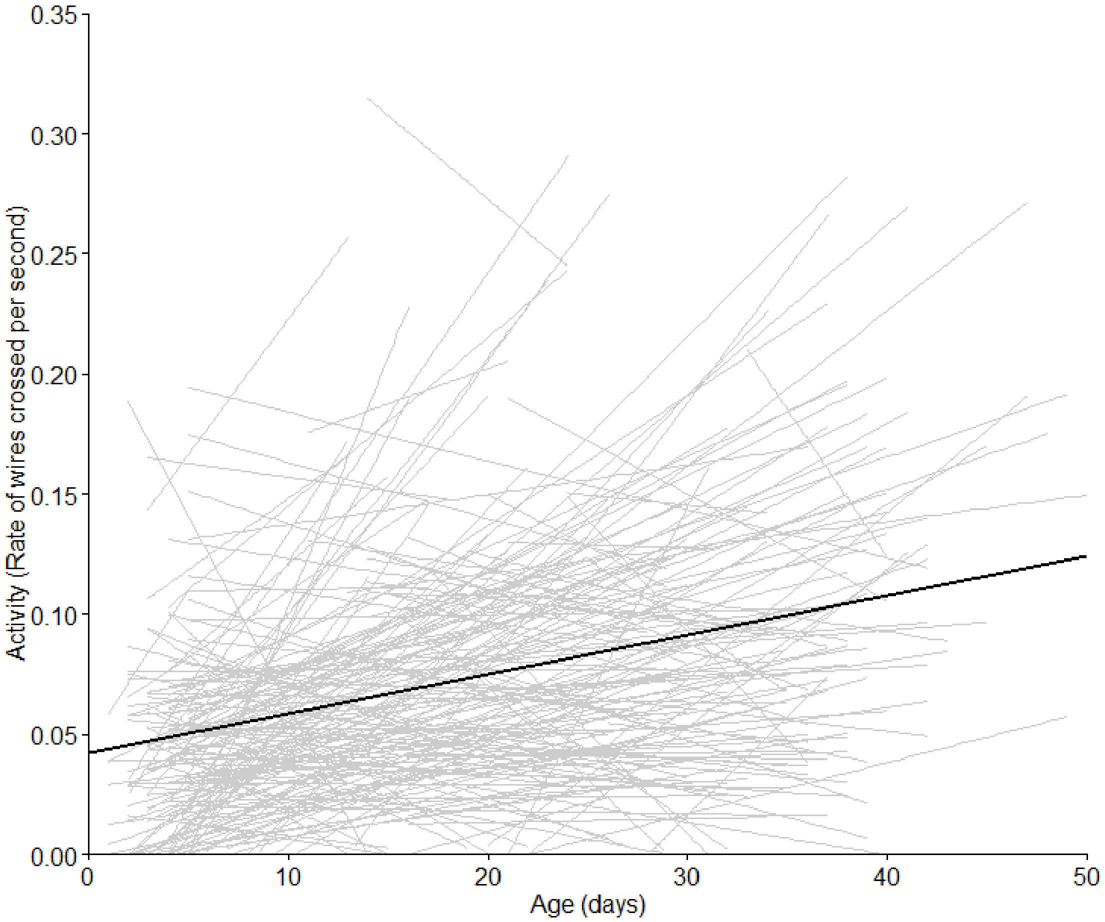

Figure 2.2. Individual plots of activity change with age, with a linear trend line through each individual’s data points in grey and a population line in black. Activity showed an important degree of among-individual variation in intercepts, but not in slopes. There was a negative intercept-slope correlation (r = -0.769. Individuals increased their activity level with age (see Table 2.2 for full results).

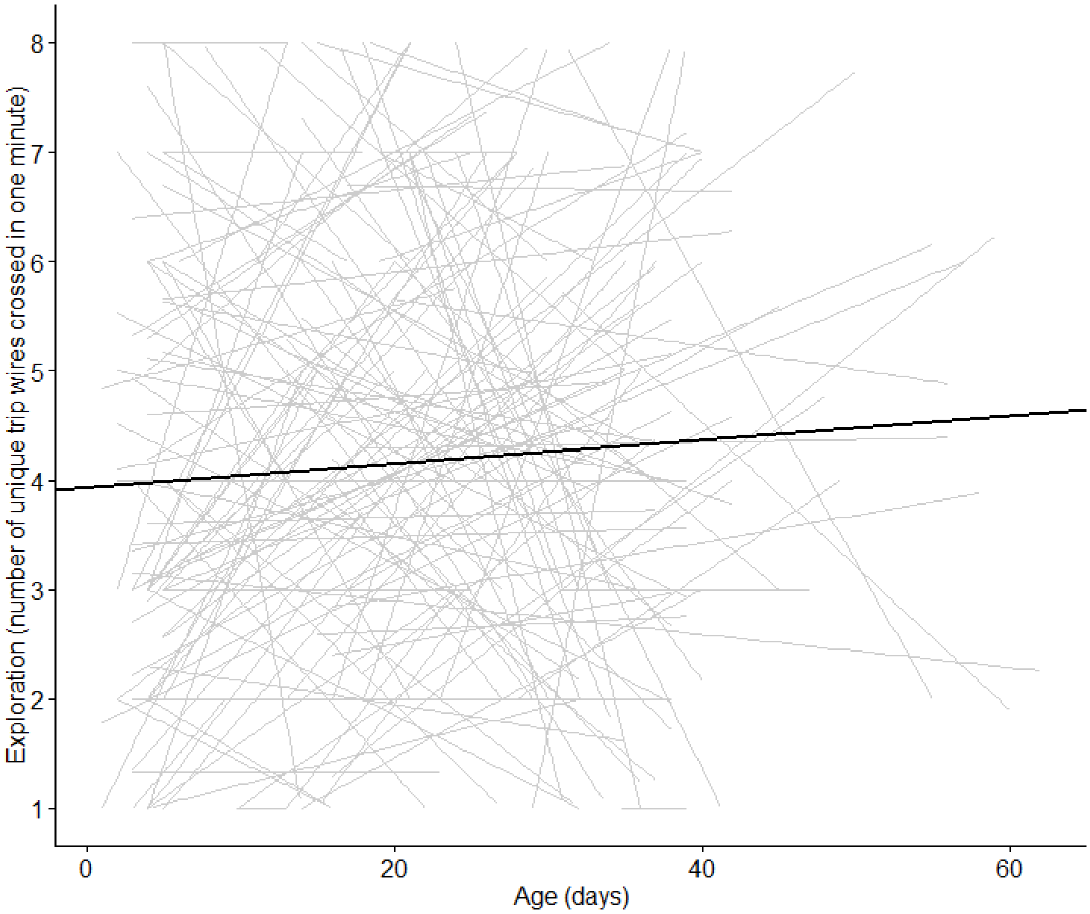

Figure 2.3. Individual plots of exploration change with age, with a linear trend line through each individual's data points in grey and a population line in black. Exploration showed among-individual variation in intercepts, but not in slopes and there was no intercept-slope correlation (r = -0.228). The fixed effect of age was non-significant, so the population did not tend to change in exploration with age (see Table 2.2 for full results).

Behavioural correlations

To incorporate exploration we used the 596 measures of shyness and activity that corresponded to the non-zero exploration scores used in the RR for exploration. None of the among-individual correlations were significant (Table 2.4). Exploration showed a significant positive residual correlation with activity, and a significant negative residual correlation with shyness. Activity and shyness showed no residual correlation. Fixed effects for this model are shown in the Appendix due to length and repetition (Table S1).

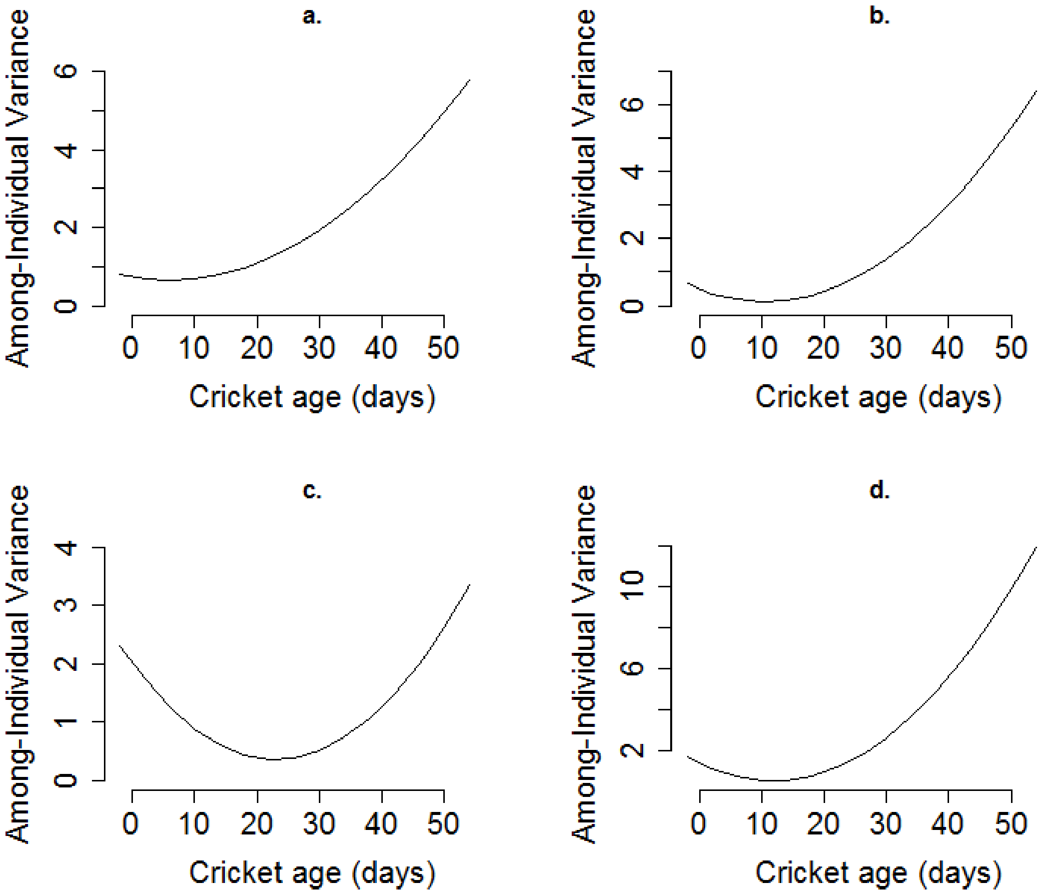

Figure 2.4. Plots of the among-individual change with age; a: tendency to leave the tube, b: shyness, c: Activity, d: exploration. Values calculated from the results of the random regressions following code in (Brommer 2013c).

Table 2.3. Results for separate univariate mixed-models of shyness, activity and exploration, with different variances estimated for the first capture (test 1) and three subsequent recaptures (tests 2-4). Given are the posterior distribution modes (PDM) and the 95% credible intervals (CRIs). Fixed effects were included in the model but not shown here as the confidence will be inflated by the use of both tests per capture.

Trait	***Component***	***Capture number***	***PDM***	***Lower 95% CRI***	***Upper 95% CRI***
Tendency to leave the tube	Among – individual variance	1	2.871	1.090	5.972
		2	1.531	0.494	3.439
		3	1.973	0.655	4.686
		4	1.124	< 0.001	4.676

	Repeatability	1	0.500	0.304	0.683
		2	0.380	0.159	0.540
		3	0.495	0.236	0.630
		4	0.361	0.033	0.632
Shyness	Among-individual variance	1	0.313	< 0.001	0.815
		2	0.285	< 0.001	0.500
		3	0.349	0.140	0.702
		4	0.002	< 0.001	0.701
	Residual variance	1	0.955	0.682	1.557
		2	1.000	0.748	1.304
		3	0.950	0.759	1.293
		4	1.540	1.106	2.164
	Repeatability	1	0.351	< 0.001	0.492
		2	0.165	< 0.001	0.358
		3	0.289	0.113	0.466
		4	0.002	< 0.001	0.341
Activity	Among-individual variance	1	2.899	1.126	5.348
		2	0.494	0.050	0.903
		3	0.523	0.056	0.976
		4	0.396	0.216	0.602
	Residual variance	1	1.937	1.136	3.539
		2	1.313	0.926	1.789
		3	1.397	1.047	1.994
		4	0.198	0.131	0.312
	Repeatability	1	0.383	0.168	0.527
		2	0.096	0.014	0.165
		3	0.096	0.018	0.177
		4	0.095	0.054	0.139
Exploration	Among-individual variance	1	0.007	< 0.001	1.425
		2	1.246	< 0.001	2.165
		3	0.007	< 0.001	1.663
		4	0.010	< 0.001	1.777
	Residual variance	1	3.036	2.013	4.349
		2	3.134	2.388	4.590
		3	3.153	2.451	4.574
		4	3.436	2.53	5.027
	Repeatability	1	0.002	< 0.001	0.379
		2	0.292	< 0.001	0.436
		3	0.002	< 0.001	0.370
		4	0.002	< 0.001	0.379

Table 2.4. Results for multivariate mixed-model of shyness, activity and exploration. Given are the posterior distribution modes (PDM) and 95% credible intervals (CRIs) of the covariances or correlations estimated. Correlations are considered significant if the 95% CRIs do not cross zero, highlighted in bold. Due to length the fixed effects are not presented here but are available in the Appendix (Table S1).

Component	*Trait(s)*	*PDM*	*Lower 95% CRI*	*Upper 95% CRI*
Among-individual variances	Shyness	0.070	0.027	0.136
	Activity	0.036	0.003	0.469
	Exploration	0.264	0.050	0.767
Among-individual covariances	Shyness & Activity	-0.003	-0.083	0.072
	Shyness & Exploration	-0.009	-0.116	0.095
	Activity & Exploration	-0.034	-0.205	0.261
Among-individual correlations	Shyness & Activity	0.004	-0.645	0.602
	Shyness & Exploration	-0.054	-0.639	0.549
	Activity & Exploration	0.183	-0.916	0.714
Residual variances	Shyness	0.783	0.698	0.890
	Activity	2.903	2.4824	3.381
	Exploration	5.654	5.043	6.354
Residual covariances	Shyness & Activity	-0.111	-0.090	0.045
	Shyness & Exploration	-0.325	-0.839	-0.360
	Activity & Exploration	2.269	1.884	2.687
Residual correlations	Shyness & Activity	-0.082	-0.159	0.009
	Shyness & Exploration	**-0.157**	**-0.242**	**-0.082**
	Activity & Exploration	**0.572**	**0.497**	**0.624**

Discussion

Among-individual variance in intercepts, but not in slopes

Assessing the dynamics of wild crickets' behaviour over adult lifespan, we found substantial among-individual variance in behaviour at mean ages among-individuals. Furthermore, only activity showed an intercept-slope interaction: Crickets with high levels of activity did not increase their activity levels with age as much as less active crickets. Moreover, it suggests that while crickets change with age in tendency to leave the tube, shyness and exploration, they do not change greatly relative to each other, and so measures at one point in life are relevant to life-history or fitness measures that are measured over a lifetime.

The amount of variation of intercepts compared to the mean intercept was greater than the among-individual variance in slopes compared to the average slope. Therefore, all traits show a very limited level of among-individual variation in the way they change with age. Coefficients of variation are not valid as the slopes can be negative, but it seems reasonable that a simple comparison between the mean and variance of an effect can be made. We were unable to test this statistically as the DIC of Poisson models in MCMCglmm is not focused correctly (Hadfield 2012), preventing us from comparing models with and without the random slope term. Dingemanse *et al* (2012) considered similar estimates of among-individual variance in slopes to show a lack of individual-specific change. We do not think that the lack of among-individual variation in slopes reflects a lack of power in our study, as the 95% CRIs are narrow (Martin *et al.* 2011). Therefore, the way the crickets' traits changed with age is not individual-specific, but governed by population-wide forces. Previous work has indicated that individuals can consistently differ in their plastic response to environmental gradients and suggested that age could be viewed as another element of the environment (Nussey *et al.* 2007; Dingemanse *et al.* 2010). Our results suggest that, at least in wild crickets, how behavioural traits change with age are not distinct traits in their own right.

Increases in among-individual variance with age

The estimates of the change in among-individual variance over time from the RRs for each trait showed identical patterns, with a drop in among-individual variance towards the mean age, followed by a large increase towards later life. This partly supports our prediction that the patterns of variance change will follow that of behavioural traits in humans (Roberts & Del Vecchio 2000) and great tits (Dingemanse *et al.* 2012). However, the curves also had properties of the U-shaped curves found in the additive genetic variance of non-behavioural traits in *Drosophila* (Tatar *et al.* 1996) and mute swans (Charmantier *et al.* 2006). Over-estimates of the variances at the extremes are likely (Promislow *et al.* 1996), so the underlying pattern is perhaps more likely to be a monotonic increase with among-individual variance over time than U-shaped.

A common assumption is that residual variance is consistent over time, however if it either consistently rises or falls then estimates of repeatability will not follow the same pattern (Brommer 2013b). Our estimates of residual variance at different captures only show such a pattern for activity, with a decrease with increasing test number. Despite this, estimates for repeatability were initially at a medium-level, before dropping. Assuming that among-individual variance is related to additive genetic variance, this suggests that the degree of heritability changes over adult lifetime (Tatar *et al.* 1996; Charmantier *et al.* 2006; Brommer 2013b). Therefore, selection could have different outcomes depending on the age of the individual. Relatively few studies have estimated gene by environmental interactions (G x E) in wild animals, and whether this change in among-individual variance is reflected in expression of additive genetic variance with age deserves investigation (Brommer 2013b).

In humans, behaviours become more repeatable as individuals age (Roberts & Del Vecchio 2000). This is thought to result from reinforcement of individual behaviour (Roberts & Del Vecchio 2000). Individual experience resulting from being more or less risk-prone or active (e.g. exploring away from the burrow and finding food or potential mates) has the potential to reinforce such behaviours in crickets, perhaps leading to an increase in consistency. For shyness and exploration no such clear pattern emerged from our models with separate estimates of repeatability at each of the captures. This appears to be driven by the very wide CRIs for among-individual variance at each time point for each trait. Only one of the estimates for shyness and none for exploration were significantly different from zero. Such “character-state” approaches are more “data hungry” than RRs (Brommer 2013b), perhaps limiting our ability to detect equivalent patterns, except if they are strong (e.g. for activity). The pattern for activity was in fact opposite to that found in humans, with a low and stable level of repeatability in tests 2-4. This may mean that selection on individual behaviour is weaker at older ages (Medawar 1952), as presumably activity is also less heritable at these older ages.

Population-level effects

Crickets left the tube more often and faster, moved about and explored their environment more as they got older. An increase in activity has been reported in the Siberian dwarf hamster, *Phodopus sungorus* (Kanda *et al.* 2012), but this contrasts with age-related declines in activity that have been reported in other insects such as the fruit fly, *Drosophila melanogaster* (Le Bourg & Lints 1992), and the housefly, *Musca domestica* (Sohal & Buchan 1981). Increasing activity as they age would allow crickets to range beyond their immediate environment to contact new mates, once they have mated (or chosen not to) with their neighbours. This suggests that in wild field crickets reproductive value is maximised in older age classes by greater risk taking, possibly because the greater residual reproductive value of young crickets favours the lower risks associated with being less active (Williams 1966; Hirshfield & Tinkle 1975; Wolf et al 2007).

The effect of selective disappearance (the fixed effect of maximum age) was significant for activity, with long-lived crickets being less active. This appears to support the Pace of Life Syndrome hypothesis, which suggests that risk-taking individuals will suffer a reduced lifespan to compensate for an increased mating rate (Réale *et al.* 2010). Whether this trade-off with mating rate features in our study system is the subject of chapter four. Summing the effects of selective disappearance and within-individual change with age gives the among-individual change with age (van de Pol & Verhulst 2006). Therefore, by adding the coefficients of the fixed effect of maximum age (which models selective disappearance) and the fixed effect of age (which models the within-individual change with age), we find values with the same sign as the fixed effect of age (0.051, -0.020, 0.043 & 0.019 for tendency to leave the tube, shyness, activity and exploration respectively). Therefore, the effect of among-individual differences in age on a trait followed the same direction as the within-individual change with age: individuals decrease in shyness over their lifetimes and older individuals are less shy than younger individuals.

In all models the fixed effect of test number was not important. Therefore, crickets did not become habituated to the assay. It has been shown elsewhere that crickets show a “forgetting curve” (Yano *et al.* 2012), which implies that experiences three-four days in the past do not affect behaviour. Returning the crickets to the wild between captures, and spacing recaptures by around ten days was clearly sufficient to prevent habituation.

Furthermore, we did not find any effect of mass. Size has been suggested to not be a good indicator of condition in this species (Rodríguez-Muñoz *et al.* 2010), and so may have limited bearing on the traits we measured.

Correlations

There was a negative intercept-slope correlation for activity. Therefore, less active crickets increased their activity more than initially more active crickets. This may simply indicate an upper limit to how active crickets can be. However, it may also indicate that initially less active crickets are compensating by more rapidly increasing their activity levels to obtain a, presumably, more beneficial level of activity. Whether activity level relates to mating success, as well as if its fits into a “pace of life syndrome”, is the subject of chapter four.

In the multivariate analysis, we found residual correlations between exploration and shyness and exploration and activity. Residual correlations can result from correlated individual plasticity, correlated measurement error, or driven by unmeasured internal or external effects (Dingemanse & Dochtermann 2013; Brommer 2013a). We controlled for environmental effects by conducting our assays in standardised laboratory conditions and included temperature of the laboratory in all our models. We also used an automated system that did not change over time to measure our behaviours. Therefore, we should avoid Brommer’s “individual gambit” when concluding that any residual correlation suggests a within-individual correlation (Dingemanse & Dochtermann 2013; Brommer 2013a; Araya-Ajoy & Dingemanse 2014) . Therefore, the significant residual correlations between exploration and both shyness and activity suggest that the traits are correlated at the within-individual level. This means that a cricket is limited in its ability to be both exploratory and shy when it suits it. A correlation between activity and exploration could “artificially” emerge if crickets that are very active end up moving about in different parts of the test arena in the first minute of the trial, giving them a high exploration score. However, there was no among-individual correlation between these traits, suggesting that more active individuals are not more exploratory, and so the within-individual correlation is genuine. Within-individual correlations indicate that the traits are influenced by a central mechanism that varies among individuals, creating individuals that are both different from each other and constrained to behave in particular ways (Stamps 1991; Sih *et al.* 2004a) c.f. “evolutionary characters” (Wagner 2001) and “behavioural characters” (Araya-Ajoy & Dingemanse 2014). Implicit to the evolutionary/behavioural characters framework is the assumption that the associations between exploration, shyness and activity are adaptive

(Bell & Sih 2007), predictions that should be tested empirically (Araya-Ajoy & Dingemanse 2014).

Conclusion

Overall we found evidence for individual-specific behaviours that are consistent over adult lifetimes. We did not however find strong evidence for individual-specific changes in behaviour over time. This suggests that there are constraints on how individuals change over time, e.g. for all crickets an increase in activity with age is beneficial or unavoidable. All traits showed a similar pattern in among-individual variance, with an increase later in life, with implications for the effect of selection at different ages. Finally, we found significant correlations between shyness and exploration and between exploration and activity within individuals, suggesting correlated plasticity within individuals in the expression of these traits and so a degree of non-independence in expression and evolutionary history.

3. Behaviour in captivity predicts some aspects of natural behaviour, but not others, in a wild cricket population

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Abstract

Examining the relevance of “animal personality” involves linking consistent among and within-individual behavioural variation to fitness in the wild. Studies aiming to do this typically assay personality in captivity and rely on the assumption that measures of traits in the lab reflect their expression in nature. We examined this rarely tested assumption by comparing laboratory and field measurements of the behaviour of wild field crickets (*Gryllus campestris*) by continuously monitoring individual behaviour in nature and repeatedly capturing the same individuals and measuring their behaviour in captivity. We focussed on three traits that are frequently examined in personality studies and that we have previously shown to be repeatable in the laboratory: shyness, activity and exploration. Laboratory activity and exploration predicted the expression of their equivalent behaviours in the wild, but shyness did not. Traits in the wild were predictably influenced by environmental factors such as temperature and sunlight, but only activity showed appreciable within-individual repeatability. This suggests that some behaviours typically studied as personality traits can be accurately assayed in captivity, but the expression of others may be highly context specific. Our results highlight the importance of validating the relevance of laboratory behavioural assays to analogous traits measured in the wild.

Key words: animal personality, exploration, *Gryllus*, laboratory, shyness, wild

Introduction

Individuals of the same species in the same population can show consistent among-individual differences in behaviour across time and contexts (Sih *et al.* 2004a; Réale *et al.* 2007). These apparent constraints on behavioural flexibility, termed “personality” have been shown to be pervasive throughout animal taxa (Bell *et al.* 2009), with a range of evolutionary and ecological consequences for individuals and populations (Wolf & Weissing 2012; Carere & Maestripieri 2013). The study of consistent among-individual differences in behaviour provides an avenue for understanding apparently non-adaptive behaviour (e.g. pre-copulatory sexual cannibalism; Johnson & Sih 2005) as well as some of the persistent variation around adaptive peaks of behaviour (Dall *et al.* 2004). The study of animal personality has undergone a recent and rapid expansion bringing difficulties associated with young disciplines, with many different definitions and techniques for answering related questions (Carter *et al.* 2013a). Nevertheless, it is widely recognised that studying animal personality in the wild is vital (Bell 2012; Niemelä & Dingemanse 2014). Studies of personality in nature allow for assessment of relevant effects on fitness (Smith & Blumstein 2008) and have the potential to identify laboratory artefacts due to artificial responses to unnatural stimuli (Niemelä & Dingemanse 2014) and the detection of differences in the expression of behaviour in wild and laboratory contexts (Archard & Braithwaite 2010).

It remains difficult to monitor the behavioural variation of individual animals in the wild, due to the workload required to capture, tag, release and then reliably track and monitor individuals in their natural habitat (but see: Desrochers 1992; Réale *et al.* 2000; Konecná *et al.* 2008; Herborn *et al.* 2010; Seyfarth *et al.* 2012; Godfrey *et al.* 2012). Rather than directly assay animals in the wild, many studies capture wild animals, conduct standardised behavioural assays in captivity, and then release them and monitor life histories and fitness traits (Dingemanse *et al.* 2004; Brown *et al.* 2005; Minderman *et al.* 2009; Amy *et al.* 2010; Cole & Quinn 2012; Patrick *et al.* 2012; Adriaenssens & Johnsson 2013; Kluen & Brommer 2013; Aplin *et al.* 2013; Bouwhuis *et al.* 2014; but see: Herborn *et al.* 2010; Briffa & Greenaway 2011; Seyfarth *et al.* 2012; Carter *et al.* 2012a). This is potentially problematic if personality assays in the laboratory do not reflect behaviour in the wild, or if single/short term assays in a novel environment do not accurately reflect an individual's behavioural type for the trait of interest (Biro 2012; Beckmann & Biro 2013 and see Edwards *et al.* 2013; Biro 2013 for further discussion). What we think is a measure of exploratory behaviour in the laboratory could actually be more analogous to susceptibility to anxiety in the wild; for example, an individual moving among many sections of an arena/box/tank as an anxious response to a novel environment (Carter *et al.* 2013a). This could lead to incorrect conclusions in relation to predictions of particular hypotheses e.g. the existence of a relationship between fitness and exploratory behaviour in certain environments (Dingemanse *et al.* 2004). Furthermore, the artificial stimulus presented in captivity might fall outside the range of stimuli normally experienced by the individual, giving it questionable relevance for understanding adaptive behaviour (Archard & Braithwaite 2010; Niemelä & Dingemanse 2014). Despite this, few studies have related captive measures of personality to wild measures of the same personality traits in the same individuals. Herborn *et al.* (2010) confirmed that in blue tits (*Cyanistes caeruleus*) captive measures of personality (neophobia and exploratory tendency) reflected analogous measures in the wild. North American red squirrels (*Tamiasciurus hudsonicus*) which scored highly for a composite measure representing activity and exploration were subsequently trapped at more different locations in the field than those with low scores (Boon *et al.* 2008). Contrastingly, Siberian chipmunks (*Tamias sibiricus*) that scored highly on an activity-exploration composite measure were trapped more often than less active/exploratory individuals, but not at a greater diversity of traps, suggesting they were less trap-shy and/or more active, but were not exploring the environment more (Boyer *et al.* 2010). Also with slightly conflicting results, van Overvel & Matthysen (2010) found that fast-exploring great tits (*Parus major*) did not increase their home range more than slow-exploring individuals did when food availability changed, but did increase the distance they travelled to visit feeders. However, the latter result could be confounded by dispersal status, as immigrants both travelled further and had higher exploration scores than locally-born individuals (van Overveld & Matthysen 2010). Others have looked for concordance among different traits, e.g. willingness to approach a mirror in captive tests and sociability in the wild (Svendsen & Armitage 1973;

Armitage 1986b,a) or shyness in captivity and activity in the wild (Fraser *et al.* 2001), but as these are not like-for-like tests they are not directly relevant here.

A further deficiency is that the majority of studies comparing individual behaviour between laboratory and wild contexts have been conducted on mammals and birds. In the one study on invertebrates, Briffa *et al.* (2008) measured the same individual European hermit crabs (*Pagurus bernhardus*) for startle response in the wild and across four laboratory observations. They found significant concordance across these five tests, but did not directly test for repeatability across wild and laboratory settings (Briffa *et al.* 2008). Invertebrate personality especially has attracted a large amount of interest (Mather & Logue 2013; Kralj-Fišer & Schuett 2014) and, for behaviours other than courtship, has been shown to be more repeatable than vertebrate behaviour (Bell *et al.* 2009). However, studies on among-individual variation in invertebrate behaviour are almost completely restricted to captivity (but see: Briffa & Greenaway 2011; Pinter-Wollman *et al.* 2012). Their small size, and the difficulty in tagging soft bodied animals or those that regularly moult contribute to this. Bell *et al.*'s meta-analysis (Bell *et al.* 2009) found wild behaviour to be more repeatable than laboratory behaviour. Therefore, one might expect wild invertebrate behaviour to be highly repeatable, as found in wild beadlet anemones (*Actinia equina*) (Briffa & Greenaway 2011), although more studies are required to confirm this as a general rule. Ultimately, we need to relate studies in the laboratory with studies in the wild in order to understand the behaviour of animals in their natural environment (Rodríguez-Muñoz *et al.* 2010). What we are lacking are direct and repeated measures of the same trait in both the wild and the laboratory in a range of taxonomic groups.

To this end, we repeatedly measured shyness (here defined as aversion to risk; Coleman & Wilson 1998), activity (general movement about an environment) and exploration (willingness to explore new areas of an environment; Réale *et al.* 2007) in the wild in a population of field crickets (*Gryllus campestris*). During the same period, we repeatedly captured the same individuals, and measured these three traits in captivity before releasing them. We also investigated what biotic (e.g. age, sex) and abiotic (e.g. weather, temperature) factors influenced wild behaviour. Finally, we quantified the importance of an individual's microhabitat at the point of measurement for its shyness. This allows us to determine whether an individual’s habitat choice could influence its observed personality (Briffa & Greenaway 2011; Westneat *et al.* 2011).

Methods

Data collection

Data were collected from April-July 2013 at the WildCrickets project site (see (Rodríguez-Muñoz *et al.* 2010) and www.wildcrickets.org for further details). We capture and tag each individual cricket, and each cricket burrow is individually identified with a unique three digit number. See previous chapter for relevant natural history information. In 2013, we placed 120 motion sensitive cameras at random among those burrows with an active cricket. These allow us to record behaviour in the natural setting and responses to stimuli. Crickets regularly move among burrows, giving a degree of independence between burrow ID and cricket ID.

Wild personality traits

Between 8/5/13 and 29/6/13, on days when the weather was suitable for the crickets to be active (>14°C and not raining; around 90% of days during the 2013 field season) we carried out a disturbance trial by walking among the cameras in the field. When walking towards a cricket, the experimenter simulates an approaching predator and triggers the cricket’s flight response into its burrow. As we passed each camera, we waved a paint brush briefly in front of it. This allows us to re-watch the video, and associate a cricket entering its burrow with the disturbance caused by ourselves rather than from another source. We scored shyness in the wild by measuring the time in seconds between the end of the disturbance (the brush last appearing on-screen) and the cricket re-emerging from its burrow. If there was a male-female pair at a burrow (5% of instances) we recorded this fact, but a shyness score was only assigned to the cricket emerging from the burrow first. For our measures of activity, we recorded the total number of times a cricket left the area under observation by the camera over a burrow each day or part of a day it was under observation. Crickets are counted as leaving a burrow if they move out of view of the camera and do not return within five minutes. Therefore, the measure of activity is the number of these “leaves” events per day. The measure of exploration is the number of unique burrows a cricket is observed at per day (or part of a day) it was under observation. Therefore, all behaviours in the wild were measured relatively continuously across the field season.

Laboratory personality traits

We recorded our initial measures of behaviour in the laboratory on crickets we caught for tagging, but prior to the tagging procedure. Once released after tagging, we re-caught crickets every 10-20 days from the first test until the cricket was no longer observed, to repeat the behavioural assays. This is a long enough gap to prevent habituation (Fisher *et al.* 2015a). Therefore, the laboratory measures were collected regularly alongside the continuously collected wild measures. See the previous chapter or (Fisher *et al.* 2015a) for full details on the laboratory assays. That work demonstrated the consistency of the personality traits over the adult life-time of the crickets under study, so we do not go into it here. In short, we measured of shyness as the time to emerge from a refuge, an assay that has been used extensively in captive crickets (Hedrick 2000; Hedrick & Kortet 2006; Niemelä *et al.* 2012b,a). Activity was scored as the rate of movement around a 290 x 201 x 212 mm plastic box, once the cricket had emerged from the tube. For exploration, we counted the number of unique virtual tripwires (set to measure activity, possible scores range from 0-8) the cricket crossed in the first minute after it emerged from the tube.

Statistical analysis

We conducted all analyses in R ver. 3.1.2 (R Core Team 2013). For shyness in the wild we removed any disturbances where the cricket was already inside the burrow long before the brush appeared on screen. Crickets did not emerge from the tube in the laboratory in 41% of trials, in which case the trial was recorded as a missing observation.

Relating wild and laboratory behaviours

We constructed separate generalised linear mixed models (GzLMMs) for each behaviour in the R package MCMCglmm (Hadfield 2010a). These models have each laboratory behaviour score as a fixed effect, and that individual’s next measured score for that behaviour in the wild as the response variable, following Herborn *et al.* (2010). A significant, positive effect of the laboratory behaviour on the wild behaviour indicates the two assays correspond to the same trait. We only used one wild behaviour measure for each laboratory score, so if two wild measures were recorded after a laboratory measure, only the first one was used. Furthermore, we never used a laboratory measure on the same day as a wild measure. We also included the number of days between the laboratory and the wild scores as a fixed effect, as well as the interaction between this interval and the laboratory behaviour score. We were interested in whether the interaction was significant (as our analyses were in a Bayesian framework, here “significant” is used as a synonym for important) as this would show whether the ability of the laboratory measure to predict the wild measure depended on the timespan between them. For activity and exploration we also included the number of minutes that crickets were under observation for the scored day as a fixed effect. We used a Poisson error structure, with additive errors and a log-link function for all models. We also included random effects of individual identity and, for wild shyness, burrow number. This also allows us to control for multiple measures per individual and per burrow, and calculate the adjusted repeatability (R_{Ad}). The R_{Ad} is (having corrected for additional variables) the proportion of total variance that is reproducible among repeated measures of a certain group and is also referred to as the intra-class correlation coefficient, in this instance the group/class being a single individual (Nakagawa & Schielzeth 2010). We calculated R_{Ad} and the 95% credible intervals (CRIs) of the wild behaviours using all data collected with multiple environmental covariates as the fixed effects. R_{Ad} scores can be compared between models to see if traits are more or less repeatable than others. For the number of samples, number of unique individuals and the mean, standard deviation and range of number of tests per individual for each analysis, see Table 3.1.

Bivariate analyses

As an alternative method to determine whether traits in the wild and the laboratory were related, we constructed a bivariate model for each trait. Entered as responses were every measure of the trait in the laboratory and every measure of the trait in the wild (see Table 3.1). The only fixed effects entered were sex and age of the individuals at the point of testing, as the other factors do not appear in both contexts. We initially included temperature in each context but these models failed to converge. For each record there is either a score for the laboratory behaviour or the wild behaviour, the other trait being recorded as a missing observation. Therefore, the residual covariance cannot be estimated so is fixed at zero. Correlations are then calculated by dividing the covariance between the two responses by the square root of the product of their variances. This can be calculated across the posterior distributions of the variances and covariances, giving a mode and 95% CRIs for each correlation.

Predictors of wild behaviour

To determine which quantifiable factors influence behaviour in the wild, irrespective of the measure in the laboratory, we constructed three separate GzLMMs, one for each trait. Every wild score for each particular trait was used as the response variable, and sex, age, date, weather and temperature were used as fixed effects. Weather and temperature were recorded by a weather station in the centre of the meadow that takes measurements every ten minutes (Vantage Pro 2, Davis instruments, California). For shyness, weather was either “sunny” or “cloudy” when the disturbance was carried out, while for activity and exploration weather was the separate (although not necessarily independent) effects of the mean amount of solar radiation and the total amount of rain on that day. Temperature (in the shade) was either the temperature at the record nearest the disturbance (for shyness, which was measured at a single point) or the mean temperature over the day (for activity and exploration, which were measured across the day). For shyness we also included the time and whether the cricket was with an individual of the opposite sex or not at the point of measurement as fixed effects. For activity and exploration we included the number of minutes the cricket was on-screen for that day as a fixed effect. All continuous fixed effects (minutes observed outside the burrow, age, date, time of day, temperature and weather for activity and exploration) were transformed by subtracting the global mean from each individual value and then dividing by the standard deviation (Jackson 2003; van den Berg *et al.* 2006). This leaves each variable in the same units: “number of standard deviations the datum is above or below the mean”, common practice in selection analyses as it allows the effect/response of different factors to be directly compared (Hunt *et al.* 2005; South *et al.* 2011).

We included interactions between sex and age, sex and weather (two separate interactions for the two weather components in the activity & exploration analyses) and, for shyness, sex and pair to determine whether the sexes differed in how they changed with age, how they responded to environmental conditions and if they responded differently to having a partner respectively. An interaction with sex and age might be expected if the sexes follow different reproductive strategies that require different rates of mate acquisition and so differences in willingness to leave the burrow and move about their environment (Schuett *et al.* 2010). A sex-weather interaction is plausible, as in this species males need to leave the burrow to sing to attract mates, a behaviour which is highly metabolically costly (Hoback & Wagner 1997; Mowles 2014) and so is likely to be weather dependent. The sexes might differ in how they respond to being in a pair as male crickets have been shown to be “chivalrous”: when in a pair it is usually the female who stays nearer the burrow and enters it first when the pair are threatened by a predator (Rodríguez-Muñoz *et al.* 2011). We also included interactions between age and weather (again, two separate interactions for activity & exploration) and age and pair (only for shyness), to determine whether crickets of different ages respond differently to environmental conditions or being in a pair respectively. An age-weather interaction is likely as direct sunlight affects the rate of cricket development (Remmert 1985), so the time spent basking in sunshine is likely to change over a cricket’s lifetime. An age-pair interaction was included as residual reproductive value is lower in old age (Williams 1966; Hirshfield & Tinkle 1975) and so could alter behaviour while with a mate in comparison to when alone. We included random effects of individual identity and, for shyness, burrow identity. Again for all models we used Poisson error structures with additive errors and log-link functions, and calculated R_{Ad} separately for individuals and burrows following Nakagawa & Schielzeth (2010). We included more fixed effects in this model than in the model comparing wild and laboratory behaviour as it has a substantially larger data set, the previous model only contained pairs of laboratory and wild measures on the same individual where the former preceded the latter.

To determine whether ignoring burrow identity (microhabitat) leads to an increased estimate of individual consistency, we removed the random effect of burrow from GLMM for shyness, and compared the new estimates of R_{Ad} with the original GLMM. The difference was considered important if the 95% CRIs of the estimate of R_{Ad} did not overlap.

Results

Total sample sizes, with the number of unique individuals, mean and range of test numbers for each analysis are presented in Table 3.1.

Table 3.1. Table showing total number of samples, number of unique individuals and mean, standard deviations and ranges for frequency of tests per individual for each analysis of each behaviour carried out. The analyses modelling the trait in either the laboratory or the wild used every available measure for those contexts, while the lab vs. wild comparison used a laboratory measure and the subsequent wild measure. For shyness in the wild, the number of unique burrows is shown in brackets next to the number of unique individuals.

Trait	***Analysis***	***Samples***	***No. unique individuals***	***Mean***	***S.D***	***Range***
Shyness	Lab vs. wild	220	153	1.44	0.65	1-3
	Laboratory	617	202	1.30	1.86	1-8
	Wild	946	147 (156)	5.28	4.25	1-16
Activity & exploration	Lab vs. wild	303	186	1.63	0.79	1-4
	Laboratory	617	202	1.30	1.86	1-8
	Wild	4087	229	17.9	11.9	1-50

Relationships between laboratory and wild behaviours

Laboratory shyness scores did not influence the wild shyness scores (Fig. 3.1; PDM = -4.37 x 10^{-5}, LCRI = -6.08 x 10^{-4}, UCRI = 7.36 x 10^{-4}, pMCMC = 0.87). The interaction between laboratory shyness and the timespan between the laboratory and wild shyness scores was not important (PDM = 1.31 x 10^{-5}, LCRI = -1.40 x 10^{-4}, UCRI = 1.49 x 10^{-4}, pMCMC = 0.90. The timespan between the laboratory and wild shyness scores did not influence the wild shyness score (PDM = -2.82 x 10^{-2}, LCRI = -9.10 x 10^{-2}, UCRI = 1.29 x 10^{-1}, pMCMC = 0.82).

Laboratory activity level was positively related to level of activity in the wild (Fig. 3.2; PDM = 5.98. LCRI = 3.99, UCRI = 8.89, pMCMC < 0.01). The CRIs for interaction between the laboratory score and the time between the measures marginally overlapped zero (interaction: PDM = -0.99, LCRI = -2.18, UCRI = 0.09, pMCMC = 0.08), while the gap between measures negatively influenced wild activity level (PDM = -0.08, LCRI = -0.17. UCRI = -1.79 x 10^{-3}, pMCMC = 0.04). The number of minutes a cricket was observed outside its burrow negatively influenced its activity score (PDM = 3.00 x 10^{-4}, LCRI = -7.06 x 10^{-4}, UCRI = -1.65 x 10^{-5}, pMCMC = 0.04).

Exploration in the laboratory tended to positively predict exploration in the wild, although this was not significant at the 95% level (Fig. 3.3; PDM = 0.08, LCRI = -0.01, UCRI = 0.15, pMCMC = 0.07). The interaction between laboratory score and time between measures, and time between measures alone, were not important (interaction: PDM = -0.02, LCRI = -0.07, UCRI = 0.01, pMCMC = 0.26; time: PDM = -0.05, LCRI = -0.13, UCRI = 0.01, pMCMC = 0.11). The number of minutes a cricket was onscreen negatively influenced its exploration score: PDM = -4.50 x 10^{-4}, LCRI = -7.90 x 10^{-4}, UCRI = -2.10 x 10^{-4}, pMCMC < 0.01).

Bivariate analyses

The results are presented in Tables 3.2-4. In summary they agree with the results of the analysis in the main text: shyness measures between the two contexts were not related, but activity and exploration measures were.

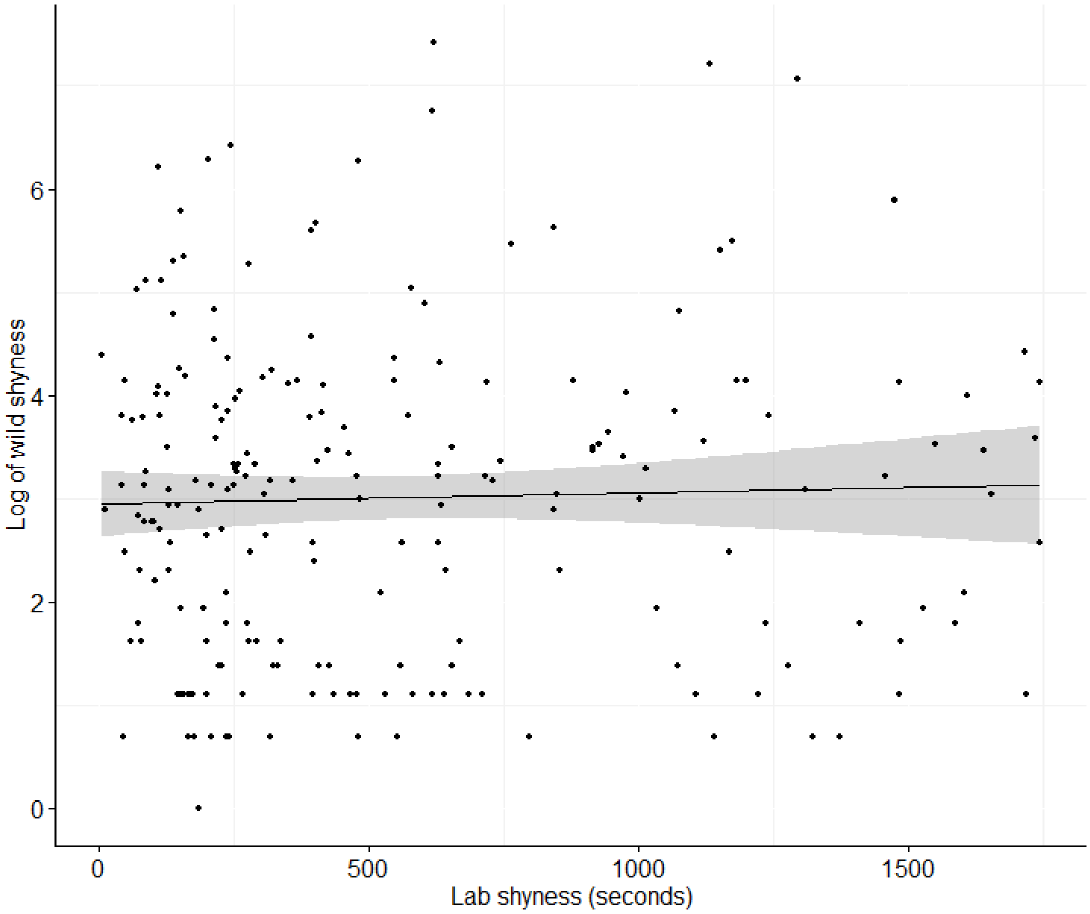

Figure 3.1. Laboratory shyness and log of wild shyness (logged to aid viewing). The line is from a simple linear model of wild shyness ~ laboratory shyness, the grey area indicates the standard errors around the estimate. There was no relationship between shyness in the laboratory and shyness in the wild (PDM ± 95% CRIs = -4.37 x 10^{-5}± -6.08 x 10^{-4} - 7.36 x 10^{4}).

Predictors of wild shyness

The results from the GzLMMs for the shyness in the wild are presented in Table 3.5. Time of day was weakly and positively related to the time a cricket took to come out of its burrow. Male crickets were shyer than female crickets. Finally, there was a significant age-weather interaction, with older crickets coming out in sunny weather more slowly than younger crickets. R_{Ad} of individuals and burrows was estimated to be 0.06 (LCRI = 0.04, UCRI = 0.12) for both.

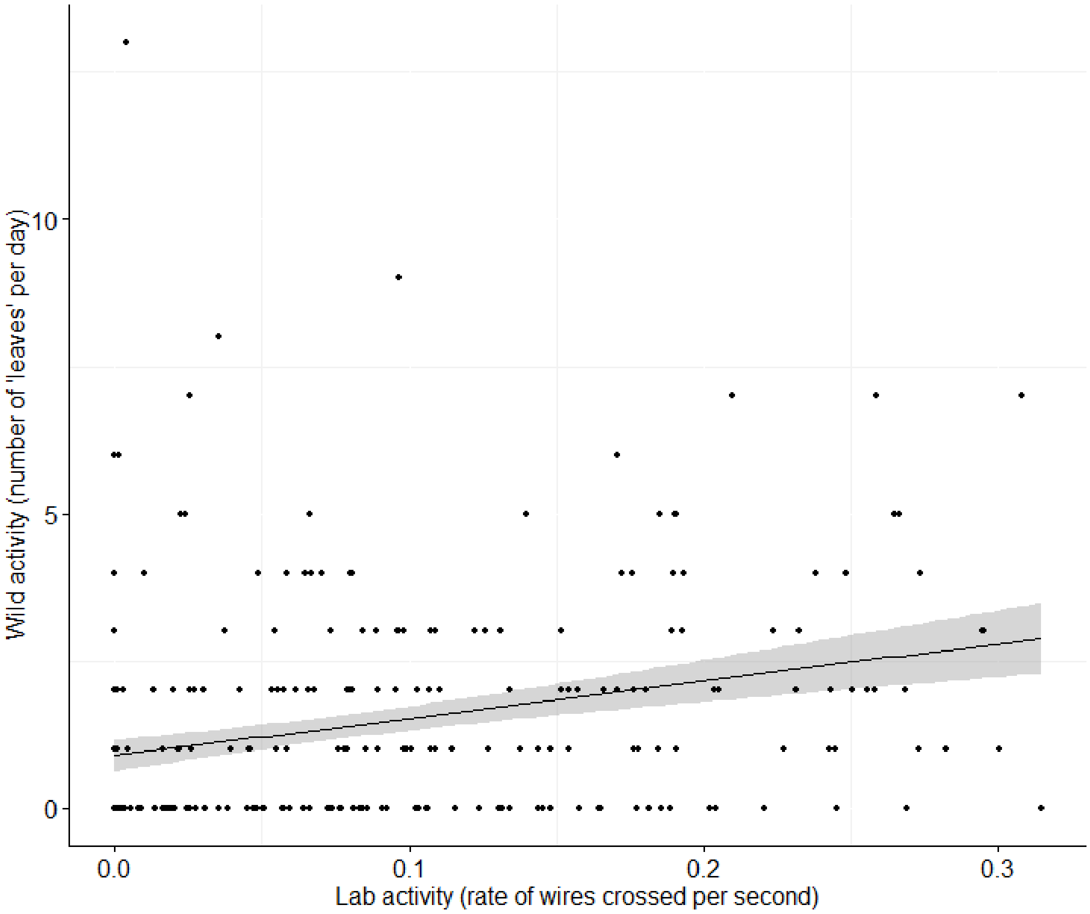

Figure 3.2. Laboratory activity and wild activity. The line is from a simple linear model of wild activity ~ laboratory activity, the grey area indicates the standard errors around the estimate. There was a significant, positive relationship between activity in the laboratory and activity in the wild (PDM ± 95% CRIs = 5.98 ± 3.99 - 8.89).

Table 3.2. Results of the bivariate model between laboratory and wild shyness. An effect is modelled as a distribution (the posterior distribution), below we give the mode of the posterior distribution (PDM) and lower & upper 95% credible intervals (LCRI & UCRI respectively). We also include the pMCMC scores, interpreted in a similar way to traditional p-values. The intercept of wild shyness is modelled as a contrast to the global intercept i.e. of lab shyness. Sex is modelled with female as the default and males as the contrast.

Trait	***PDM***	***LCRI***	***UCRI***	***pMCMC***
Intercept	5.766	5.629	5.933	NA
Intercept – wild shyness	-1.431	-1.621	-1.258	NA

Sex on lab shyness	-0.056	-0.284	0.150	0.533
Sex on wild shyness	-0.124	-0.271	0.021	0.094
Age on lab shyness	-0.220	-0.303	-0.165	<0.001
Age on wild shyness	0.062	-0.028	0.142	0.171
V_A *of lab shyness*	0.237	0.139	0.395	NA
V_A *of wild shyness*	0.029	0.015	0.063	NA
CoV_A *lab -wild shyness*	0.011	-0.038	0.064	NA
Correlation lab -wild shyness	0.287	-0.309	0.631	NA

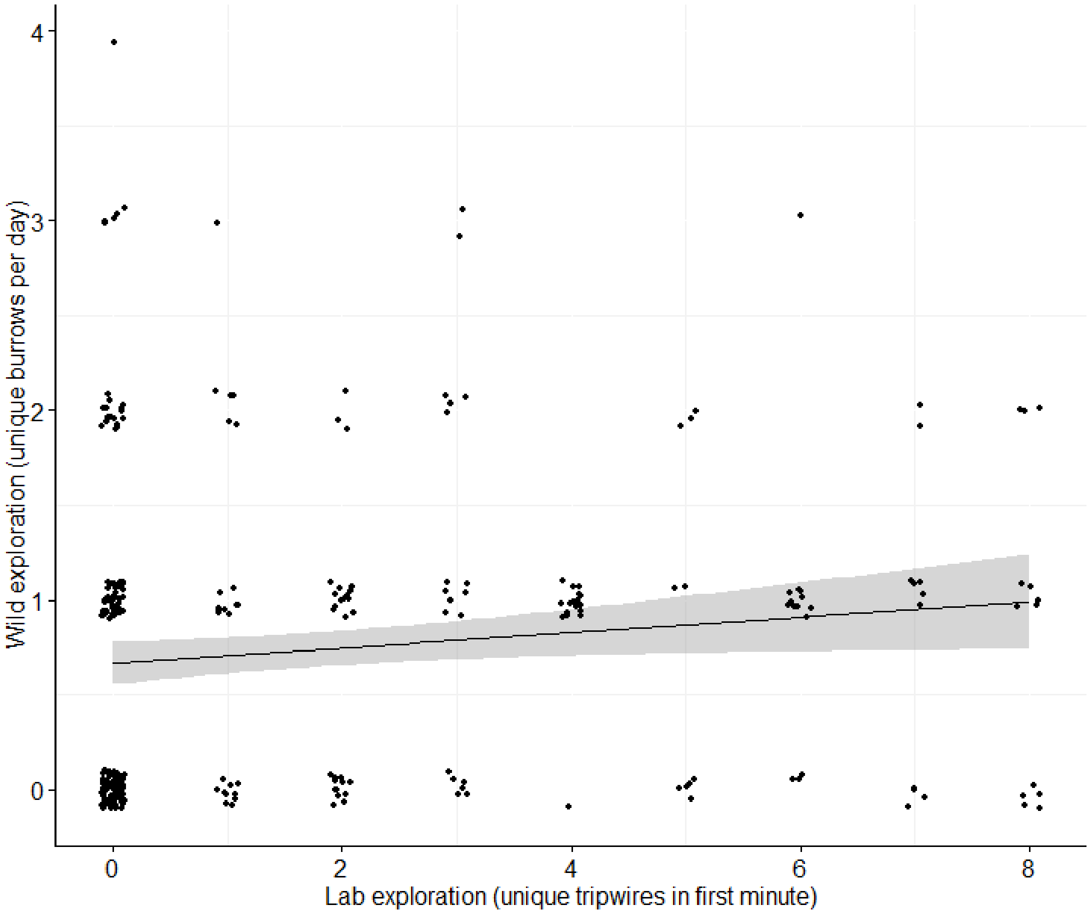

Figure 3.3. Laboratory exploration and wild exploration. The line is from a simple linear model of wild exploration ~ laboratory exploration, the grey area indicates the standard errors around the estimate. There tended to be a positive relationship between exploration in the laboratory and exploration in the wild (PDM ± 95% CRIs = 0.08 ± -0.01 - 0.15). Points are offset on both x and y axes to aid viewing when there are multiple points with the same x and y scores, which were always integers.

Table 3.3. Results of the bivariate model between laboratory and wild activity. An effect is modelled as a distribution (the posterior distribution), below we give the mode of the posterior distribution (PDM) and lower & upper 95% credible intervals (LCRI & UCRI respectively). We also include the pMCMC scores, interpreted in a similar way to traditional p-values. The intercept of wild activity is modelled as a contrast to the global intercept i.e. of lab activity. Sex is modelled with female as the default and males as the contrast.

Trait	***PDM***	***LCRI***	***UCRI***	***pMCMC***
Intercept	3.435	3.047	3.789	NA
Intercept – wild activity	-3.457	-3.861	-3.197	NA
Sex on lab activity	-0.103	-0.735	0.294	0.446
Sex on wild activity	-0.329	-0.577	-0.136	0.002
Age on lab activity	0.968	0.868	1.092	< 0.001
Age on wild activity	0.676	0.623	0.738	< 0.001
V_A *of lab activity*	2.977	2.301	4.055	NA
V_A *of wild activity*	0.499	0.386	0.658	NA
CoV_A *lab -wild activity*	0.666	0.451	0.997	NA
Correlation lab -wild activity	0.546	0.406	0.706	NA

Table 3.4. Results of the bivariate model between laboratory and wild exploration. An effect is modelled as a distribution (the posterior distribution), below we give the mode of the posterior distribution (PDM) and lower & upper 95% credible intervals (LCRI & UCRI respectively). We also include the pMCMC scores, interpreted in a similar way to traditional p values. The intercept of wild exploration is modelled as a contrast to the global intercept i.e. of lab exploration. Sex is modelled with female as the default and males as the contrast.

Trait	***PDM***	***LCRI***	***UCRI***	***pMCMC***
Intercept	0.172	-0.130	0.398	NA
Intercept – wild exploration	-0.791	-1.001	-0.492	NA
Sex on lab exploration	-0.115	-0.475	0.238	0.564
Sex on wild exploration	-0.169	-0.372	-0.031	0.026
Age on lab exploration	0.695	0.532	0.798	< 0.001
Age on wild exploration	0.580	0.512	0.632	< 0.001
V_A *of lab exploration*	0.705	0.442	1.256	NA
V_A *of wild exploration*	0.224	0.148	0.312	NA
CoV_A *lab -wild exploration*	0.267	0.135	0.432	NA

Correlation lab -wild exploration	0.652	0.389	0.840	NA

Table 3.5. Predictors of wild shyness. An effect is modelled as a distribution (the posterior distribution). Below we give the mode of that distribution (PDM) and the lower & upper 95% credible intervals (LCRI & UCRI, respectively). We also include the pMCMC scores, interpreted in a similar way to traditional p-values. Sex is modelled with female as the default and males as the contrast and weather is modelled with “cloudy” as the default and “sunny” as the contrast. Effects significant at the 95% level are highlighted in bold.

Factor	***PDM***	***LCRI***	***UCRI***	***pMCMC***
Intercept	3.068	2.801	3.332	<0.001
Sex	-0.379	-0.805	-0.072	0.028
Age	-0.132	-0.385	0.228	0.587
Pair	0.689	-0.348	1.583	0.221
Temperature	-0.063	-0.221	0.065	0.315
Weather	-0.072	-0.367	0.274	0.804
Date	-0.087	-0.374	0.172	0.525
Time	**0.116**	**0.016**	**0.252**	**0.032**
Sex:age	0.039	-0.121	0.361	0.409
Sex:weather	0.280	-0.152	0.765	0.168
Sex:pair	0.041	-0.895	1.486	0.726
Age:weather	**0.350**	**0.104**	**0.571**	**0.005**
Age:pair	-0.061	-0.605	0.342	0.654
Among-individual variance	0.203	0.112	0.375	NA
Among-burrow variance	0.197	0.111	0.352	NA
Residual variance	2.482	2.192	2.692	NA
Repeatability of individuals	0.061	0.040	0.120	NA
Repeatability of burrows	0.062	0.037	0.119	NA

Microhabitat and shyness

In the model for wild shyness the PDMs of among individual variance and among burrow variance were both 0.20 (Table 3.5). The R_{Ad} of both individuals and burrows was 0.06. When the random effect of burrow was removed from the model, the PDM of the among-individual variance rose to 0.26 (LCRI = 0.17, UCRI = 0.46) and the R_{Ad} to 0.10 (LCRI = 0.06, UCRI = 0.16).

Predictors of wild activity

We recorded 4097 measures of activity in the wild for 229 individuals. The results are presented in Table 3.6. Crickets were more active on sunnier and warmer days, as well as when they were older, whereas a lower activity was found on rainy days. Females were more active than males. There was a significant, positive age:rain interaction, so older crickets were more active and exploratory when it was raining than younger crickets. There was a significant, positive sex:age interaction; males increased activity levels more when older, so the difference in activity between males and females was lower in older crickets. Crickets that were on screen for longer recorded higher activity levels. The significant, negative age:sun interaction indicates that older crickets were less active than expected when it was sunny. Finally, crickets were more active at later dates. R_{Ad} of individuals was calculated to be 0.21 (LCRI = 0.17, UCRI = 0.27).

Table 3.6. Predictors of activity in the wild. An effect is modelled as a distribution (the posterior distribution), below we give the mode of the posterior distribution (PDM) and lower & upper 95% credible intervals (LCRI & UCRI respectively). We also include the pMCMC scores, interpreted in a similar way to traditional p-values. Sex is modelled with female as the default and males as the contrast. Effects significant at the 95% level are highlighted in bold.

Factor	***PDM***	***LCRI***	***UCRI***	***pMCMC***
Intercept	0.050	-0.045	0.191	0.223
Minutes	**0.117**	**0.084**	**0.167**	**< 0.001**
Sex	**-0.227**	**-0.407**	**-0.065**	**0.011**
Age	**0.135**	**0.031**	**0.238**	**0.014**
Temperature	**0.060**	**0.005**	**0.109**	**0.045**
Sun	**0.219**	**0.178**	**0.280**	**< 0.001**
Rain	**-0.172**	**-0.225**	**-0.090**	**< 0.001**
Date	**0.447**	**0.351**	**0.580**	**< 0.001**
Sex:age	**0.131**	**0.045**	**0.216**	**0.003**
Sex:sun	0.032	-0.049	0.114	0.416
Sex:rain	0.022	-0.114	0.102	0.957
Age:sun	**-0.110**	**-0.141**	**-0.065**	**< 0.001**
Age:rain	**0.089**	**0.047**	**0.160**	**0.001**
Among-individual variance	0.248	0.200	0.356	NA

Residual variance	0.324	0.278	0.374	NA
Repeatability	0.210	0.169	0.267	NA

Predictors of wild exploration

For exploration we recorded 4097 measures of 229 individuals. The results are presented in Table 3.7. Crickets explored more when older, when the sun was stronger and less when it was raining. Furthermore, there was a significant age:rain interaction, so older crickets were more exploratory when it was raining than younger crickets. The weak positive sex:age interaction indicates that males increased their exploration more as they aged than females did. Older crickets were less exploratory than expected when it was sunny, as indicated by the negative age:sun interaction. Finally, crickets were more exploratory at later dates. R_{Ad} of individuals was calculated to be 0.12 (LCRI = 0.08, UCRI = 0.15).

Table 3.7. Predictors of exploration in the wild. An effect is modelled as a distribution (the posterior distribution), below we give the mode of the posterior distribution (PDM) and lower & upper 95% credible intervals (LCRI & UCRI respectively). We include also the pMCMC scores, interpreted in a similar way to traditional p-values. Sex is modelled with female as the default and males as the contrast. Effects significant at the 95% level are highlighted in bold.

Factor	***PDM***	***LCRI***	***UCRI***	***pMCMC***
Intercept	-0.335	-0.432	-0.260	< 0.001
Minutes	-0.024	-0.067	0.012	0.236
Sex	-0.080	-0.209	0.041	0.184
Age	**0.175**	**0.077**	**0.250**	**0.001**
Temperature	0.011	-0.044	0.062	0.835
Sun	**0.265**	**0.217**	**0.321**	**< 0.001**
Rain	**-0.093**	**-0.165**	**-0.017**	**0.007**
Date	**0.307**	**0.217**	**0.397**	**< 0.001**
Sex:age	**0.083**	**0.002**	**0.166**	**0.050**
Sex:sun	0.038	-0.045	0.112	0.482
Sex:rain	-0.042	-0.159	0.051	0.300
Age:sun	**-0.087**	**-0.124**	**-0.045**	**< 0.001**
Age:rain	**0.101**	**0.033**	**0.150**	**< 0.001**
Among-individual variance	0.120	0.082	0.157	NA
Residual variance	0.045	0.033	0.059	NA
Repeatability	0.117	0.083	0.146	NA

To summarise, shyness in the laboratory and the wild were not related, but activity was positively associated between the two contexts, and exploration tended to be. Shyness was not at all repeatable in the wild (R_{Ad} = 0.06). Activity, and to a lesser degree exploration, showed a modest degree of repeatability in the wild (R_{Ad} = 0.21 & 0.12 respectively). Based on whether the 95% CRIs of the estimates of R_{Ad} overlapped or not, repeatability activity in the wild was significantly higher than the repeatability of shyness and exploration in the wild, which were not different. All behaviours in the wild could be predicted by various biotic & abiotic factors.

Discussion

Relating captive and wild behaviours

We found a relationship between individuals' activity and exploration in the laboratory and the wild, but no such relationship for shyness. For shyness, this suggests that either we have in fact measured two different and unrelated traits, or that expression of this behaviour is highly context specific (Fox *et al.* 2009). The very low repeatability of shyness in the wild suggests that shyness expression in the wild is context specific. Therefore, the natural setting has a high "situational strength" for crickets, i.e. it has a strong influence on behaviour and so masks among-individual differences (Uher 2011). This is not a general rule for poikilotherms however; beadlet anemones (*A. equina*) show a high repeatability of startle response in the wild (Briffa & Greenaway 2011). Shyness in the laboratory may therefore reflect responses to the stress of the artificial situation, rather than behavioural tendencies on a bold-shy continuum. The stimulus for the shyness test was necessarily different between the laboratory and the wild, as we could not bring each cricket's burrow into the laboratory. Such compromises will be necessary for many species when moving from the wild to the laboratory, although in some cases stimuli can be replicated e.g. (Briffa *et al.* 2008). The fact that such a low R_{Ad} was observed in the wild indicates that studying among-individual behavioural differences may be more viable in tightly controlled conditions for some traits.

Unlike shyness, activity showed a relationship between laboratory and wild measures. Activity could be viewed as a more fundamental property of an animal’s behaviour, reflective of differences in basal metabolic rate (BMR) (Careau *et al.* 2008) rather than more complex combinations of cost-benefit trade-offs. BMR commonly shows large intra-specific variability (Careau *et al.* 2008), and for activity it is easy to see how consistent differences in individual BMR could lead to consistently different levels of activity across contexts. It is interesting that our measures of activity in the two contexts were quite different (movement around a box in <30 minutes and movement to and from burrows over the course of an entire day), yet still showed a strong relationship. Clearly, assays designed to test the same fundamental trait in different environments can achieve the same goal. There was also a tendency for a larger gap between assays to decrease the strength of the relationship. This suggests that within-individual change in behaviour over time can reduce the ability to detect relationships between contexts.

Exploration showed a weaker relationship between laboratory and wild measures, with lower repeatability in the wild than activty. Exploratory behaviour may be a more complex trait than activity, reflecting trade-offs a cricket makes based on its current condtion, goals/requirements and the environmental conditions. This may have weakened our ability to capture individual differences in the wild, while we were able to detect individual differences in the laboratory (Fisher *et al.* 2015a). However, we still found a positive relationship, despite our assays of exploration being quite different. In particular, laboratory exploration was measured over only one minute, yet was still related to exploration in the wild, which was measured over an entire day.

Ultimately, these results indicate the need to be careful when relating personality traits measured in the laboratory to traits in the wild, as a relationship might exist for some traits but not others. Either researchers need to validate their measurements by comparison with an analogous behaviour in the wild, or make every effort to ensure they are not in fact measuring something else e.g. a stress response.

Predictors of wild shyness

The factors predicting shyness in the wild were time of day, sex and a weather-age interaction. Time of day was weakly and positively related to the delay before a cricket re-emerged from its burrow. Field crickets move less among burrows at night, likely as a result of the decreased ambient temperature (Rost & Honegger 1987) and possibly because of the threat of shrew and hedgehog predation. Therefore, as dusk approaches the advantage of ceasing daily activity and retreating into a safe refuge increases. Male crickets re-emerged from their burrows more quickly than female crickets. Males need to be outside of the burrow to sing in order to attract mates which, depending on male size, increases reproductive success (Rodríguez-Muñoz *et al.* 2010). The correlation between number of mates and number of offspring in wild *G. campestris* is higher in males than females (Rodríguez-Muñoz *et al.* 2010). Therefore, males may benefit more from leaving a burrow to sing and potentially attract new mates than a female does in leaving the burrow to find new mating partners. Finally, there was a significant age-weather interaction, with older crickets re-emerging in sunny weather less quickly than expected. When young, adult crickets need to bask often to accelerate their development to sexual maturity (typically three-six days post-emergence; Remmert 1985). However, once sexual maturity is reached, the energy from the sun might accelerate the aging process, making individuals less willing to be exposed. In cloudy weather this factor is removed, so young individuals have less need to emerge from the burrow.

The low estimate of R_{Ad} for wild shyness score indicates that shyness of wild crickets is dictated by external conditions (some of which we identify here) rather than by the identity of the individual. This contrasts with the beadlet anemone (*A. equina*), which showed a high level of R_{Ad} for a startle response (Briffa & Greenaway 2011). However, Briffa & Greenaway (2011) pointed out that unmeasured aspects of the microhabitat, e.g. position in the pool or exposure to currents and predators, could be important for sedentary species such as anemones. Indeed, in the laboratory where these factors are absent *A. equina* show intermediate levels of R_{Ad} (Rudin & Briffa 2012). Briffa & Greenaway (2011) also note that repeatability of analogous behaviours can vary greatly among invertebrate phyla, suggesting that we need further work to understand why, in the field, crickets (*G. campestris*) show low repeatability in willingness to take risks (this study), hermit crabs (*P. bernhardus*) show intermediate consistency (Briffa *et al.* 2008) and anemones (*A. equina)* show high consistency (Briffa & Greenaway 2011). This could be due to the mobility of the animals in question. Mobile species that experience a range of conditions might show low repeatability in the wild, while more sedentary species with a stable microhabitat might show high repeatability. It has also been suggested that among-individual behaviour variation is non-adaptive, and instead arises from constraints in development (Duckworth 2010). Whether taxa specific developmental pathways lead to these differences should be investigated.

Microhabitat and shyness

Accounting for microhabitat only slightly reduced our estimate of individual R_{Ad} for shyness in the wild (from 0.10 to 0.06), with the 95% CRIs of these scores overlapping substantially. There was also little variance in shyness attributed to among burrow differences. This suggests that either all burrows are very similar or that the differences among them do not affect cricket behaviour. The crickets dig the burrows themselves in the autumn and spring (Rodríguez-Muñoz *et al.* 2010), which allows them to choose a location and orientation. They also move among burrows throughout the course of the season, abandoning some and regularly using or digging others (Rost & Honegger 1987; Rodríguez-Muñoz *et al.* 2010). This allows them to move if the burrow they are using does not match their preferences, suggesting that differences among those burrows used by crickets do not have a great effect on this measure of shyness.

Predictors of wild activity & exploration

Crickets were more active and explored more when the sun was stronger and less when it was raining. Crickets were unsurprisingly more active when it was warmer, but not more exploratory. Therefore, although temperature drives more general movement about the environment, it does not cause crickets to visit new areas. This also demonstrates the importance of direct sunlight, rather than simply ambient temperature, in influencing cricket behaviour. Females were more active than males. In this species, males typically sing at burrows to attract mates while females move among them, which may drive this difference in activity. The sexes were however equally exploratory, so the higher activity shown by females was to repeatedly visit the same burrows, rather than to employ their additional activity to visit multiple different burrows and males in the same day. Females of this species benefit from mating multiply (Rodríguez-Muñoz *et al.* 2010), but might visit males across different days rather than within the same day. Crickets were more active and exploratory when older. An increase in these traits with age was also found in the laboratory assays (Fisher *et al.* 2015a). A lower residual reproductive value at old age may increase risk-taking behaviour, and so increase the willingness of a cricket to move around its environment to find mates (Williams 1966; Hirshfield & Tinkle 1975). Furthermore, older crickets were more active and exploratory when it was raining than younger crickets, perhaps as older crickets are more willing to take risks involved in being active and exploratory while it is raining. Alternatively, older crickets might have a more robust physiology or be more highly chitinised, allowing them to be move about the environment despite the rain. Males increased activity levels more when older, so the difference in activity between males and females was lower in older crickets. This might reflect the diminishing return for females in continually acquiring new mates, whereas for males the return is probably near-linear (Snook 2014). Males also increased their exploration more as they aged than females did, although this interaction was very weak. Crickets that were on-screen for longer recorded higher activity levels, but did not record higher exploration levels. This likely results from the fact that a cricket can potentially move between neighbouring burrows in a few seconds, so visiting many burrows does not require being on-screen for a long period of time. Older crickets were less active than expected when it was sunny, and also less exploratory. This complements the finding that older crickets are slower to emerge from the burrow when it is sunny, perhaps as a response to the accelerating effects of sunshine on senescence processes. Finally, crickets were more active and exploratory later in the field season. This could be a response to the limited window in which to acquire mates, as at the end of the season in July there are very few other crickets alive. Individuals who are alive at later dates might need to be more active and exploratory to find mates.

Personality in the laboratory and wild traits

Previous work has found relationships between cricket personality in captivity and sexual signalling (Hedrick 2000), immune response (Niemelä *et al.* 2012b) and predation pressure (Hedrick & Kortet 2006). Furthermore, work on laboratory personality measures in our study population has revealed relationships with aging (Fisher *et al.* 2015a). This, along with relationships between laboratory and wild assays in two out of three of the traits we measured here, suggests that personality measured in the laboratory is not irrelevant to adaptation in the wild. For shyness at least, the laboratory can be said to have "low situational strength", allowing among-individual differences to be detected (Uher 2011). However, it seems odd that an environment as unnatural as the laboratory would have such a low impact on cricket behaviour. Indeed, the trait we measured in the laboratory might not be the trait we thought it was at all. Crucially, to determine whether shyness (and activity and exploration) observed in the laboratory is relevant or not to selective forces in nature, it must be compared to fitness-relevant traits of the same individuals in the wild e.g. social interactions and life history. Previous work has demonstrated relationships between personality traits measured in captivity and fitness (Dingemanse *et al.* 2004; Adriaenssens & Johnsson 2013), competitive ability (Cole & Quinn 2012), territoriality (Amy *et al.* 2010), social network position (Aplin *et al.* 2013) and rate of promiscuity (Patrick *et al.* 2012), although no relationship with environmental sensitivity (Minderman *et al.* 2009) and only a weak relationship with BMR (Bouwhuis *et al.* 2014).

Alongside the ability to detect among-individual differences in a controlled environment, an additional strength of laboratory studies is the ability to conduct experimental manipulations to test hypotheses. Such manipulations are typically very difficult in the wild. However, in some systems direct experimental manipulations in the wild are feasible. For example, in the field crickets we could alter burrow characteristics such as grass cover to determine if crickets respond to the characteristics of their microhabitat with behavioural changes. The ability to perform a variety of experimental manipulations with limited resources is another advantage to studying invertebrates.

Conclusions

There were relationships between some behaviours we measured in the lab and their analogues in the wild. This cautions against assuming that ecologically relevant measures of personality can easily be made by removing animals from their natural context. Assays that appear superficially similar may in fact measure different dimensions of personality. Existing literature outlines a variety of relationships between captive personality assays and natural and sexual selection in wild vertebrates, while some types of study systems and questions will necessarily require animals be brought into captivity. Nevertheless, every effort should be made to ensure such assays are good proxies for the particular trait of interest as expressed in the wild.

4. Direct evidence for a pace-of-life syndrome in wild crickets: long- and short-term consistency alongside within-individual change

This chapter is currently in review:
David N. Fisher, Morgan David*, Tom Tregenza and Rolando Rodríguez-Muñoz. Direct evidence for a pace-of-life syndrome in wild crickets: long- and short-term consistency alongside within-individual change (in rev.). *Am. Nat.*

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Abstract

Behaviour varies among- and within-individuals over the long- and short-term. Understanding the extent to which these levels of temporal variation are independent is crucial for a holistic understanding of why behavioural variation exists. Short- and long-term consistencies are rarely quantified simultaneously in the wild, despite their potential value for evaluating models of behavioural variation. For instance, the pace-of-life syndrome hypothesis suggests that differences in long-term consistent behaviour (personalities) result from divergent life-history strategies, with more active/risk-taking individuals reproducing rapidly but dying young. However, direct support for this hypothesis is lacking from studies on wild animals, and completely absent for wild invertebrates. We regularly measured the activity of wild adult field crickets at both short and long intervals over their entire adult lives. This allowed us to separately quantify behavioural consistencies over short- and long-terms and the level of individual variability. We found support for a pace-of-life syndrome, confirming the negative trade-off between mating rate and lifespan based on activity level. There was also considerable variation attributed to short-term consistency, indicating state-dependant behaviour. Furthermore, crickets increased activity with age, although this effect accounted for less variance than either type of consistency. Our results reveal how behaviours are influenced by predicted syndromes, and demonstrate the contribution of different hierarchies to overall behavioural variation.

Keywords: behavioural type, Gryllus, life-history, pace-of-life, personality, plasticity, wild behaviour, variance

Introduction

Behavioural traits have the potential to vary enormously both within- and among-individuals, and over much shorter timescales than most other traits. Despite this plasticity however, consistent differences among-individuals in both average behaviour and degree of plasticity are widespread, with a range of evolutionary and ecological implications (Bell *et al.* 2009; Dingemanse *et al.* 2010; Wolf & Weissing 2012; Dingemanse & Wolf 2013). Quantifying and understanding this variation has been a major focus in biology in recent decades (Pigliucci 2005). Short-term repeatability over the course of a few hours or days (David *et al.* 2012) may relate to individuals' "states" (Houston & McNamara 1999), with longer term repeatability over individuals' lifespans (Bell *et al.* 2009) being described in terms of behavioural type or "personality" (Dall *et al.* 2004). Partitioning among-individual variance in behaviour into these short- and long-term temporal consistency levels and also quantifying the degree of within-individual variation allows us to measure their relative contribution to the total variance in individuals' behaviour. This allows accurate interpretation of the importance of these different hierarchies of variation, for instance allowing us to compare the relative importance of personality type compared to changes with age or condition. Furthermore, this approach allows us to identify which levels of variation we understand well and which we do not (Westneat *et al.* 2014).

As an example, field crickets show consistent among-individual variation in activity levels over their adult lifetime and across contexts (Fisher *et al.* 2015a,b). Moving around in the natural environment allows them to encounter potential mates, but may also increase their chances of encountering a predator. This potential balancing selection on activity levels can lead to a flat fitness function for activity level (Mangel & Stamps 2001), or a behavioural polymorphism for average activity (Wolf *et al.* 2007a). The absence of a single adaptive peak of behaviour may therefore allow long-term among-individual behavioural differences to persist in populations. Crickets may also be repeatable over shorter periods of time e.g. when responding to features of their environment such as temperature (Doherty 1985), that are stable over short periods of time. However, crickets show considerable within-individual variation even between identical tests only 30 minutes apart (Fisher *et al.* 2015a), indicating they are not completely consistent even within-contexts.

Current theory suggests that long-term behavioural consistency should be part of a syndrome that links behaviour to a stable life-history strategy (Stamps 2007; Réale *et al.* 2010). More active crickets should also have higher mating rates, but also shorter lifespans (alongside other differences) i.e. they possess a fast “pace-of-life syndrome” (POLS), compared to less active, slower mating but longer lived individuals in the same population. These potential syndromes have attracted a great deal of recent interest (Eccard & Herde 2013; Le Galliard *et al.* 2013; Niemelä *et al.* 2013; Shearer & Pruitt 2014; Montiglio *et al.* 2014a; Watts *et al.* 2015; Hall *et al.* 2015), but studies of personality in natural systems have not investigated the types of potential trade-off between the major life history traits of mating rate and lifespan that are fundamental to the POLS hypothesis.

Feedbacks between state and behaviours consistent in the short-term can promote or retard the development of long-term behavioural consistency (McElreath *et al.* 2007; Wolf *et al.* 2007b; Luttbeg & Sih 2010; Sih *et al.* 2014b). Long-term differences among-individuals would also result in frequent short-term differences among those individuals, independent of whether those individuals were actually in different states at any given point in time. Only by estimating both at once can we confirm that an individual’s state-dependent behaviour is an additional level of variation to its personality (see Fig. 4.1). Yet simultaneously quantifying both short- and long-term behavioural consistency is rarely attempted (but see David *et al.* 2012 for a two-step approach). Finally, individuals may change consistently in response to some environmental variable. If that variable is not accounted for, individuals may be judged to be inconsistent in their behaviour, even if the level of their behaviour is consistently different from others in the population along the environmental gradient (Nussey *et al.* 2007; Dingemanse *et al.* 2010).

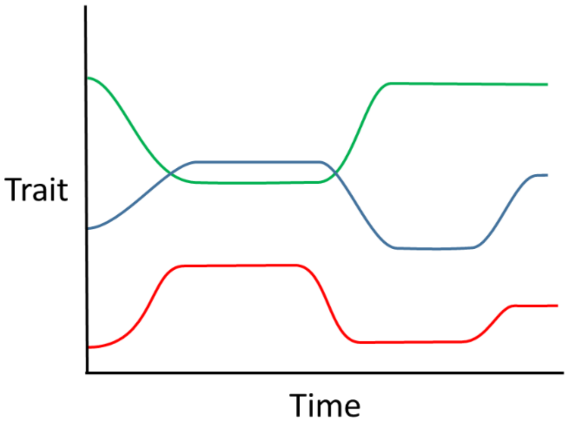

Figure 4.1. Different individuals (blue, red and green) change in the value of some behavioural trait (e.g. boldness) over time. They differ on average over the whole observation period (showing long-term differences - personalities). Additionally, over the short-term, they vary in trait expression, the adaptive component of which will presumably relate to variation in state. At any given time point, red and blue are consistently different but their short-term variation is correlated, indicating some shared factor affecting their state-dependent behaviour in a similar way. In contrast, green and blue are more consistently similar in the overall level of their behavioural expression, but their state-dependent element varies more independently of one another. The similarities between blue and green are more complex combinations of personality and short-term state. This is not apparent unless individuals are both studied over longer periods of time, and their short- and long-term consistency are simultaneously quantified.

To investigate these different levels of among- and within-individual consistency and variability, we collected activity measures regularly over the lifetime of wild adult field crickets (*Gryllus campestris*). We took multiple measures each time we captured the crickets, as well as re-capturing them at regular intervals. This allowed us to quantify both short- and long-term consistency. We were firstly interested in whether crickets possessed, independent of one another, both, long- and short-term among-individual differences in behaviour i.e. both personalities and state-dependant behaviour. If these were confirmed, we could then attempt to quantify the variables that influence each of them. For state-dependant behaviour, we expected that activity would increase with temperature (as found in both the wild and the laboratory; Fisher *et al.* 2015a,b), age (as we have already shown in this population; Fisher *et al.* 2015a, possibly as a response to lower residual reproductive values at older ages e.g. Hall *et al.* 2015) and condition (as high-condition individuals may be more willing to take risks e.g. Martín *et al.* 2006). Each of these would be consistent within a capture event, and so would promote short-term consistency. For personality, a POLS would explain long-term behavioural consistency if there is a positive relationship between activity and mating rate, and a negative relationship between activity and lifespan, flattening the fitness function (Mangel & Stamps 2001; Stamps 2007; Réale *et al.* 2010). We could then compare the relative amounts of variance explained by these measures of consistency to long-term within-individual variation due to factors such as aging, and the remaining un-accounted for individual variability. This would indicate the relative importance of these levels of consistency and variation relative to the total variation in cricket behaviour.

Methods

Study subjects

The study was carried out at the “WildCrickets” project field site in Northern Spain, see (Rodríguez-Muñoz *et al.* 2010) and www.wildcrickets.org for further details. *G. campestris* is univoltine and adults are active in the months April – July following overwintering as nymphs in burrows they dig themselves. At the start of this adult activity period we randomly placed 120 video cameras over burrows with nymphs, allowing us to record the emergence date and subsequent behaviour of adult crickets. These cameras record 24 hours a day using infra-red light at night. If a burrow monitored by a camera is observed not being used by a cricket for several days, we moved the camera to a burrow where a cricket has recently been observed. Migration to and from neighbouring fields is very limited as a result of surrounding unsuitable habitat and barriers to dispersal on all sides of the meadow (Bretman *et al.* 2011).

Data collection

We watched the video recordings to catalogue cricket behaviour such as movement amongst burrows, mating (successful matings being identified as where transfer of a spermatophore was visually confirmed), fighting and predation events. Individuals were observed for 57.8 ± 28.9% (mean ± standard deviation) of their adult lifespan. The vast majority of important events that crickets engage in (mating, fighting, singing, avoiding predators and oviposition) take place at burrows, so we are confident that we captured nearly all of the relevant behaviour (Rodríguez-Muñoz *et al.* 2010). To complement the video recordings, we directly observed burrows without a camera in the field for presence of crickets and their identity on a daily basis. As crickets rarely move among burrows as late instar nymphs, this allowed us to determine emergence dates for individuals at burrows without cameras by recording when an adult was observed where previously there had been a nymph. Crickets were tagged three or four days (3.76 ± 2.81) after they emerged. We blocked the burrows while tagging or assaying the crickets trapped from them, to prevent other animals, including other crickets, from moving in. If a cricket's death was not directly observed, its death date was set as the day after it was last observed.

Behavioural trials

Once caught, we weighed the crickets and carried out behavioural tests to assay their activity. Tests occurred in a temperature controlled room (19.8 °C ± 0.59), in a clear plastic box (290 x 201 x 212mm) monitored from above by a camera. Crickets were placed in an opaque tube (80 x 20mm), simulating a refuge like a cricket burrow, and placed in individual boxes. Using iCatcher, a digital video recording software (www.icode.co.uk), eight virtual trip wires were set across each box, each covering a different area of the box. Activity was quantified as the number of virtual trip wires a cricket crossed after it left the refuge, see (Fisher *et al.* 2015a) for further details on experimental set-up. This test predicts activity level in the wild (Fisher *et al.* 2015b). If an individual did not leave the tube within 30 minutes (41% of trials) a missing observation was recorded, as giving a cricket the minimum activity score would inflate the individual repeatability scores if a cricket did this consistently. Crickets were tested twice each time they were caught, with a 30-minute intervals between these, to quantify short-term behavioural consistency.

The first time an individual was caught and after the behavioural tests had finished, we fixed a small waterproof vinyl tag to each cricket's thorax using cyanoacrylate glue (Rodríguez-Muñoz *et al.* 2010). Each tag had a unique code, allowing individual identification without disrupting natural behaviour. We also took photos of the crickets from above, and used ImageJ (Schneider *et al.* 2012) to measure the width of widest part of their thorax. Crickets were then released back to the burrows we trapped them from. Subsequently, we re-caught, re-weighed and re-tested each individual cricket at time intervals of around ten days and continued until the individual was no longer observed alive, allowing us to quantify long-term behavioural consistency.

Statistical analyses

We built two generalized linear mixed models in R (ver. 3.0.2; R Core Team 2013) using the package "MCMCglmm" (Hadfield 2010a), a full model and an intercept only model. Each cricket's activity scores were the responses, with different sets of fixed effects but identical random effect structures for the two models. We set an offset as the log of the number of seconds a cricket spent outside the refuge, effectively modelling activity as a rate. We included two random effects: individual identity and the unique combination of individual identity and capture number. The latter effect quantifies the among-individual, within-capture variance, and so short-term differences (state-dependant behaviour). The variance attributed to individual identity is then interpreted as the among-individual, among-test variance i.e. long-term consistency (personalities). We also allowed the effect of age to vary at the level of the individual. This type of model (known as a random regression or random slope model) fits a slope for each individual, as well as an intercept, allowing individuals to change differently over time, rather than a single population wide effect of age (Henderson 1982). These models allow the integration of the study of behavioural consistency and plasticity (Nussey *et al.* 2007; Dingemanse *et al.* 2010).

The full model contained variables that could contribute to a POLS, and so explain long-term consistency, as well as variables that could explain an individual's state, and so short-term consistency. The POLS variables were: lifespan (days), lifetime mating success, future mating rate (FMR), and sex, as well as the interaction between sex and FMR. The interaction models the possibility that investment in future mating opportunities affects the sexes differently (e.g. Dammhahn 2012). Cameras were moved around the meadow, so each individual was only monitored for around half its adult lifetime. Therefore, lifetime mating success (number of successful matings) was divided by the log of the total number of minutes a cricket spent under observation and FMR was calculated by dividing the observed number of matings from the date of the assay until the cricket's death by the log of the number of minutes the cricket was monitored for from the date of the assay until the cricket's death. Using untransformed monitoring effort made no qualitative difference to the effects of FMR and lifetime mating success (not shown). The variables that we examined in relation to short-term behavioural consistency were: temperature of the laboratory (°C), condition (mass / thorax width), age (number of days since emergence at date of test) and an age x temperature interaction, as previous analyses indicated that age x weather interactions can influence behaviour (Fisher *et al.* 2015b). As the individual's lifespan term models the among-individual effect of age, the fixed effect of age can be interpreted as an within-individual effect (van de Pol & Verhulst 2006). The intercept model included none of these fixed effects apart from age, which was retained to aid interpretation of the random regression.

Each continuous variable was mean centred and transformed to unit variance so all were on the same scale, enabling the effect sizes to be directly compared (Hunt *et al.* 2005; Schielzeth 2010). We excluded all crickets that were observed for less than 300 minutes in total in the field. This removes individuals for which our information is likely to be relatively inaccurate. We used a Poisson error structure, a log-link function and additive errors. We set expanded, non-informative priors for the among-individual and residual variances. We used 300,000 iterations, with the first 50,000 discarded and then 1/10 subsequent iterations kept to estimate parameter effects. The models were checked to confirm convergence of parameters and lack of auto-correlation between estimates. Deletion testing cannot be performed on Bayesian models, and the deviance information criterion for non-Gaussian models in MCMCglmm is not focused correctly (Hadfield 2012). Instead, alongside assessing the importance of the fixed effects, we examined the conditional (proportion of variance explained by the fixed and random effects) and marginal (fixed effects only) R^2 values, and how the variance components relating to short- and long-term consistency changed between the full and intercept-only models. This allowed us to determine which aspects of the variance we were able to explain. R^2s were calculated following (Nakagawa & Schielzeth 2013) with a modification for use with random regression models (Johnson 2014).

Results

We monitored 172 different individuals in the wild for a mean of 408 hours each and also measured their behaviour in the laboratory. Individuals were captured between one and five times (mean ± standard deviation: 2.54 ± 1.43), with 438 assays of activity in the laboratory recorded. The fixed effect estimates from the full model with all terms are illustrated in Fig. 4.2, and the among-individual variance components for the full and intercept-only model are illustrated in Fig. 4.3. In the full model there were similar and appreciable amounts of among-individual among-test variance (long-term consistency) and among-individual, within-capture variance (short-term consistency). High FMR tended to be associated with increased activity (Fig. 4.4), although the 95% credible intervals (CRIs) marginally crossed zero. More active crickets had shorter lifespans (Fig. 4.5). Activity was positively related to age, although there was little among-individual variance in the change with age (mode of among-individual variance in change of activity with age = 0.004; Fig. 4.6). The temperature x age interaction was negative but the 95% CRIs marginally crossed zero, indicating that at hotter temperatures older crickets tended to be less active than expected. Temperature, sex, condition, lifetime mating success and the sex x FMR interaction did not affect activity.

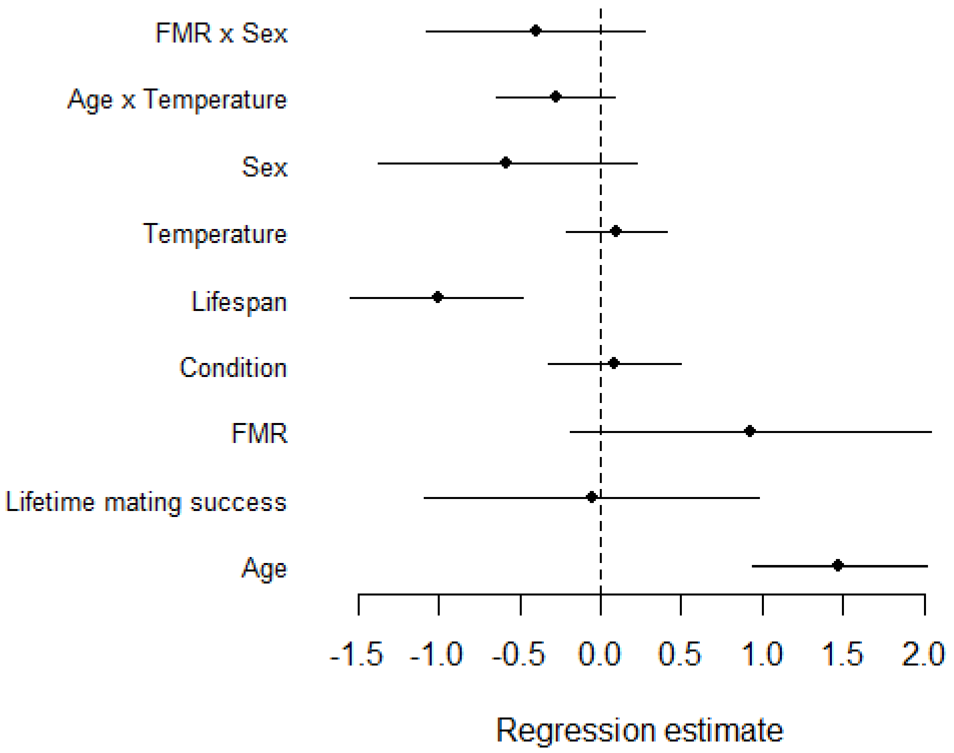

Figure 4.2. Coefficient plot showing the mean and 95% credible intervals for the posterior distributions of the regression estimates for each term in the model. Each continuous variable was transformed to the same units, so the effect sizes are directly comparable. For sex, female was set as the default with males modelled as the contrast, so the effect size indicates the mean difference of males from females. The effects are directly from the model, hence are on a log scale.

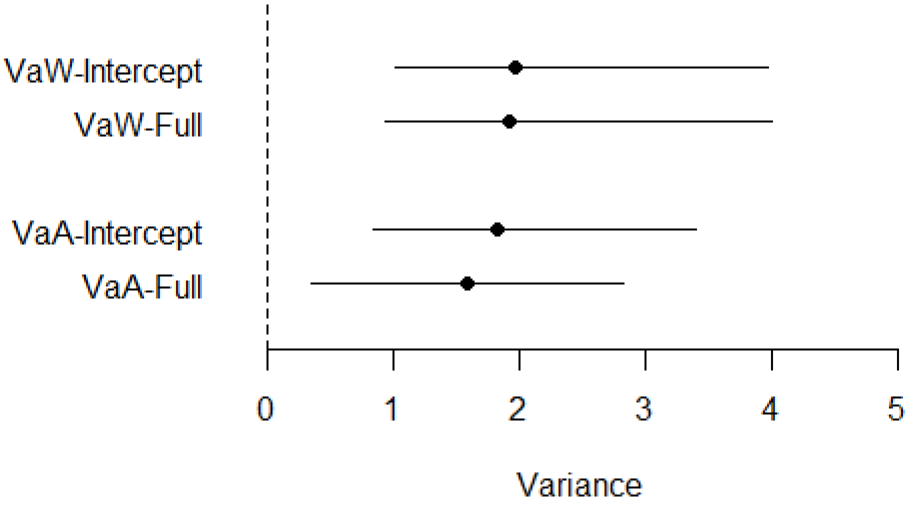

Figure 4.3. Plot of the modes of the variance components and their 95% credible intervals. VaW refers to the among-individual, within-capture variance i.e. short-term consistency or state-dependent behaviours. VaA refers to the

among-individual, among-test variance i.e. long-term consistency or personality. “Intercept” and “Full” refer to the estimates from the intercept only model and the model with all terms respectively.

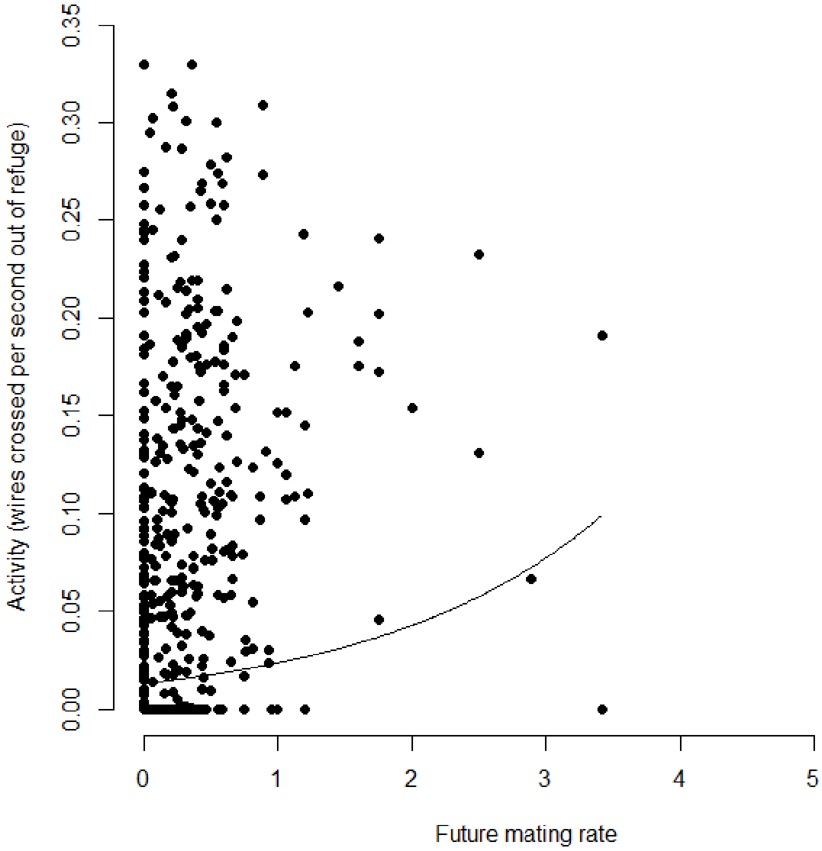

Figure 4.4. High future mating rates were associated with high activity, although the 95% credible intervals marginally crossed zero. The line is from a predictive model of activity with a range of future mating rate values from the real data, and the mean age and lifespan of the crickets in this study as fixed effects. This model was run in lme4 (Bates *et al.* 2012), using a Poisson error structure, an offset of time spent outside of the refuge and the same random effect structure as the models in the main test. This was conducted in lme4 as the predict function for MCMCglmm cannot accept simulated data frames at this point. Note that the relatively large number of zero scores for activity causes the line to be relatively low.

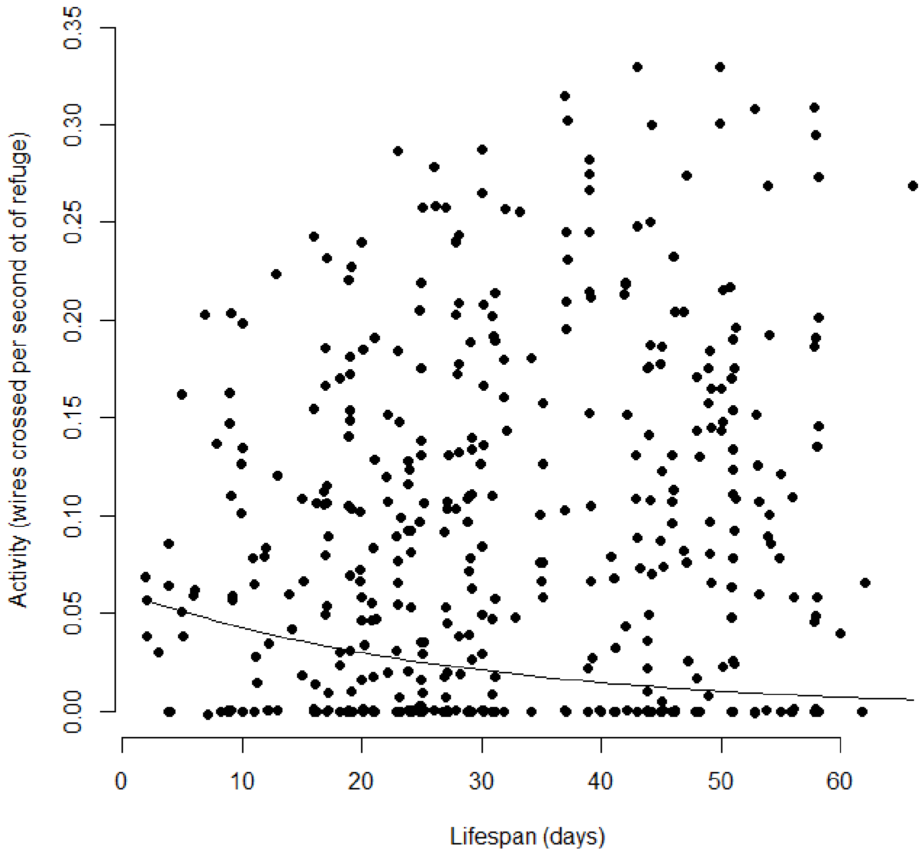

Figure 4.5. Short lifespans were associated with high activity. The line is from a predictive model of activity with a range of lifespans from the real data, and the mean age and future mating rate of the crickets in this study as fixed effects. This model was run in lme4 (Bates *et al.* 2012), using a Poisson error structure, an offset of time spent outside of the refuge and the same random effect structure as the models in the main test. Note that the relatively large number of zero scores for activity causes the line to be relatively low.

The fixed effects explained 17.7% of the total variation, giving a marginal R^2 of 0.177. The average amount of among-individual, among-test variation accounted for 10.7% of the variance and the among-individual, within-capture variation accounted for 16.5% of the variance, giving a conditional R^2 (the proportion of variance explained by both the fixed and random factors) of 0.450. The intercept only model showed a proportional change of the among-individual, within-capture variance of 0.029, and a proportional change of the among-individual, among-test variance of 0.335. This means that removing the fixed effects causes these variance components to increase (Nakagawa &

Schielzeth 2013), although only marginally for the among-individual, within-capture variance.

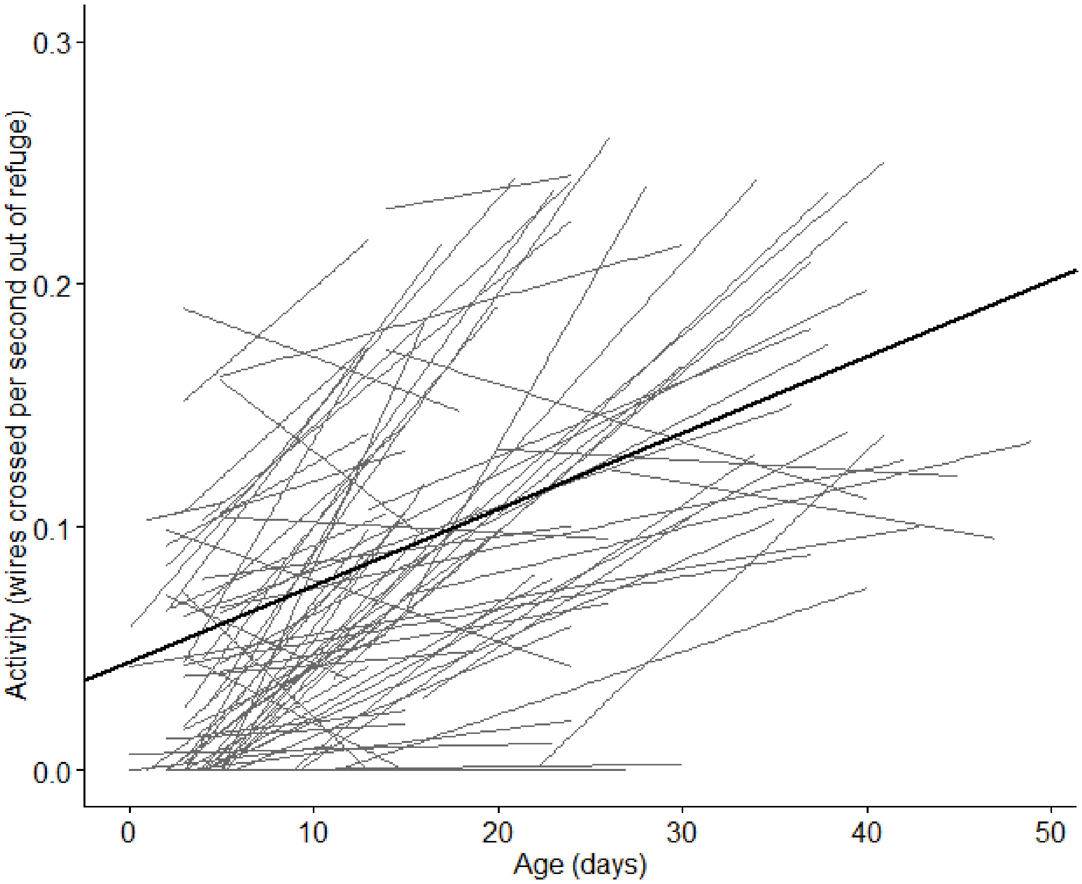

Figure 4.6. Activity increased with age, but with limited among-individual variance in the change with age. Each grey line is a line of best fit through the activity scores from an individual cricket, as we modelled each cricket as having a unique change with age using random regression. The black line is the population change with age, from a simple regression of age on activity. Drawn using ggplot2 (Wickham 2009).

Discussion

Personalities and state-dependent behaviours

We found considerable consistency in behaviour over both the short- and long-term. Field crickets exhibit among-individual differences in long-term behavioural tendencies (personality) and short-term, presumably state-dependent, differences among-individuals. It seems likely that both of these patterns of variation will have fitness consequences and hence be subject to selection. By quantifying both levels of variation simultaneously, our results demonstrate that short- and long-term behavioural consistencies exist with some independence from one-another. However, it is still possible that processes at one level of consistency produce consistency at another level. For example positive feed-backs between risk-taking behaviour and condition could result in individuals that consistently take more risks over their lifetime than others (Luttbeg & Sih 2010), although this particular process seems unlikely in our system as condition did not influence activity.

Substantial outstanding variance at both the state-dependant and personality level was apparent in the full model. So, while we have partitioned the variance at those temporal levels to these random effects, we have not identified the source of the variance e.g. what traits of the individual or the context account for it. If we had identified which traits of an individual, e.g. its life-history strategy, accounted for the long-term differences among-individuals, then the among-individual among-test variance would approach zero when modelling this life-history strategy (Nakagawa & Schielzeth 2010). The same is true for short-term consistency; we may have identified that crickets have some short-term consistency, but the fact that this variance component is not zero indicates that we do not completely understand what its basis is.

Short-term behavioural consistency

Of the variables meant to explain short-term variation, only age was significant at the 95% level. Furthermore, there was only a slight increase in the among-individual, within-capture variance from the full to the intercept only model, which included the effect of age, indicating the other terms had very little explanatory power. There also remained an appreciable amount of variance attributed to short-term individual differences in the full model, which means that crickets are consistent in the short-term for reasons we were unable to quantify.

To allow accurate cost/benefit analysis, decisions individuals make at each time point are predicted to include considerations of their state (Houston &

McNamara 1999). For example, chin-strap penguin chicks (*Pygoscelis antarctica*) allow predatory birds to approach them more closely and flee shorter distances when they are healthier (Martín *et al.* 2006). Assuming that an individual cricket's behaviour is an adaptive response to its state, these results suggest that we have not effectively modelled individual states. Testing theories for why individuals make these decisions requires that we are able to quantify an individual's state in all systems of interest. This is challenging however when definitions typically read something like: "the state of an animal refers to all those features that are strategically relevant, i.e. features that should be taken into consideration in the behavioural decisions in order to increase fitness" (Wolf & Weissing 2010). There are a large number of different models that relate state to behavioural consistency (reviewed in Sih *et al.* 2014b), so in each study system and for each model, serious consideration should be given to what are appropriate state variables. For *G. campestris* at least, environmental temperature and condition appear to be relatively poor predictors of state.

Age however was positively related to activity level. We have previously interpreted this as a response to lower residual reproductive values in old age (Fisher *et al.* 2015a). Consistent residual reproductive values or future fitness expectations have been suggested to lead to behavioural polymorphisms within-populations (Wolf *et al.* 2007a). The effect of age was weaker in hotter temperatures, which we have previously attributed to the potential accelerating effects of temperature on senescence (Fisher *et al.* 2015b), although this remains to be formerly tested. The fixed effect of age accounted for around 8% of the variance in cricket activity levels. This is lower than the variance accounted for by both personalities and state-dependent behaviour separately, indicating the relative importance of these different sources of variation in this population.

Long-term behavioural consistency

Activity and lifespan were negatively related, while there was a tendency for crickets with a higher FMR to be more active. Crucially, these two appear to cancel each other out, as there was no relationship between activity level and lifetime mating success. These finding are in concordance with the POLS hypothesis, suggesting that long-term among-individual behavioural differences are based on among-individual differences in overall life-history strategy (Biro & Stamps 2008; Réale *et al.* 2010; David *et al.* 2015). Similar relationships have now been found in a number of systems (Hawlena *et al.* 2009; Adriaenssens & Johnsson 2011; Dammhahn 2012; Montiglio *et al.* 2014a; Dosmann *et al.* 2015; Hall *et al.* 2015; although these are not always simple or in the predicted direction: Réale *et al.* 2009; Kluen *et al.* 2013; Montiglio *et al.* 2014b; David *et al.* 2015), but this is the first where a flat relationship between mating success and a trait related to risk-taking alongside trade-offs between lifespan and mating rate has been shown. It is also the first such investigation in wild invertebrates, but see Niemela *et al.* (2015) for an analogous boldness-lifespan trade-offs in another wild population of *G. campestris*. Individuals of both sexes that have more matings have a higher lifetime fitness, measured as number of offspring surviving to adulthood (Rodríguez-Muñoz *et al.* 2010). Therefore, using successful matings as a proxy for fitness is reasonable. Furthermore, that both sexes benefit from promiscuity (Rodríguez-Muñoz *et al.* 2010) explains why the effect of FMR on activity was similar between the sexes. Previous research on grey mouse lemurs (*Microcebus murinus*) found a relationship between future reproductive investment and risk-taking only in males (Dammhahn 2012). Studies on more species are therefore required to determine whether sex differences in the POLS are dependent on the mating system or some other form of sexual selection, as sexual selection could both generate and maintain both among-individual differences and within-individual consistency (Schuett *et al.* 2010).

Due to these pace-of-life syndrome based consistent differences in behaviour between individuals, our intercept only model had a proportional increase in the among-individual, among-test variance compared to the full model. This indicates that our fixed effects absorbed some of the variance that would otherwise have been attributed to the random effect. This was not complete however, and there was still an appreciable amount of variance among-individuals, among-tests in the final model. This means there are still factors outstanding, such as developmental processes (Duckworth 2010), variation in parasite burden (Poulin 2013), or differences in genetic quality (Rowe & Houle 1996) that cause individuals to be consistently different from each other in the long-term.

Variability of individuals

In the full model, 26% of the variance was attributed to within-individual variation and measurement error. We attempted to minimise measurement error by using a comprehensive monitoring protocol and excluding individuals monitored for less than 300 minutes, so this variance is probably predominantly genuine variance within-individuals. This within-individual variability was greater than the amount attributed to fixed effects (18%), and was outstanding after accounting for those fixed effects, including the long-term within-individual change with age. This pattern of substantial unexplained within-individual variance is repeated across many studies on individual-level behaviours; the average proportion of variance explained by among-individual differences is 37% (Bell *et al.* 2009), leaving 63% attributed to within-individual variance and measurement error. It therefore remains problematic that there is so much variance that we cannot account for. Low explanatory power is common in ecological studies (Low-Décarie *et al.* 2014), so this is not necessarily a field-specific problem. It does suggest however that if the current approaches can only explain on average less than half of a population's behaviour, then new approaches may be required. In particular, abandoning the assumption of homoscedasticity of residual variance to investigate variation in within-individual variance may prove fruitful (Stamps *et al.* 2012; Westneat *et al.* 2012, 2014; Dingemanse & Wolf 2013; Briffa *et al.* 2013). For example, hierarchical general linear models allow the user to explain individual variation in predictability through interactions with fixed effects (Cleasby *et al.* 2014). Alternatively, non-linear approaches, through individual-based modelling (Lehmann 2009) or complex-system based approaches (Bradbury & Vehrencamp 2014) may be better suited to the complex dynamics observed in the natural world than the linear-modelling approaches that dominate animal behaviour variation research.

Conclusions

We found both short- and long-term among-individual differences in cricket activity levels. Both of these accounted for more variance in cricket behaviour than the (still significant) aging process, while condition, sex and environmental temperature were unimportant. Long-term (personality) differences were partly attributed to a life-history syndrome, providing support for the POLS hypothesis, in particular demonstrating crucial trade-offs that had not been shown to date. However, substantial variance in both long- and short-term among- individual consistency remained unexplained. Accounting for the variables that explained the short-term differences through identifying the state variables that are most relevant to our study organism is an outstanding challenge. A similarly large challenge remains accounting for the substantial degree of within-individual variability. This challenge to true across all taxa in Bell *et al.*'s meta-analysis (Bell *et al.* 2009), indicating it should be a priority for all researchers interested in explaining variation in individual behaviour (Cleasby & Nakagawa 2011; Westneat *et al.* 2014; Cleasby *et al.* 2014).

5. Comparing pre- and post-copulatory mate competition using social network analysis in wild crickets

This chapter is published as:

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Abstract

Sexual selection results from variation in success at multiple stages in the mating process, including competition before and after mating. The relationship between these forms of competition, such as whether they trade-off or reinforce one-another, influences the role of sexual selection in evolution. However, the relationship between these two forms of competition is rarely quantified in the wild. We used video cameras to observe competition among male field crickets and their matings in the wild. We characterised pre- and post-copulatory competition as two networks of competing individuals. Social network analysis then allowed us to determine: 1) the effectiveness of pre-copulatory competition for avoiding post-copulatory competition 2) the potential for divergent mating strategies and 3) whether increased post-copulatory competition reduces the apparent reproductive benefits of male promiscuity. We found: 1) limited effectiveness of pre-copulatory competition for avoiding post-copulatory competition; 2) males do not specifically engage in only one type of competition; 3) promiscuous individuals tend to mate with each other, which will tend to reduce variance in reproductive success in the population and highlights the trade-off inherent in mate-guarding. Our results provide novel insights into the works of sexual competition in the wild. Furthermore, our study demonstrates the utility of using network analyses to study competitive interactions, even in species lacking obvious social structure.

Key words: *Gryllus*; cryptic female choice; male competition; sexual selection; sperm competition.

Introduction

Competition for mates has a potent influence on evolution. Females may prefer particular males and dominant individuals can monopolise access to females (Birkhead & Pizzari 2002; Andersson & Simmons 2006), leading to variance in fitness that drives selection. Additionally, in both internally and externally fertilising species, once matings are achieved there is still room for further sexual selection through processes such as sperm competition (Parker 1970) and cryptic female choice (Thornhill 1983). This divides sexual selection into two arenas of competition: pre- and post-copulatory ("episodes of selection" according to Pizzari *et al.* 2002). These arenas of competition are however not necessarily independent (Yasui 1997; Tomkins *et al.* 2004). A number of studies have identified negative associations across species between sexual dimorphism in body size (an indicator of males' ability to monopolise access to females) and relative testes size (an indicator of the stength of post-copulatory selection) (Heske and Ostfeld 1990; Poulin and Morand 2000). This pattern is consistent with the hypothesis that intense pre-copulatory competition leads to reduced post-copulatory competition between individuals. Furthermore, ability in pre- and post-copulatory competition within-individuals can be positively related (e.g. Matthews *et al.* 1997; Hosken *et al.* 2008), negatively related (e.g. Pizzari *et al.* 2002; Simmons and Emlen 2006; Demary and Lewis 2007; Engqvist 2011) or show no relationship (e.g. Lewis *et al.* 2013; reviwed by Mautz *et al.* 2013). If ability in pre- and post-copulatory competition is negatively related within-individuals, then divergent male morphs specialising in either mode of competition, such as those found in the beetle *Onthophagus binodis* (Cook 1990), can evolve. If there is a genetic correlation between ability in the two types of competition the rate of evolutionary change in traits will be increased if the correlation is positive and retarded if it is negative (Andersson and Simmons 2006; Mautz *et al.* 2013).

If males with many matings are disproportionately more likely to mate with females who also have a higher than average numbers of partners, their reproductive success will be reduced due to a loss of paternity through sperm competition (Sih *et al.* 2009). This will lower the variance in reproductive success in the population, and weaken pre-copulatory selection (e.g. Danielsson 2001). The relationship between mating rate and reproductive success could even be completely reversed if the positive association between male and female mating rate is strong enough (McDonald & Pizzari 2014). Alternatively, if males who mate frequently also achieve high exclusivity, then the variance in reproductive success will instead increase. Therefore, the potentially major implications for fitness and evolution of both these arenas of competition makes understanding the relationship between them important (Preston *et al.* 2003; Hunt *et al.* 2009; Sbilordo and Martin 2014).

In the field cricket *Gryllus campestris* individuals live in and around burrows they dig as nymphs in the autumn and continually enlarge as they grow. *G. campestris* will only share their burrow with a member of the opposite sex once they are adult and fights occur intra-sexually in both males and females. Fights are assumed to be contests for access to mating partners and burrows that provide protection from predators (Alexander 1961; Rodríguez-Muñoz *et al.* 2011). Both sexes seek out multiple mates *(Rodríguez-Muñoz et al.* 2010) so males are frequently in sperm competition (Tyler *et al.* 2013). This mating system, with its high levels of both pre- and post-copulatory competition provides an opportunity to study the relationship between these types of male-male competition. We tested the following three sets of predictions:

1) Different patterns of dominance could lead to different relationships between pre- and post-copulatory competition between males. If dominant males prevent others from mating by evicting them from burrows, within a pair of crickets there would be a negative relationship between the intensity of pre- and post-copulatory competition. Alternatively, males may fight more when they are of a similar fighting ability, and so a clear dominance hierarchy cannot be established. In such a situation, a female may not be able to choose between them, and so mate with them both. This would result in positive associations within a pair for the intensity of the two types of competition.
2) If some individuals can consistently evict others from burrows, this could then lead to individuals specialising in either pre- or post-copulatory competition. This would result in negative relationships within-individuals between engagement in pre- and post-copulatory competition. However,

crickets are thought to possess flexible mating strategies (Buzatto *et al.* 2014), so we do not expect individuals to consistently trade-off between the two types of competition. Instead, positive relationships based on condition or quality seem more likely (e.g. Hosken *et al.* 2008).

3) While males may attempt to dominate one another to maximise their reproductive success, females may mate multiply with both dominant and non-dominant males. This would tend to reduce the success of dominant males through sperm competition, resulting in a reduction in the variance in reproductive success and pre-copulatory selection within a population (Sih *et al.* 2009). The use of mating success as a proxy for reproductive success could then lead to misleading results. Alternatively, males who are successful at acquiring matings may also be successful at preventing females from remating, which would have the opposite effect.

Directly comparing pre- and post-copulatory competition to investigate these predictions is a challenge. Although pre- and post-copulatory competition differ in how the individuals interact, the time and spatial scale they interact at and the currency of victory, they can both be represented in the same way: as a social network. Links (“edges” in network terminology) can be drawn between individuals (“nodes”) if they engage in pre- or post-copulatory competition with each other (McDonald *et al.* 2013), representing the population as a network. For example, two males can be linked if they fight one another for access to a female, or they can be linked by both mating with the same female within a timeframe which places them in sperm competition with one another. Alternatively, an entire mating system can be represented as a network of male-female links. This network approach allows the researcher to quantify each individual’s unique social and competitive environment, thus providing more accurate estimates of the selection that a population is under (McDonald *et al.* 2013).

The networks can be analysed using social network analysis (SNA). For instance, the centrality measure “degree”, which is the number of unique edges a node possesses, can be *used* to quantify the intensity of competition an individual is experiencing (McDonald *et al.* 2013). Recent reviews have highlighted that SNA can be used even with animals not typically considered “social” (Krause *et al.* 2009; Sih *et al.* 2009; Krause *et al.* 2011; McDonald *et al.*

2013; Pinter-Wollman *et al.* 2013; McDonald and Pizzari 2014; Kurvers *et al.* 2014). For example, Muniz *et al.* (2014) examined differences between territorial and sneaker males using social networks of male harvestmen (Se*rracutisoma proximum*). They found that territorial males experienced less sperm competition on average, but the amount was more variable than for sneaker males. Meanwhile, in mating networks of the Asian red palm weevil (*Rhynchophorus ferrugineus*) males show greater variance in the number of unique individuals they interact with than females, suggesting that males are under stronger sexual selection (Inghilesi *et al.* 2015).

To build on these applications of SNA, we observed the interactions and movements among burrows of a wild population of field crickets (*G. campestris*). Burrows are dug by nymphs in the autumn, and are used to avoid predators and adverse weather conditions. *G. campestris* is univoltine and adults are active between April and July. Sexual activity begins two-five days after the final moult to adulthood, when males start to sing from their burrows to attract mates and both sexes move among burrows in search of mates. Observing males fighting each other, and mating with the same female allows us to construct networks of pre- and post-copulatory competition in order to test the three sets of predictions presented above.

Methods

Data collection

Observations were made at the “WildCrickets” project site in Northern Spain (Rodríguez-Muñoz *et al.* 2010). Each spring since 2006, we have located and marked each burrow at our study site. Around mid-April, to coincide with when adults start to emerge, we placed cameras over burrows with nymphs, allowing us to record the emergence dates and subsequent behaviour of adult crickets. We have completed video analysis of cricket interactions for the years 2006 and 2013 and these are the data used in this study. There were 64 cameras in 2006 and 120 in 2013, and the total adult population sizes were 151 and 239, respectively. In both years, at the peak of the season there were more burrows than cameras, so we moved cameras from burrows that had recorded no activity for two-three days to monitor as many individuals as possible. In 2006 individuals were observed for a mean of 11.8 ± 10.7 days (mean ± standard deviation) and in 2013 they were observed for 13.6 ± 10.1 days. The majority of behaviour related to reproductive success takes place at the burrows (Rodríguez-Muñoz *et al.* 2010). We also directly observed burrows without a camera, to assess when the resident nymph became an adult. Late instar nymphs rarely move among burrows, so we can be confident that we correctly assigned emergence dates to most of the population.

Three or four days after each cricket emerged as an adult, we trapped it and glued to its thorax a unique visible tag with a one or two character code. This allowed individual identification without disrupting natural behaviour. Following this tagging process we released the cricket back to the burrow we trapped it from. The burrow was blocked while the cricket was being tagged to prevent other animals, including other crickets, from usurping the burrow. We then watched the video recordings to record cricket behaviour such as movement amongst burrows, mating, fighting and predation events for each individual until its death. When the death of a cricket was not directly observed, we assigned the last observation date as the date of death. Migration in and out of the study area is relatively low (Rodríguez-Muñoz *et al.* 2010; Bretman *et al.* 2011), so we are confident that if a cricket is no longer observed it has died rather than moved to a new area.

Network construction

We constructed two networks, each representing a type of male-male competition:

i. Fighting. We linked one male to another if it arrived at a burrow and fought the resident. This ranges from flaring mandibles to wrestling (Alexander 1961). The strength of the interaction was a count of the number of times the cricket arrived at a burrow and fought a particular opponent. This network was therefore weighted and asymmetrical (directed).

ii. Sperm competition. Insects store sperm in their spermatheca, and multiple paternity has been demonstrated in field crickets, so males mating to the same female will be in sperm competition (Bretman and Tregenza 2005; Tyler *et al.* 2013). Using only matings where a spermatophore was successfully transferred, we created a network of mating between males and females. This is distinct from a typical network in that the matrix is rectangular, and links only exist between two types of individuals, never between two of the same type of individual (a bipartite network). We then linked males if they mated with the same female. Two males were interacting more strongly with each other if they mated many times with the same females. A male interacted with another with equal strength if they both mated once with two females or if they each mated twice with a single female. Our rationale being that each spermatophore represents a unit of investment by the male, competing for a share of the female's eggs. In both situations, ignoring order effects and assuming equal competitive ability, a male has equal chance of fertilising each available egg, regardless of whether they are split across two females or one. This network was asymmetrical, with one male having a link to another male equal to the total number of times the first male mated with any female also mated by the second male, and vice versa.

Similarity in space and time

Two individuals are likely to be in greater pre- and post-copulatory competition if they overlap in space and time compared to a pair that did not. To account for this, we constructed matrices of individuals' temporal and spatial overlap during their adult lives. The former was simply the number of days that each pair of adult crickets were alive at the same time, a symmetrical relationship. For spatial overlap we linked males via their interactions with burrows. Encounters between individuals away from burrows are likely to be very rare because individuals spend the vast majority of their time in the immediate vicinity of burrows, typically leaving only when moving to another burrow. Each male's strength of interaction with a particular burrow was equivalent to the amount of time he was observed there. Males were then connected to other males who also used each particular burrow. These edge weights, and so the matrix, was initially asymmetrical, as each male using a burrow would have spent different amounts of time there. To obtain a single value for each pair that represented how close in space they were, the matrix was symmetrised by taking the geometric means of the two values. For pairs of values, the geometric mean is the square root of their product. This effectively gives greater weight to values close together rather than those further apart. For example, the geometric mean of five and five is five, but the geometric mean of one and nine is three. Both of these pairs would have an arithmetic mean of five, but we do not think they represent equal strengths of interaction, which the use of the geometric mean captures more accurately. Two males that spent longer at the same set of burrows as each other (but not necessarily at the same time) were more strongly connected.

Network analyses

For prediction (1), about relationships between the intensity of pre- and post-copulatory competition within pairs of competing males, we used an extension of quantitative assignment procedure to multiple regression: MRQAP (Krackhardt 1988). We used an ordinary least squares (OLS) network regression with the sperm competition network as a response variable and the network of fighting as a predictor variable. We controlled for each pairs' similarity in time and space by adding the matrices for spatial and temporal overlap as covariates. To independently estimate the effect of each of the predictor variables on the response variable, the test was performed using Dekker semi-partialling for the permutation tests (see Dekker *et al.* 2007) in the R package "sna" (Butts 2008b). This was necessary as the covariates were significantly correlated (Mantel tests, 2006: $r = 0.354 – 0.544$; 2013: $r = 0.184 – 0.442$, $p < 0.001$ in all cases). We symmetrised the fighting and sperm competition networks, to give a single value for an edge between two individuals indicating how strongly they were linked in competitive interactions, rather than how much one interacted with another. This was done by taking the geometric mean of the two edge weights as for the spatial closeness network. This allows us to determine whether the level of sperm competition within each pair was positively, negatively or not associated with the frequency of fighting within the pair. For each predictor variable, we subtracted the mean pair-wise interaction strength from each value to centre the values over zero, and divided by the standard deviation of all pair-wise interaction strengths. This means that each variable was on the same scale (number of standard deviations the datum is above/below the mean), which aids interpretation (Hunt *et al.* 2005; Schielzeth 2010).

For prediction (2), about the correlation within-individuals in engagement in pre- and post-copulatory competition, we correlated an individual's degree between the fighting and sperm competition networks. We repeated this using individual “strength”, i.e., the total number of interactions an individual instigated, regardless of who they were with. This is distinct from the previous analysis, which compares the within-pair relationships between networks, and used the original, directed/asymmetric networks. Therefore, to test predictions (1) and (2) we looked at both within-pair and within-individual relationships between pre- and post-copulatory competition.

For prediction (3), if promiscuous males mate with promiscuous females, we took each connection in the male-female mating network and correlated the degrees of the individuals at either end. This measure is known as “degree correlation”; a positive correlation indicates that individuals with many connections are connected to other individuals with many connections, whereas a negative correlation indicates that individuals with many connections are primarily connected to individuals who are connected to few others (Newman 2002, 2003). We compared the observed correlation with the correlation found in 1000 simulated networks. For the simulated networks we first multiplied together the spatial and temporal overlap matrices, to create a network that only contained non-zero values for pairs of crickets that were both alive at some point and were observed to use the same burrow at least once. This network represented all possible connections. We then took a random sub-sample of the edges in this network 1000 times, to give 1000 random networks with, on average, the same density as the observed network, and calculated the degree correlations in each network. This accounted for non-zero degree correlations that could arise through spatial and temporal structuring. P-values were obtained as the proportion of simulated values with more extreme correlations than the observed network (Simpson 2015).

Results

There were 74 males in 2006 and 119 in 2013. In 2006 there were 35 males that never used the same burrow as another male, and 23 such males in 2013. These isolated individuals were not considered for the analyses of interactions, as they could not contribute to sexual selection through fighting and were unlikely to contribute through sperm competition. The frequency of these individuals was higher in 2006 than 2013 (35/74 and 23/119, respectively).

Individuals were observed for a similar mean amount of time in each year, so this difference presumably reflects the lower population density in 2006.

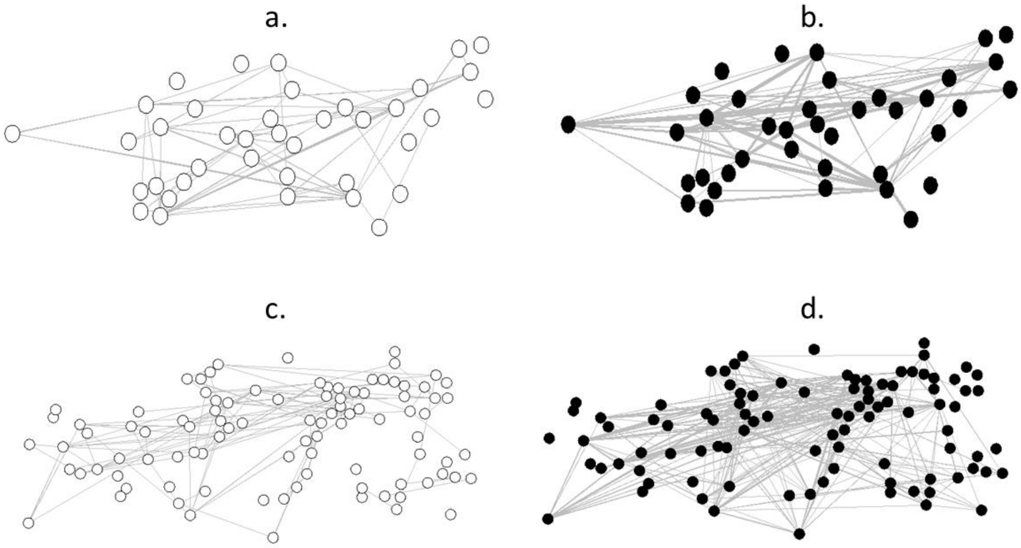

Figure 5.1. Plots of the networks in 2006 (a & b) and 2013 (c & d). The networks of fighting are plotted with open circles (a & c), the sperm competition network with solid circles (b & d). Lines indicate males that either fought each other (fighting) or mated with the same female (sperm competition). Each male is plotted in the same position in each network, based on his emergence location as an adult, so individuals occupy the same position in the fighting and sperm competition networks.

Not every male necessarily interacted in every network; for instance if they fought, but never successfully mated with a female, they would score zeros for sperm competition with all other males but would still be included in the analyses. Plots of each network are shown in Figs. 5.1 a - d. Each male possessed a similar degree in the fighting network as the sperm competition network in 2006 (medians of 1 & 2 respectively, Wilcoxon test, $W = 633$, $N = 39$, $p = 0.194$) but males had a higher degree in the sperm competition network in 2013 (medians of 1 & 2.5 for the fighting and sperm competition respectively, Wilcoxon test, $W = 3280$, $N = 96$, $p < 0.001$).

1) Within-pair intensity of pre- and post-copulatory competition

The results of the OLS network regression are presented in Table 5.1. In both years, the networks of fighting and the matrices of spatial and temporal overlap were significant, positive predictors of the networks of sperm competition.

Table 5.1. Results of OLS network regression for the effect of fighting frequency, spatial similarity and overlap in lifespan on the level of sperm competition between males. Each of the predictor variables has been mean centred and scaled to unit variance, so effect sizes are comparable.

Year	***Predictor***	***Coefficients***	***p-value***	***Model statistics***	
2006	Fighting	0.446	0.002	Residual standard error	2.132
	Space	1.160	< 0.001	Degrees of freedom	737
	Time	0.374	0.003	R^2	0.385
2013	Fighting	0.186	< 0.001	Residual standard error	0.824
	Space	0.215	< 0.001	Degrees of freedom	4560
	Time	0.134	< 0.001	R^2	0.187

2) Within-individual correlation between engagement in pre- and post-copulatory competition

An individual’s degree in the fighting network was positively correlated with its degree in the sperm competition network (Fig. 5.2; Spearman’s rank correlations, 2006: N = 39, S = 4000, rho = 0.595, p < 0.001; 2013: N = 96, S = 62500, rho = 0.576, p < 0.001). This result was maintained if an individual’s strength was used in place of degree (2006: N = 39, S = 3640, rho = 0.631, p < 0.001; 2013: N = 96, S = 64500, rho = 0.563, p < 0.001).

3) Promiscuous crickets tend to mate with each other

There was a positive degree correlation in the male-female mating network in 2006, but there was no correlation in 2013 (Spearman’s rank correlations, 2006: N = 93, rho = 0.193, permutation p-value = 0.003; 2013: N = 246, rho = 0.068, permutation p-value = 0.300). Plots of the simulated vs. observed correlations are shown in Fig. 5.3.

Discussion

We found that (1) males were in stronger sperm competition with the males they fought more; (2) males that fought many different males were also in sperm competition with many different males; (3) there is a positive relationship between the promiscuity of a male and the promiscuity of the females he mated with but it is only statistically significant in 2006. We address each of these findings in turn.

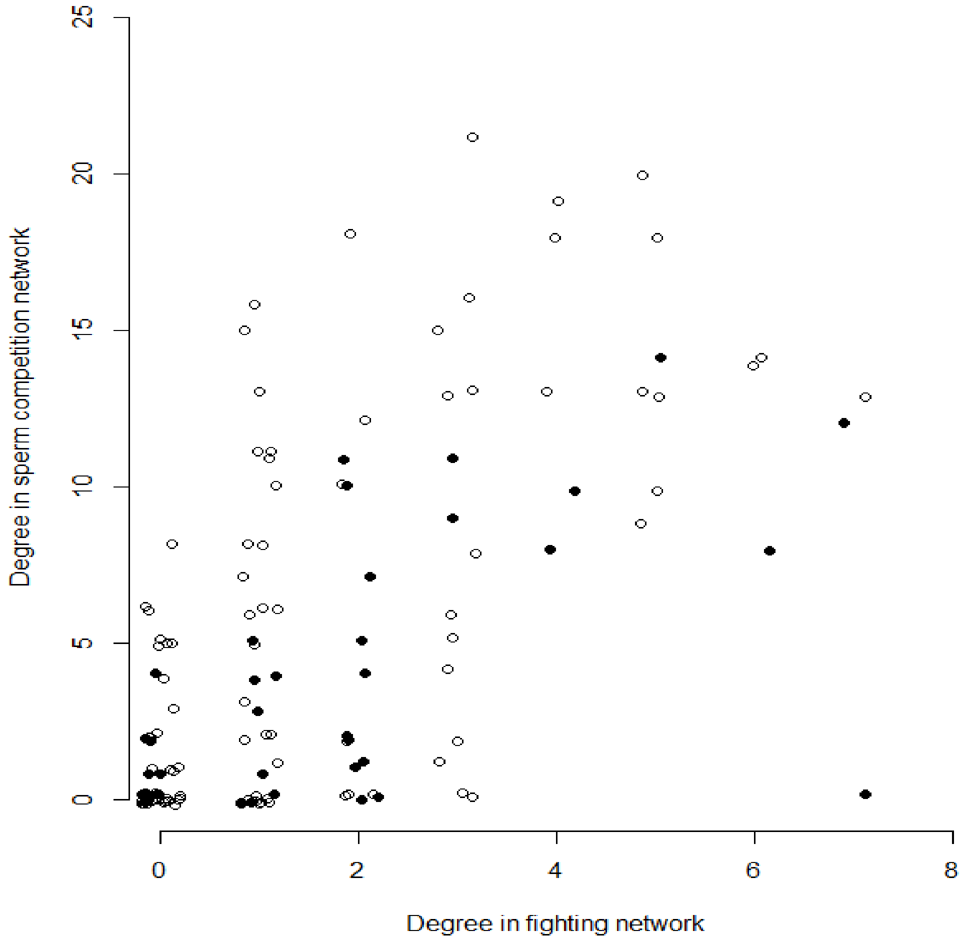

Figure 5.2. Each male’s degree in the fighting network against his degree in the sperm competition network. Filled circles = 2006, open circles = 2013. There were strong positive correlations in both years (2006: rho = 0.594; 2013: rho = 0.576). A small value has been added to each point at random to reveal that there are multiple points for some x and y values.

Within-pair and within-individual correlations between pre- and post-copulatory competition

Males that emerged as adults nearer each other engaged in more intense sperm competition. Similar results have been found in harvestmen (S. *proximum*), where harems of females that were close together were more likely to be invaded by the same “sneaker” male (Muniz *et al.* 2014), while trees (*Prunus mahaleb*) near each other tend to be visited by the same pollinators

(Fortuna *et al.* 2008). The temporal overlap of male ejaculates is necessary for sperm competition to occur (Wigby & Chapman 2004), and individuals typically reduce competition by segregating themselves in time (e.g. Alanärä *et al.* 2001).

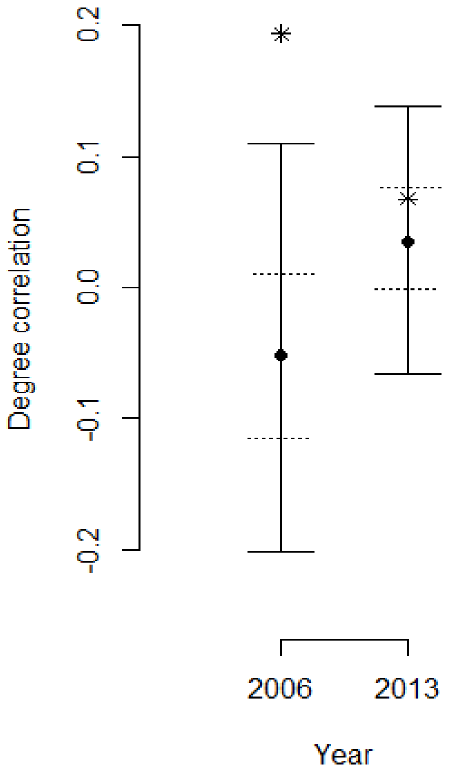

Figure 5.3. Plots of the simulated and actual correlations between male degree and female degree from the mating network in each year. The solid points indicate the medians, dashed horizontal lines the 50% quantiles and the solid horizontal lines the 95% quantiles. Simulated networks possessed only links between crickets that overlapped in both space and time, and were on average the same density as the original network (see Methods). The observed value for each year is plotted as an asterix. The correlation in 2006 (0.193) was greater than 99.7% of simulated correlations, while the correlation in 2013 (0.068) was greater than 70% of simulated correlations.

However, we are unaware of any studies in wild animals that explicitly demonstrate that the degree of spatial and temporal overlap of adult males increases the intensity of sperm competition between them. It seems probable that this is a pattern that is likely to be a general feature of spatially structured populations. This finding highlights how decisions made by mothers over factors such as egg laying site or nest location (Refsnider and Janzen 2010; Mitchell *et* *al.* 2013) or aspects of phenology such as laying date (Einum and Fleming 2000; Skoglund *et al.* 2011), can strongly influence the competitive environment of offspring.

Even after accounting for temporal and spatial factors, the number of fights between a pair of males was positively related to their level of sperm competition. This suggests that pre-copulatory competition may not always be an effective means of avoiding post-copulatory competition. This is true in various systems, for instance some male giant cuttlefish (*Sepia apama*) change markings to look like females, allowing them to mate with females guarded by larger males (Norman *et al.* 1999), while female brown capuchin monkeys (*Sapajus apella*, formerly *Cebus apella*) solicit copulations from subordinate males towards the end of their oestrus cycles (Janson 1984). As this relationship between pre- and post-copulatory competition does not appear to be explained by patterns of space use or phenological equivalence, some other factor must be driving males in one form of competition to be more involved in the other type. One possible explanation is that there is some consistency among females in their preference for males of a particular type. Males of this type will be more likely to be in sperm competition with one another because they receive a disproportionate share of matings. If males that are similar in their attractiveness to females are also more similar in their fighting abilities then they may be evenly matched in fights, which may lead to them having repeated fights with one another as they seek to establish dominance. The two perquisites for this possibility have been established in other animals. Consistent female preferences for certain male types have been shown in a number of species in laboratory settings (Howard & Young 1998; Forstmeier & Birkhead 2004; Cummings & Mollaghan 2006; Ihle *et al.* 2015). Furthermore, escalation of fights between male butterflies typically occurs when each male considers himself to be the resident of the territory, a role which normally settles contests (reviewed in Kemp and Wiklund 2001). Similarly, prolonged contests between female house finches (*Carpodacus mexicanus*) only occur between females most closely matched in condition and body size (Jonart *et al.* 2007). Therefore, fighting behaviour may be an emergent property of equality in sexual competition, rather than a means of imposing inequality.

Our observation of a positive correlation in degree within-individuals between networks indicates that individuals that instigated many fights were also engaged in a lot of sperm competition. This may be related to our earlier observation that pairs of males in pre-mating competition were more likely to be in post-mating competition. We interpreted this as likely being the result of closely matched males tending to fight frequently, and also being unable to exclude one another from females and hence experiencing high sperm competition. This within-pair correlation could drive within-male correlations in pre- and post-copulatory competition because males that happen to encounter an opponent of similar competitive ability will experience a lot of fights and a lot of post-copulatory competition, whereas males that only encounter opponents of divergent fighting ability will tend to have fewer fights and experience less sperm competition. The positive correlation between degrees in each network could potentially amplify the reproductive success of good condition or high quality males if abilities in pre- and post-copulatory forms of competition are correlated through links to condition or quality (e.g. Matthews *et al.* 1997; Hosken *et al.* 2008). There is a large reproductive skew observed amongst males in this population (Rodríguez-Muñoz *et al.* 2010), suggesting that this may be occurring. This type of skew in mating success is common in social animals, due to control of mating opportunities by dominants or strong benefits of kin-directed altruism (Engh 2002; Hager and Jones 2009; Ryder *et al.* 2009; Cant *et al.* 2010). This skew in crickets and other non-social animals could be driven by differences in longevity, as the number of fights instigated and copulations achieved is expected to increase over time. Together, these results suggest that males must be adapted to both pre- and post-copulatory competition, as they will typically be engaged in both. This therefore makes the evolution of alternative male morphs unlikely. As crickets do not have a particularly unusual mating system, it seems likely that this correlation will be typical of species where the potential for males to monopolise females or resources is limited (Andersson and Simmons 2006; Buzatto *et al.* 2014).

Promiscuous crickets mate with each other

Promiscuous individuals positively assorted in both years, although it was not significant at the 95% level in 2013. Therefore, in 2006 at least, apparently successful males faced higher sperm competition for each of their matings than did less promiscuous males. This would have tended to reduce the variance in reproductive success across the population (Sih *et al.* 2009). This could result from positive assortment by attractiveness due to both females and males exercising choice of mates. Such mutual mate choice has been found in a number of animals, for example in a cichlid fish (*Pelvicachromis taeniatus*), large body size was favoured by both sexes but larger individuals were more choosy, resulting in positive assortment by body size (Baldauf *et al.* 2009). Furthermore, the strength of sexual selection acting on male and female fruit flies (*Drosophila serrata*) has been shown to be approximately equal, with a low genetic correlation suggesting independent evolution of sexually selected cuticular hyrdocarbon profiles (Chenoweth & Blows 2003). Therefore, males who are preferred by females may also prefer particular females, who are attractive to all males. This would result in the individuals with the highest mating rates mating with each other; the pattern we observe here. This positive correlation between mating rates also indicates that males with many mating partners are less successful at preventing females from remating than those who only mate with a few different females. This trade-off between the mating rate of a male and the fidelity of his partners may explain the considerable variance in mate-guarding behaviour in this population (Rodríguez-Muñoz *et al.* 2011). Similar results have been found in Prarie voles (*Microtus ochrogaster*), where males who entered the territories other other males most frequently also had their own territories invaded more often (Okhovat *et al.* 2015). Our results support the argument that, in systems with frequent post-copulatory competition, using the number of matings as a proxy for reproductive success may lead to the over-estimation of the fitness of males who mate often (Preston *et al.* 2001). This should encourage more studies into the fitness determinants of polyandrous species in the wild (Preston *et al.* 2003; Rodríguez-Muñoz *et al.* 2010; McFarlane *et al.* 2011; Thompson *et al.* 2011; Sardell *et al.* 2012).

Conclusions

Following recent calls (McDonald *et al.* 2013; McDonald and Pizzari 2014) we used methods of data analysis not commonly used in the field of sexual selection to provide insights into male-male competition in a wild population. By simultaneously considering pre- and post-copulatory sexual competition among individuals of an entire population, as well as both individual and pair-wise relationships between the two types of competition, we have addressed a range of questions relevant to promiscuous mating systems. We found that males are unlikely to specialise in either pre- or post-copulatory competition, nor can they use the former to avoid the latter. This supports the idea that in species where males are unable to monopolise access to females the evolution of alternative male phenotypes is unlikely. Furthermore, the structure of the mating network may reduce variance in reproductive success, reducing the usefulness of mating success as a proxy for reproductive success, and suggests that males who mate more often may lose more paternity through sperm competition.

6. Wild cricket social networks show stability across generations

This chapter is currently in review at *Peerage of Science*

Abstract

A central part of an animal's environment is its interactions with conspecifics. There has been growing interest in the potential to capture these interactions in the form of a social network. Such networks can then be used to examine how relationships among individuals affect ecological and evolutionary processes. However, in the context of selection and evolution, the utility of this approach relies on social network structure persisting across generations. This is an assumption that has been difficult to test because networks spanning multiple generations have not been available. We constructed social networks for six annual generations over a period of eight years for a wild population of the cricket *Gryllus campestris*. Through the use of exponential random graph models (ERGMs), we found that the networks in any given year were able to predict the structure of networks in other years for some network characteristics. We also found that the capacity of a network model of any given year to predict the networks of other years did not depend on how far apart those other years were in time. Our results indicate that cricket social network structure resists the turnover of individuals and is stable across generations. This would allow evolutionary processes that rely on network structure to take place. We also found that the capacity of a network model to predict the structure of a network in another year was influenced by the difference in population size between those years. This may indicate that scaling up findings on social behaviour from small populations to larger ones will be difficult. Our study also illustrates the utility of ERGMs for comparing networks, a task for which an effective approach has been elusive.

Keywords: exponential random graph models, Gryllus, network comparison, population structure

Introduction

Alongside elements of their environment such as climate, resource availability and predation risk, animals are also adapted to their social environment. This is comprised of the social interactions with con-specifics, through mating, fighting, playing, grooming or associating in the same group. This social environment can be characterised as a social network, where individuals (“nodes”) are connected with others that they interact or associate with via links called “edges” (Downing & Royle 2013). Having been adopted from the study of human social behaviour, the study of animal social networks is now out of its infancy, with studies across a range of taxa and addressing a wealth of different questions (Croft *et al.* 2008; Whitehead 2008; Krause *et al.* 2014; Hasenjager & Dugatkin 2015; Farine & Whitehead 2015).

Studies on animal social networks typically construct a social network from a single continuous period of observation. This allows one to make conclusions about ecological processes over the time period that relates the social environment to other aspects of the animals’ ecologies, for example their exposure to disease (Fenner *et al.* 2011; Bull *et al.* 2012; Weber *et al.* 2013) or group decision making (Bode *et al.* 2011; Farine *et al.* 2014). Studies on networks rarely extend to timescales that would allow evolutionary processes. This is probably because most animals studied through social network analysis are relatively long-lived vertebrates e.g. dolphins, baboons or great tits. Studies over multiple generations therefore take decades, and so are uncommon (Clutton-Brock & Sheldon 2010). This is problematic, as we do not know the extent to which the characteristics of the social network structure of populations persist across generations. Qualitatively similar processes predicting the structure of social networks have been found in sperm whales (*Physeter macrocephalus*) (Christal *et al.* 1998) long-tailed manakins (*Chiroxiphia linearis*) (Edelman & McDonald 2014) and spotted hyenas (*Crocuta crocuta*) (Ilany *et al.* 2015) in different years, but none of these studies spanned multiple generations. Shizuka *et al*. (2014) demonstrated that distinct communities of golden-crowned sparrows (*Zonotrichia atricapilla*) persisted across three seasons, despite high turnover of individuals. However, two generations at most may have featured in this study, limiting conclusions relating to stability across evolution time.

If social network structure does not resist the turnover of individuals, then evolutionary processes facilitated by the presence of a social network may not actually occur. For example, the evolution of cooperation is facilitated by a viscous social network, allowing co-operators to preferentially interact with each other and avoid cheats (Santos *et al.* 2006; Ohtsuki *et al.* 2006; Nowak 2006). However, if the structure of the network changes from generation to generation, then a cooperative strategy that exploits aspects of the social network in one generation might not be successful in the next, preventing it from persisting in the population. Evolutionary processes and responses such as this cannot take place if the social network structure is unstable, in the same way that animals cannot evolve a particular thermal tolerance if the temperature of their environment fluctuates randomly over generations.

We wanted to determine whether a population showed consistent social network structure across independent generations by studying a species with non-overlapping generations. Independent generations are necessary, as one keystone or despotic individual could have a large influence on network structure over time if they were long-lived (McComb *et al.* 2001; Sih & Watters 2005; Lusseau 2007). We assessed whether the factors predicting the structure of social networks in a population of wild field crickets (*Gryllus campestris*) were consistent across years by using model parameters based on networks in one year to simulate networks from other years. If networks from a year could be used to accurately simulate the characteristics of networks from others, it would indicate that social network structure is conserved over time. We also related the ability of one network to predict another with the difference in time (years) between them and the difference in total population size between them.

Methods

Study system & data collection

The field cricket *G. campestris* is a univoltine species. Adults emerge early in spring having overwintered as nymphs in burrows they dig themselves and are active from April-July. Once sexually mature, adult males start singing to attract mates, and both sexes move around burrows to find mates (Rodríguez-Muñoz *et al.* 2010). They will also fight members of the same sex for access to burrows or mating partners (Alexander 1961), although we do occasionally observe aggressive interactions between the sexes (authors pers. obs.). This allows us to construct social networks between individuals that either mate with or fight each other.

Our study site is a meadow of approximately 20 by 40 metres, located on a north facing slope in a valley in Northern Spain. We have been studying *G. campestris* there since 2005, with a generation each year. Such timescales are long enough to allow contemporary evolution (Reznick 1997), with adaptations with major implications for fitness able to occur in only one generation (Christie *et al.* 2012). Once nymphs become active after overwintering, we located each burrow at our study site and marked it with a unique number. We placed video cameras over burrows with an active individual before any adult emergences were observed. Cameras recorded cricket activity 24 hours a day, seven days a week using infrared illumination at night. Nymphs rarely move among burrows (Rodríguez-Muñoz, pers. obs.). Therefore, the camera footage along with direct observations of burrows without cameras allowed us to determine when each individual became an adult. Two-three days after it emerged as an adult, we caught each cricket and fixed a unique waterproof vinyl tag to its thorax with cyanoacrylate glue. This allows non-invasive identification of individuals recorded on the video. Following this, we released crickets back to the burrow we caught them from. Crickets use burrows to hide from predators such as robins and shrews, and spend most of their life in the immediate vicinity of burrows, usually within the frame of our cameras. They will share burrows with members of the opposite sex while mating with them, but will fight members of the same sex when they approach. Therefore, the vast majority of cricket social interactions take place at burrows, and so are recorded by our cameras. If we did not directly record the death of a cricket we set it as the day after we last observed it. Migration in and out of our population is limited by surrounding unsuitable habitat (Bretman *et al.* 2011), so we are confident that the majority of crickets active in the population are caught and tagged. Of the years since

2005, we have completely analysed the video from 2006-08 & 2011-13, so we present those years in this study.

Social interactions are either fighting, which typically only occurs within the sexes, and mating. Here we present social networks based on both types of interactions, so that all individuals could theoretically interact with each other. We directly record interactions rather than infer associations, so there is no need to compute an association index (Croft *et al.* 2008; Whitehead 2008). We linked individuals if they were ever observed to mate or fight with one another, with the strength of the link defined by the number of interactions between them. This gives weighted, symmetrical (undirected) networks.

Exponential random graph models

We used exponential random graph models (ERGMs, also known as p* models) to quantify the networks' properties (Wasserman & Pattison 1996). These have previously been used in animal behaviour research to investigate the structure of dominance hierarchies in pukeko (*Porphyrio melanotus melanotus*) (Dey & Quinn, 2014), and the structure and stability through time of cooperative leks in male long-tailed manakin (*Chiroxiphia linearis*) (Edelman & McDonald 2014). ERGMs are similar to logistic regression models and have been developed to model the presence and strength of edges in a network (Snijders *et al.* 2006; Krivitsky 2012). This makes it possible to determine which variables contribute to non-random network structure, which can provide insights into the social processes forming the network (Lusher *et al.* 2012). Variables predicting edge formation and strength can be structural properties of the network (for instance the presence of a mutual association creating an association between two individuals: "triadic closure"), properties of the individuals (for instance their sex), or properties of a relationship between two individuals (for instance their genetic relatedness). Which predictor variables are chosen depends on the interests of the researcher and the available data, as for a regression (Lusher *et al.* 2012). Effect sizes for each variable are arrived at through a stochastic process of model fitting. Importantly, by estimating multiple different processes in one model, each term is calculated relative to the others, and so shared influence on edge formation is accounted for. Once coefficients for each variable have been estimated, these can be used to simulate a range of new, otherwise random networks to compare with the original network. Furthermore, coefficients from one model can be applied to simulations based on a different network. This allows one to determine how well the parameters predicting one network predict the observed structure in other networks.

Efficacy of network simulation

We first determined how well fully parameterised models simulated various network metrics compared with much reduced models. This would tell us whether our models were effective at simulating realistic networks. For the network in each year we fitted an ERGM with the same effects using the packages “ergm” (Hunter *et al.* 2008) and “ergm.count” (Krivitsky 2015) in R ver. 3.0.2 (R Core Team 2013). The effects in this full model were:

- Conway-Maxwell-Poisson (CMP) distribution. This models the tendency for the distribution of edge weights to be under- or over-dispersed relative to a theoretical Poisson distribution, analogous to a quasi-Poisson parameter in a glm (Krivitsky 2015).
- Non-zero. This models the tendency for networks to be sparse e.g. individuals are not connected to every other individual in the network. This is a common attribute of social networks (Snijders *et al.* 2010).
- Transitive ties. This models triadic closure, the tendency for crickets to interact with those with whom they share a mutual 3rd interaction. This is a common property of social networks (Croft *et al.* 2008).
- Main effect of sex. This models any sex differences in total interaction strength, summed across all interactions. Both sexes are promiscuous (Rodríguez-Muñoz *et al.* 2010) and males cannot control access to females (Rodríguez-Muñoz *et al.* 2011) so we do not expect major sex differences in interaction frequency. Females are modelled as the default with males as the contrast.
- Node-matching by sex. This models the tendency for crickets to interact more or less with individuals of the same sex as themselves. As matings (inter-sex; 4311 recorded in total in 2006-08 & 2011-13) are more common that fights (typically intra-sex; 1628 recorded in total in 2006-08 & 2011-13), we expect this to be negative.
- Emergence location closeness. This dyadic covariate contains information on the closeness (the inverse of distance) between the adult

emergence co-ordinates of each pair of crickets. We expect this variable to be positive, as individuals emerging closer together should interact more.

If the initial run of a model did not achieve convergence (as indicated by the ergm.count package) we then re-ran the model, using the estimated coefficients of each parameter as new starting values for the next run. This either lead to satisfactory convergence or only made small differences to the coefficients, indicating the parameter values were relatively stable and thus were reliable. We then simulated 100 new networks based on all the coefficients from the model, and 100 new networks using only the CMP and non-zero parameter coefficients. Comparison of these two sets of 100 networks for each year would indicate how effective our model was at reproducing elements of the real cricket social network. The elements we chose were the mean path length (or geodesic distance) of the network, the degree correlation of the network, and the clustering coefficient. The mean path length is the average number of steps (edges) on the shortest route between all possible pairs of individuals (Albert & Barabási 2002). Individuals that are separated from each other completely are recorded as having an infinite distance between them, and these path lengths were not used in the analysis. The degree correlation is the correlation between the degree (the number of unique connections) of the individuals at either end of each edge (Newman 2003). The clustering coefficient is the ratio of open triads (where two crickets are connected to a third but not to each other) to closed triads (where all three are connected) and is a measure of local edge density (Holland & Leinhardt 1971). In theory, any network metric could be used, we chose these as they are commonly used and represent features of the network with global implications based on local connections. We then calculated “predictive distances” for each year and for each network metric. These were simply the difference between each of the 100 simulated values and the real value for each network metric, for each year, for both the simulations with all parameters and the simulations with the reduced parameters. We then compared the absolute size of these using Wilcoxon rank sum tests, to determine whether the simulation with all terms gave significantly shorter predictive distances than the reduced-term simulations.

Within- and between-year simulation comparison

The above analysis looks at capacity for an ERGM to simulate a network based on a model from the same year, hereafter a “within-year” comparison. We also wished to determine whether ERGMs from the other years could accurately simulate a network in a different year, a “between-year” comparison. If they could, we would have evidence of similarity, and so stability, of network characteristics across years.

We took the model parameter coefficients from the full model for each year, and used them to simulate 100 new networks from each other year. We entered the original network and its exact characteristics (population size, sex ratio, total number of interactions and emergence location of individuals) into these simulations, so the simulations were as realistic as possible. We then calculated predictive distances as before for each set of simulations. Therefore, alongside the 100 predictive distances for the model in 2006 predicting the clustering coefficient in 2006 (within-year comparison), we had 100 predictive distances for the model in 2006 predicting the clustering coefficient in 2007 (between-year comparison), and so on. We then took the mean of each of these set of 100 values and compared the between-year comparisons with the within-year comparisons using Wilcoxon rank sum tests.

Predictive distances and other population characteristics

We compared the sizes of the mean predictive distances between years to the difference in time (number of years) and differences in population size (number of individuals) between those years. For this we used Mantel tests (Mantel 1967) in the package vegan (Oksanen *et al.* 2013) to account for the fact that we compared each year to multiple others, who were also involved in multiple comparisons, like a network. We calculated a Spearman’s rank correlation coefficient as the distribution of values was non-normal. A positive relationship between distance in time and predictive distance would indicate that the networks were changing over time, weakening the relationships among them. No relationship would be taken as further evidence of network stability across generations. Network size is an important axis of variation, so networks that are more different in size may be worse at predicting each other. In which case we expect a positive relationship between predictive distance and difference in population size.

Results

Predictors of cricket social networks

The variable estimates for each year are shown in Table 6.1. The CMP parameters were all positive, indicating over-dispersion, and the non-zero parameters were all negative, indicating that most possible edges did not exist/were zero i.e. crickets tended not to be connected to all others. The transitive ties parameters were positive, indicating that the presence of a mutual connection increased the likelihood that two crickets would interact. The main effect of sex was generally weak and negative with relatively large standard errors, indicating only a weak tendency for males to interact slightly less often than females. The node-matching by sex was negative, indicating that intersexual interactions were more common than intrasexual interactions. The dyadic effect of emergence location was positive, confirming that individuals emerging close together interacted more. Each effect is estimated while accounting for the other effects, so the process of triadic closure is significant even given that crickets emerging near each other are more likely to interact.

Table 6.1. Parameter estimates from ERGMs in each year, with standard errors in brackets. CMP stands for Conway-Maxwell-Poisson distribution; see main text for description of terms.

Parameter	***2006***	***2007***	***2008***	***2011***	***2012***	***2013***
CMP	0.923 (0.013)	0.783 (0.010)	0.914 (0.058)	0.743 (0.012)	0.958 (0.012)	0.600 (0.082)
Non-zero	-7.109 (0.436)	-6.389 (0.192)	-4.287 (0.282)	-6.622 (0.231)	-5.805 (0.476)	-6.377 (0.176)
Transitive ties	1.954 (0.208)	1.373 (0.090)	0.654 (0.136)	1.571 (0.113)	1.508 (0.230)	1.323 (0.077)
Sex	-0.096 (0.024)	0.059 (0.017)	-0.092 (0.109)	-0.019 (0.015)	-0.107 (0.028)	-0.073 (0.042)
Node-match by sex	-0.411 (0.030)	-0.399 (0.036)	-0.685 (0.162)	-0.339 (0.023)	-0.430 (0.035)	-0.020 (0.081)
Emergence location	0.390 (0.036)	0.391 (0.066)	0.269 (0.113)	0.594 (0.0425)	0.143 (0.055)	0.679 (0.199)

Full vs. reduced simulations

For mean path length, the full simulations gave significantly smaller predictive distances than the reduced simulations in all years apart from 2012, when the full simulations actually gave larger predictive distances (all Wilcoxon rank sum tests, $p \leq 0.001$ in all cases).

For degree correlation the reduced simulations gave smaller predictive distances in all years (all Wilcoxon rank sum tests, $p \leq 0.038$ in all cases) except 2012, where the difference was not significant (Wilcoxon rank sum test, $p = 0.080$) and in 2013, where the full simulations gave significantly shorter predictive distances (Wilcoxon rank sum test, $p < 0.001$).

For clustering coefficient the full simulations gave significantly smaller predictive distances in all years (all Wilcoxon rank sum tests, $p < 0.001$) except 2008, where the full and reduced models gave equal predictive distances (Wilcoxon rank sum test, $p = 0.085$). Box plots for all these comparisons are shown in Appendix A (Figs. S1-3).

From these results we concluded that our models were effective for predicting path lengths and clustering coefficients, but not degree correlations. Therefore, we did not consider degree correlations for the rest of the analyses.

Predictive distance within vs. between years

The predictive distances for the within- and between-year comparisons are shown in Fig. 6.1a. (path length) & b. (clustering coefficient). For both path length and clustering coefficient the within-year comparisons gave equal predictive distances to the between-year comparison (Wilcoxon rank-sum tests, path length: $W = 70$, n (within-year) = 6, n (between-year) = 30, $p = 0.418$; clustering coefficient: $W = 61$, n (within-year) = 6, n (between-year) = 30, $p = 0.233$).

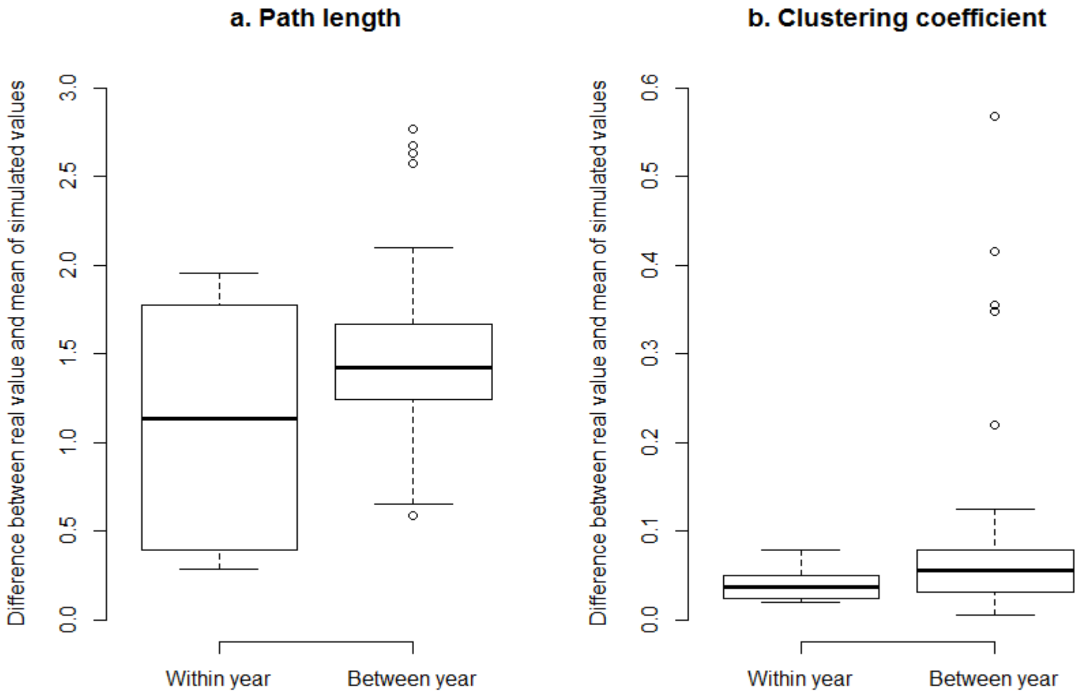

Figure 6.1. Box plots of the predictive distances for the within- and between-year comparisons for path lengths (a.) and clustering coefficient (b.). The y-axis indicates the differences between the observed and simulated network measures. Network models were able to predict the true network both within and between years; for both network measures the difference between the within-year and between-year comparison was non-significant (see results).

Correlates with predictive distance

There was no significant relationship between number of years apart and predictive distance for either path length (Fig 6.2a; Mantel test, rho = -0.169, p = 0.733) or clustering coefficient (Fig 6.2b; Mantel test, rho = -0.107, p = 0.708). There were positive, albeit marginally non-significant relationships between difference in population size and predictive distance for path length (Fig. 6.2c; Mantel test, rho = 0.481, p = 0.056) and clustering coefficient (Fig. 6.2d; Mantel test, rho = 0.488, p = 0.060).

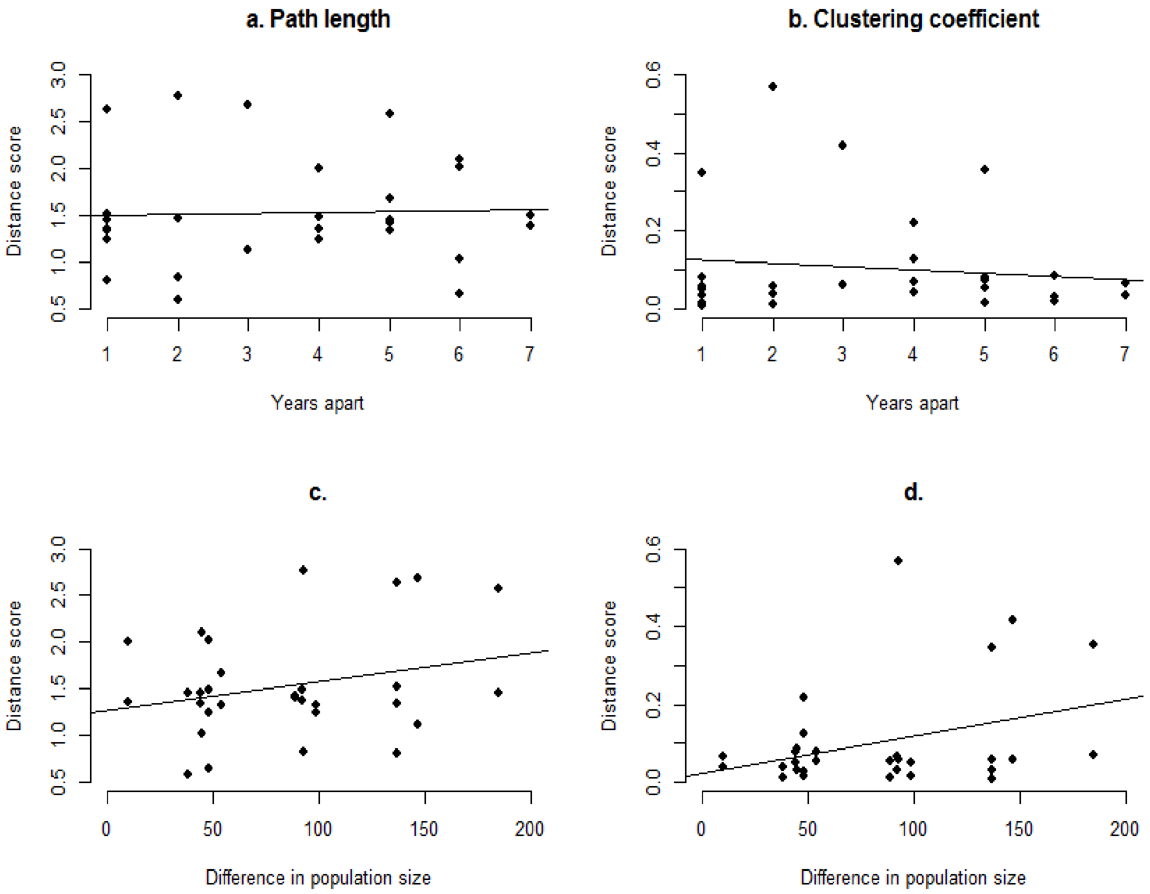

Figure 6.2. Plots of the predictive distance for the between year comparisons against the difference in time between each pair of compared years (a. & b.) and the difference in population size between each pair of compared networks (c. & d.). Plots a. & c. show this relationship for predicted path lengths, b. & d. for predicted clustering coefficient. Plotted are the means of the 100 predictive distances for each comparison: the difference between the mean of the simulated values and the real value. Distance in years did not affect the ability of models to predict other networks (no correlation: Mantel test, rho = -0.169 & -0.107), but were worse at predicting the path lengths of other networks when they were initially parametrised on networks with different population size (increased predictive distance with increased difference in population size: Mantel test, rho = 0.481 & 0.488; see results). The lines are from simple regressions of the variable on the x axis on the predictive distance. These were not informed by the Mantel tests but help visualise the result.

Discussion

Predictors of cricket social networks

We found that cricket networks were sparse, like most social networks, and the interaction strengths were over-dispersed, suggesting fewer weak interactions and more strong interactions than expected under a Poisson distribution. This may be evidence of preferred associations, with crickets avoiding most individuals to interact strongly with particular others. Consistent mate-choice by females has been shown in captivity in various species (Howard & Young 1998; Forstmeier & Birkhead 2004; Cummings & Mollaghan 2006; Ihle *et al.* 2015), and individual male traits such as singing frequency and body mass influence mating success in this species (Rodríguez-Muñoz *et al.* 2010), so for mating interactions this seems plausible in this system. Male crickets that are in sperm competition are also more likely to fight (Fisher *et al.* 2016), so crickets may have consistent fighting opponents as well. Crickets interacted more strongly with those that emerged near to them, which was expected, and illustrates the importance of accounting for spatial factors in species whose interactions are likely to be strongly spatially-structured.

We also found that males interacted slightly less often than females, although the reverse was true in 2007 and the standard errors tended to be relatively large. In this polyandrous species both sexes benefit from multiple mating and show highly skewed reproductive success (Rodríguez-Muñoz *et al.* 2010) and females may compete strongly with other females to maintain access to the safety of burrows or to prevent sperm-limitation (Wedell *et al.* 2002; Slatyer *et al.* 2012). Therefore, it is not surprising that there are only small differences between the sexes in the rate of mating and fighting. The sex-matching parameter was negative in all years, although not significant in 2013. This was expected, as mating is more common than fighting, but simulating this helps create more realistic networks. As fighting between a pair of males is related to increased sperm competition between the pair (Fisher *et al.* 2016) fighting may not be an effective behaviour for avoiding post-copulatory competition, and along with potential costs of injury may explain why it is not more common.

Path length and clustering coefficients were generally simulated more effectively by the full simulations than the reduced simulations. The exception was 2012, for which the full model was not better at simulating clustering coefficients or path lengths. Exactly what was different about 2012 is unclear. Our models were however not effective at predicting degree correlations. Accurately predicting degree correlations in social networks based on randomisations is recognised as difficult (Newman & Park 2003) hence this is not necessarily a failing unique to ERGMs. We have found that mating networks show positive degree correlations (Fisher *et al.* 2016), yet most random networks show null or negative degree correlations (Estrada 2011). This indicates there are some aspects of cricket behaviour that our ERGMs did not capture, such as positive assortment by some trait or aspect of “quality”.

Stability of networks across generations

The coefficients of each model were largely consistent in size and sign each year, and the predictive power of the ERGMs was equal for within- and between-year comparisons for both network metrics considered. This indicates that networks were comparable between years. We also found no influence of number of years apart on predictive distance between networks. Therefore, the fundamental properties of cricket social networks that we captured do not appear to diverge over time. Together, these results provide strong support for the idea that some of the characteristics of cricket social networks are stable across generations. This would allow the population to adapt to the social environment in the form of the social network structure. Furthermore, if networks are stable over evolutionary time, evolutionary processes such as the evolution of cooperation through directed reciprocity could occur (Santos *et al.* 2006; Ohtsuki *et al.* 2006; Nowak 2006). This is a key assumption of these models of cooperation and of models of selection acting via social networks (Krause *et al.* 2007; McDonald *et al.* 2013). The only direct evidence for cooperation in our species is when males and females share a burrow (Rodríguez-Muñoz *et al.* 2011). Our point is that, for the first time, we have shown that social network structure in the wild is relatively stable across generations, resisting the regular turnover of individuals. This is necessary before any kind of evolutionary processes can take place across networks.

Predictive distance increases with difference in population size

We found positive relationships between the predictive distance between years and the difference in population size between those years. These were marginally non-significant in both years treated independently, but as the Mantel test is regarded as overly conservative (Legendre & Fortin 2010) and since we found the same pattern for both metrics, we are confident that predictive distances do increase as the population sizes diverge. This is despite the fact that we entered the exact properties of the population for these simulations. This therefore indicates that the network changes in some unexpected way as it changes in size, as otherwise the larger networks would simply scale up accurately from the smaller networks. As a general rule it is not surprising that network similarity is based on size; network size is an important axis of variation (Croft *et al.* 2008). What this suggests is that studies on the social behaviour of small populations, say in captivity or at times of year when individuals live in smaller groups, may not be easily scaled up to situations where the animal lives in larger groups. Many studies on social behaviour in captivity have the express aim of understanding the implications of behaviour for ecological processes such as information or disease transmission in the wild (e.g. Boogert *et al.* 2003). Our findings indicate a need for caution in attempting to transfer this research between contexts.

Using ERGMs to investigate and compare networks

We have used ERGMs to explicitly compare different networks. The effective comparison of networks of different sizes, from different populations of one species, or across species has long been the subject of study and debate (Faust & Skvoretz 2002; Faust 2006). However, as highlighted by a recent review: “Comparing networks across contexts (e.g. between populations or species) remains one of the main challenges in network analysis” (Farine & Whitehead 2015). Part of this challenge is related to differences in data collection among different systems (Farine & Whitehead 2015). Yet this has clearly not stopped comparative studies in other fields. We suggest that, as we have demonstrated here, ERGMs can be used to predict the structure of the network of one species or population from the parameters of another. This will likely reveal a range of networks that are successfully able to predict each other, and a range that cannot. Comparison of similar and dissimilar factors between these different networks, e.g. differences in data collection method vs. differences in population size vs. differences in taxonomic group, will then allow us to determine specifically what makes one observed network different or similar to another. Once we understand how factors such as the method of data collection influence the parameter estimates of an ERGM, we can then account for it to explore more interesting questions, such as the phylogenetic conservation of complex social behaviours (Kasper & Voelkl 2009).

Conclusions

Overall, we found stability in some social network metrics across generations, and consistency in factors affecting social network structure. This would allow the cricket population to evolve in response to social network structure. Alongside our study spanning eight generations, the existence of other studies with long-term data sets of social behaviour in populations (Whiten *et al.* 1999; Wells 2003; Dantzer *et al.* 2012; Aplin *et al.* 2015b), should mean that soon we should be able to actually detect evolutionary changes occurring in response to variation in social structure. However, our observation that networks more different in size were worse at predicting one-another indicates that social structure may not be consistent between contexts where population sizes differ, such as across seasons or between captivity and the wild. Alongside Edelman and McDonald (2014), we have confirmed that ERGMs are a reproducible method for some network metrics by arriving at similar results (size and sign of coefficients) in different years. We have also demonstrated that ERGMs can be used to compare networks distinct in time, and would encourage other researchers to use ERGMs as an effective tool for investigations into network structure and comparisons.

7. Social network dynamics: incorporating individual traits and temporal variation using stochastic actor-orientated models

This chapter is currently in a second round of peer review after being re-submitted following review:
David N. Fisher, Amiyaal Ilany*, Matthew J. Silk** and Tom Tregenza. Social network dynamics: incorporating individual traits and temporal variation using stochastic actor-orientated models (in rev.) *J. Anim Ecol.*

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Abstract

Animals are embedded in dynamically changing networks of interactions with conspecifics. These dynamic networks are fundamental aspects of their environment, creating selection on behaviours and other traits. However, most ecological network-based approaches are constrained to considering networks as static, despite several calls for such analyses to become more dynamic. We introduce a method from sociology that could be used to answer a range of questions in ecology. Stochastic actor-orientated models (SAOMs) are a class of individual-based models that simulate both the dynamic change in social interactions and individual traits over time, while incorporating various relationships between the two. SAOMs can also include a range of individual and dyadic, constant and varying covariates. This allow the investigation of topics such as information or disease transmission over a varying network, co-development of social and other personality types and the response of social groups to changing environmental conditions. We describe the potential applications, data requirements of SAOMs, provide an extensive walk through for model fitting and inference with R code and a sample dataset. We outline how the unique properties of animal social networks are handled within a SAOM, including extensions to multiple association strengths and controlling for elements of data structure. We aim to allow any interested researcher with no more than standard statistical training to implement a SAOM. Researchers can then extend the basic method to tackle a range of existing questions in ecology and explore novel lines of questioning. This should enhance the use of dynamic modelling techniques among behavioural and other ecologists. This will improve our understanding of networks of animal interactions, their change over time and the evolutionary and ecological processes that influence and depend on these networks.

Key words: animal communities; dynamics, individual based models, network-based diffusion analysis, social networks, transmission

Background

Social networks in ecology

All animals are embedded in networks of interactions with conspecifics. These networks represent the social environment of individuals, which influences various evolutionary and ecological processes (Proulx *et al.* 2005; Bascompte 2007; Kurvers *et al.* 2014). By simultaneously considering both the traits of the individuals in these networks and their patterns of interactions, networks have been used to study diverse subject areas, such as disease epidemiology and individuality (Danon *et al.* 2011; Weber *et al.* 2013), and the dynamics of group formation (Bode *et al.* 2011; Wilson *et al.* 2014). The importance of links between individual variation and group-level processes is increasingly well appreciated (Farine *et al.* 2015b), and networks are especially useful as a tool to quantify the social environment to which animals are presumed to be adapted. For instance, by quantifying an individual’s social network we can gain insights into the social information available to an individual (Aplin *et al.* 2012; Atton *et al.* 2012; Farine *et al.* 2015a), the diseases it is exposed to (Hamede *et al.* 2009; Bull *et al.* 2012), the intensity of local competition it experiences (Oh & Badyaev 2010; Formica *et al.* 2011; Fisher *et al.* 2016) and the strength of its cooperative interactions (Voelkl & Kasper 2009; Apicella *et al.* 2012).

Typically these networks of interactions are analysed as being static i.e. a network is built that summarises social interactions over a period of time, and this network is related to the processes of interest. However, this ignores the fact that individuals will change their interaction patterns over time (Blonder & Dornhaus 2011; Blonder *et al.* 2012). If a relationship between two traits exists (e.g. social connectedness and individual dominance) change in one could drive change in the other, but it is impossible to tease apart which trait drives this relationship when only observing the product. This is true of many processes; for instance, if infected individuals show different levels of behaviour, are they infected because of their behaviour or did the infection change their behaviour? Without an experiment, inference of causality is difficult, but strong evidence can be provided where a process or behaviour is observed to consistently happen before, and lead to a change in, another process or behaviour. This is outside the scope of static network analyses as it requires an element of time-ordering to be incorporated into the analyses (Blonder *et al.* 2012; Pinter-Wollman *et al.* 2013). By modelling change in the network over time, it is possible to identify not only how social and non-social processes drive each other (Burk *et al.* 2007), but also what processes govern the development of network structure (Kossinets & Watts 2006). Furthermore, transmission dynamics, such as the spread of information or disease across a population, can be examined and factors important for contraction and transmission of disease identified (e.g. Aplin et al 2014).

Despite the evident potential in the dynamic network analysis approach, applications in ecology remain relatively limited (but see: Blonder & Dornhaus 2011; Jeanson 2012; Wilson *et al.* 2014; Aplin *et al.* 2014; Ilany *et al.* 2015). This may be due to the complexity of the analytical techniques involved. Recent calls for the implementation of dynamic network analyses (e.g. Pinter-Wollman *et al* 2013) provide little information on practical application. Furthermore, contemporary introductions on social network analysis for ecologists state that “temporal dynamics represent a significant analytical challenge” and that tools developed by computer scientists “are not realistic for many animal social networks” (Farine & Whitehead 2015). This indicates that we require more accessible methods. Here, we describe an accessible method for the dynamic analysis of networks: stochastic actor-orientated models (SAOMs). These are flexible and powerful enough to be applied to a wide range of questions. Additionally, SAOMs can incorporate individual and pairwise covariates, and the temporal covariation of traits alongside social interactions. This allows researchers to tackle a very wide range of questions in a single framework.

Actor-orientated models

SAOMs are a class of individual based models. Individual, agent, or actor-orientated models characterise the behaviour of each actor (individual) in the system, rather than calculating an average effect over a population. The latter approach can be problematic if even small non-linear dynamics occur (Lehmann 2009). Additionally, linear-modelling based approaches are often inappropriate for network-based analyses, as the assumption of independence of data points is clearly violated when individuals are embedded in an entire network of connections (Croftv 2008; Croft *et al.* 2011; Whitehead 2008; Snijders 2011). However, to date, there have been only limited applications of SAOMs by those investigating interactions among real animals over time, despite this being identified by the review of DeAngelis and Mooij (2005) as an area where individual based models could be of use (but see Jones 2011; Ilany *et al.* 2015).

There have been recent developments in SAOMs for the study of human social behaviour (Steglich *et al.* 2006; Steglichv 2010; Burk *et al.* 2007; Snijders *et al.* 2010; Snijders *et al.* 2013). These developments have the potential to enable behavioural ecologists to explore a broad suite of interesting questions. Questions tackled in the human research literature include how music preferences and drug taking habits develop within and among friendship groups (Steglich *et al.* 2006) and how unethical behaviour can spread within organisations (Zuber 2014). Such questions have clear analogies for non-human animal behaviour (such as the spread of a novel foraging technique through a group; Boogert *et al.* 2008; Allen *et al.* 2013; Aplin *et al.* 2014), indicating this method’s potential. Yet the applications to understand animal behaviour are currently limited. Jones (2011) investigated patterns of interactions in farmed salmon (*Salmo salar*), and found that fish were either consistent givers or receivers of aggression, suggesting social personality types (Krause *et al.* 2010; Wilson *et al.* 2012). More recently, Ilany *et al.* (2015) investigated the long-term dynamics of spotted hyena (*Crocuta crocuta*) social networks. Some of their key findings were that: 1) hyenas form sparser networks in years with high rainfall; 2) hyenas tend to form ties with individuals with whom they share a mutual connection and 3) female hyenas are more flexible than males in their social bonding tendencies, possibly reflecting their dominance in hyena groups (Ilany *et al.* 2015). These are fundamental insights into how and why animal groups possess their observed structure. Nonetheless, these examples do not fully exploit actor-based models. Specifically, there is the potential to model multiple traits changing over time, not just social interactions, and the variables that affect them. Alongside traits of the individuals in the network, environmental conditions can also be incorporated. Furthermore, the effect of the network structure beyond immediate connections on the formation of new ties can be modelled. Therefore, combining the change in a trait over time, social interactions, group behaviour and/or transmission dynamics are all within the scope of SAOMs.

Below we highlight the potential of SAOMs by providing two more detailed examples of their possible application. We also discuss how to apply SAOMs to animal social networks, which present some unique challenges compared to human social networks. We then outline the types of data and minimum requirements when modelling with SAOMs, and provide a description of the modelling process. A walk through example with complementary R code and data sets to repeat the analysis are available in the online supporting information (http://hdl.handle.net/10871/20067). We focus on the application of SAOMs using the simulation package “SIENA” (Simulation Investigation for Empirical Network Analysis; Snijders *et al.* 2010) implemented through the R package RSiena (Ripley *et al.* 2015; available from http://r-forge.r-project.org/R/?group_id=461).

Examples

1: Disease transmission

A primary interest for those studying epidemiology is how individual behaviour relates to infection at the individual and the population level (Tompkins *et al.* 2011). If a disease is transmitted directly, its spread depends on the social interactions of the entire population, making it a network-based problem. With a SAOM, being infected or not can be modelled as a dynamically changing trait with multiple levels (e.g. uninfected, infected but dormant, infective). This can then be influenced by 1) an individual's characteristics (e.g. sex, condition); 2) its network position (e.g. connectedness) and 3) the characteristics of other individuals it interacts with (including their own disease state). This allows the tendency to be infected to be influenced by the infection status of those you interact with at a particular time point, allowing the spread of a disease across a dynamically changing network to be modelled. The researcher can then explore whether the infection status alters the rate or choice of interactions, or the tendency to be targeted with interactions. As well as modelling disease status as more complicated than infected/uninfected, differences between classes (e.g. sex) in infection or transmission rates can be examined (McDonald *et al.* 2014). If desired, the change in infection status could be constrained to going from uninfected to infected, with returns to an uninfected state being impossible (Ripley *et al.* 2015; Greenan 2015). A similar framework can be applied to information transmission, to model the spread of an innovation across a population (Greenan 2015). This has previously been investigated using network-based diffusion analysis (NBDA; Aplin *et al.* 2012, 2014; Atton *et al.* 2012; Allen *et al.* 2013; Boogert *et al.* 2014; Farine *et al.* 2015) with Hobaiter *et al.* (2014) extending traditional NBDA to account for the build-up of interactions over time. However, SAOMs explicitly model both the change in network over time and the change in a trait over time as mutually connected dependant variables. This allows their covariance, the direction of any causal relationship(s) and the effect of external variables on the dynamic change in both networks and the trait to be modelled (rather than just accounted for), beyond what is possible with NBDA.

2: Behavioural types & networks

In social network analysis, each individual is modelled with a specific social environment. Researchers then determine how individual differences in network traits such as degree or betweenness have consequences for the individual. This indicates that individual-level behavioural traits are important for ecological and evolutionary processes. A similar conclusion has been reached by behavioural ecologists (Koolhaas *et al.* 1999; Dall *et al.* 2004; Réale *et al.* 2007), with within-population, among-individual differences in behaviour observed to be widespread (Bell, Hankison & Laskowski 2009). These "personalities" (Dall *et al.* 2004) are linked to fitness (Smith & Blumstein 2008) and a range of ecological and evolutionary consequences (Wolf & Weissing 2012). SAOMs offer the opportunity to integrate these two branches of individual specific behaviours from social and non-social domains, by modelling both as responses. This allows the researcher to explore the variables that affect both change in social and non-social traits over time. For instance, a researcher could model how the level of e.g. risk-taking behaviour relates to the number of social interactions, after accounting for variables such as condition. This would allow ecologists to determine whether there are social personality types (Krause *et al.* 2010; Wilson *et al.* 2012), and whether they are consistently associated with a suite of other personality traits expressed in non-social contexts i.e. as part of a "behavioural syndrome" (Sih *et al.* 2004; Sih *et al.* 2014). Additionally, researchers could investigate if "social-carry over effects", where social interactions influence the expression of a behaviour, are important (Niemelä & Santostefano 2015). Furthermore, it has been observed that animal social groups show homophilly, in that individuals of similar behavioural types are more likely to associate (Aplin *et al.* 2013; Wilson *et al.* 2014; Carter *et al.* 2015). This could result from "selection" where individuals choose to associate with those of a similar behavioural type, or "influence" where individuals change their behavioural type to match that of those they associate with (Steglich *et al.* 2006, 2010; Burk *et al.* 2007). Identifying exactly which process is more influential is important as it is suggestive of the cognitive process occurring and therefore the selection pressures at work, yet cannot happen unless the change in traits is ordered in a dynamic analysis. Finally, it has been suggested that repeated social interactions lead to an increase in within-individual consistency (Bergmüller & Taborsky 2010; *et al.* 2013). Evidence is mixed however (Laskowski & Bell 2014; Laskowski & Pruitt 2014; Modlmeier *et al.* 2014). SAOMs can be used to investigate this question with existing longitudinal datasets, allowing broader trends to be identified.

An outline of SAOMs

SAOMs model the gradual change in the network and traits of the individuals across discrete time points using hidden Markov models. This models network change as a continuous time Markov process with unobserved states in which the state of an actor at time *t+1* depends only on its state at time *t.* Individuals are recorded as associating at time point *t*, or not associating at time point *t* i.e. the networks are binary. Traits can take a wider range of values; see below. Changes in traits and associations between each network time-period are modelled separately as transitions among states in the overall “state space”. This state space is comprised of all possible combinations of network position and trait (Burk *et al.* 2007). The fact that transitions are modelled as a continuous-time Markov processes means that likely trajectories between each observation are calculated and any changes made are assumed to depend only on the current state of the network and traits. Information about the past is not included by default and is assumed to not bring any additional predictive power (Burk *et al.* 2007; Snijders *et al.* 2010). Covariates containing information about the past can be included in models (T. Snijders, pers. comms.) but this is beyond the scope of this review. While the focus on the present state may initially seem an oversight, it should be noted that SAOMs model states e.g. “X and Y are currently connected”, rather than events e.g. “X interacted with Y” (Snijders *et al.* 2010), so information on long-term bonds in included. However, even if researchers have recorded events rather than states, these data can still be used in a SAOM. Events can be aggregated to infer states (Snijders *et al.* 2010) e.g. “X and Y were grooming each other four days out of seven this week, so they are socially affiliated”. If states of association cannot be accurately inferred then the use of a SAOM is not recommended. The duration of each time period will be determined by the study system, the questions being asked and the resolution of the data available. Some studies of human associations have used yearly censuses (e.g. Steglich *et al.* 2006), although shorter time frames are more likely to be used in studies of animal social networks; for instance we used eight days in the example (see online supporting information).

Between these time points, it is assumed that individuals gradually optimise their position in the network according to a utility function (they either seek to maximise the value of a preference function or minimise the value of a tension function). This is based on their links with others in the network and the links between these others, short-term preferences and unknown tendencies (modelled as residual/random deviance; Burk *et al.* 2007). This occurs over a series of mini-steps in which one individual at a time has the opportunity to take one of a range of permitted actions to change its state (including doing nothing at all). The process of the change in ties or a trait consists of two elements: the rate function and the objective function. The rate function (or “change opportunity process”) models the frequency of changes by the individuals. This rate of change can depend on existing network structure and properties of the individual. The objective function (or “change determination process”) models the probability of particular changes occurring when the individual has the opportunity to make them. This framework requires an assumption that an individual controls its outgoing ties (but importantly in the case of animal social networks, not necessarily for an actor to be purposeful in its actions). Whilst a further assumption of this process is that individuals have complete knowledge of the network, the fact that an individual’s local network is key in determining its probability of network change means that individuals typically only need limited information to act as they do (Snijders *et al.* 2010). RSiena can use both directed and undirected networks. For undirected networks SAOMs are flexible to allow multiple definitions of tie formation that can correspond to the studied system (Ripley *et al.* 2015). For example, in some species a tie requires the agreement of both individuals to form, whereas in others one individual may join others, forcing its presence. For further details on the types of tie formation possible in undirected networks see the RSiena manual (Ripley *et al.* 2015).

Applying SAOMs to animal social networks

SAOMs offer great potential as a tool to study dynamic animal networks. However, due to some the assumptions mentioned above some care needs to be taken when determining whether their use is appropriate within a given study system. Three principal concerns are that i) SAOMs can only model binary network data, ii) they are not designed to deal with situations where “states” cannot be reliably inferred , i.e. when there is uncertainty surrounding network edges (Lindström *et al.* 2013; Farine & Strandburg-Peshkin 2015) and iii) methods of data collection may bias the network (Franks *et al.* 2009).

Binary networks

Reducing weighted networks to binary networks can have major implications in animal social network analysis (Franks *et al.* 2009; Farine 2014). However, through the use of “ordered” networks, RSiena can make use of networks of different interaction strengths. Essentially, a binary network of “strong” associations among a population is entered alongside another binary network of “weak or stronger” associations. The model then estimates what influences weak association formation and dissolution, and then what predicts the transitions between weak and strong associations. This avoids some of the problems associated with “filtering”, where ties below a certain threshold are removed, as ties can be represented as belonging to a small set of different strengths. Determining these association strengths still requires a degree of thresholding however, which can be problematic if weak ties are important (Granovetter 1973; e.g. Farine 2014) and “filtering” ties in this manner can lead to incorrect network metrics (Franks *et al.* 2009). Therefore, SAOMs are likely to be most appropriate when high-resolution data make it possible to construct networks over relatively short time periods during which limited additional information is provided by assigning a wide range of weights to interactions. As SAOMs split the data collected into distinct time periods, information on repeated associations is still retained, in the form of interactions being present in multiple time periods rather than a single interaction with a weight. There will be many areas of research where the presence/absence of an edge is adequate information to answer questions of interest, and SAOMs are likely to be especially useful in these cases. Methods to analyse networks with edge weights drawn from a greater range through (the related) exponential random graph models are continually being developed (Krivitsky 2012), so in the future SAOMs may be able to include such information.

Edge uncertainty

Animal networks have greater potential to contain uncertainty than human networks, as we must infer unobservable social states from observable behaviours. Ideally, we would use SAOMs when no inference of social relationships is required. However, if association-based methods are used (i.e. meaningful social relationships are inferred from spatio-temporal occurrence or repeated interactions (e.g. Sundaresan *et al.* 2007; Shorrocks & Croft 2009;

Aplin *et al.* 2012; Allen *et al.* 2013; Ilany *et al.* 2015) during network construction then a high level of confidence that these associations represent the true states of association is required. For some study systems and some methods, this may require a large number of observations (Lusseauv 2008; Franks *et al.* 2009; Farine & Strandburg-Peshkin 2015). This however does not preclude their use (e.g. Ilany *et al.* 2015) as long as the inference of associations is a confident one. As we mentioned above, if you cannot reliably infer states of association from your data, we do not recommend the use of SAOMs.

Biases introduced by the method of data collection

When collecting data in the field the method of data collection may influence the network structure e.g. individuals might possess many mutual associations with each other if all individuals in a group are linked when they were observed together. As outlined by Franks *et al.* (2009), performing enough censuses or surveys can ameliorate this issue. Furthermore, there are additional features of SAOMs that allow one to control for various factors that may bias results: Particular structural network terms, or dyadic covariates, can be used to model aspects of the social network that could have arisen from the method of data collection. This then allows conclusions about hypotheses of interest to be made having accounted for the confounding factors. We describe this approach in more detail after outlining the types of variables SAOMs can incorporate.

Ultimately, all measurements made when studying animal behaviour are estimates of a true value. As long as any major biases are accounted for, transitions from one network to the next should still approximate real changes in the animals' social environments. Therefore, it should be possible for a researcher to use their prior knowledge of a system to determine when they have arrived at a set of social networks appropriate for analysis using SAOMs.

Data types and requirements

SAOMs allow structural properties of the network and covariates to affect both the probability of a network change occurring (the objective function) and the rate at which change occurs (the rate function). Descriptions of some of the network and trait processes that SAOMs can model that are of interest to ecologists, including those mentioned in our examples above, are provided in Table 7.1, and we implement some examples in R code in the online supporting information. A complete list is available in the RSiena manual (Ripley *et al.* 2015). The SAOM framework can estimate the importance of a variety of structural network processes (e.g. the tendency of individuals to form associations with individuals with whom they already share a mutual associate: “triadic closure”) on how networks change. Modelling these kind of structural processes allows the researcher to determine how particular aspects of individuals’ social environments, such as the presence of a mutual associate, influence their decision on association partners. Such effects also enable researchers to control for structure in the data or biases generated by the method of data collection (see below). The inclusion of covariates (both at the level of the individual and the dyad) enables the role of individual traits and other relationships between individuals in influencing network structure to be assessed. Furthermore, interactions between effects and covariates can be specified. For instance, in some social systems it might be hypothesised that males are more likely to form coalitions than females. An interaction between sex and triadic closure can then be specified, and its importance evaluated. Finally, behaviours or traits can be considered as response variables alongside network change, allowing their change to be directly modelled alongside the change in social interactions.

Table 7.1. A list of possible effects of interest to ecologists that can be modelled with SAOMs in the SIENA software. This is not a complete list of possible effects; see the SIENA documentation for full details. In general a positive value for the effect indicates the process outlined is occurring, but if otherwise this will be described. Effect type indicates whether the effect is a structural term, a covariate influencing the network, or if it involves the relationship between tie formation and the change in a trait, and whether the effect is relevant for undirected and/or directed networks. “Ego” refers to the individual who is initiating the interaction, “alter” to the receiver of the interaction.

Effect name	***Effect type***	***Description***	***Behavioural process***
Ego/alter effects on tie formation	Covariate, directed & undirected	Effect of traits of the individual on the ties it sends/receives	Individuals of different sex, age or personality having different likelihood to form ties
Ego/alter effects on rate	Covariate, directed & undirected	Effect of traits of an individual on rate of change of interactions	Individuals of different sex, age or personality forming or dissolving ties at different rates
Ego-alter trait interactions	Covariate, directed & undirected	Properties of both individuals on the chance of tie formation between them	Positive: ties form within classes/homophilly e.g. intra-sex aggression Negative: ties form between classes e.g. producer-scrounger
Outdegree	Structural term, directed	Number of existing associations of an individual on its tendency to form new associations	Positive: Social behavioural types e.g. consistently social or non-social individuals Negative: optimising group size
Popularity/ indegree	Structural term, directed & undirected	Tendency for individual to associate with those with many connections	Attractive/susceptible phenotypes for affiliative/aggressive interactions
Triadic closure	Structural term, directed & undirected	Tendency of individuals to associate with “friends of friends”	Coalition/clique formation
Reciprocity	Structural term, directed	Individuals repeat interactions with those that interact with them	Preferred associations, tit-for tat cooperation
Balance	Structural term, directed & undirected	Tendency to have/lack the same ties as another associate	Partner choice copying, community formation
Three cycles	Structural term, directed	Directed behaviour from X to Y, Y to Z and Z to X.	Positive: generalised reciprocity Negative: linear dominance hierarchies
Influence	Network-behaviour co-dynamic,	Change in an individual’s behaviour due to the	Social learning and culture or disease transmission

	directed & undirected	behaviour of their associates	
Selection	Network-behaviour co-dynamic, directed & undirected	Forming ties due to the behaviour of the other individuals	Positive: partner choice based on phenotype Negative: avoidance of aggressive or diseased individuals
Dyadic covariates	Covariate, directed & undirected	Properties of a relationship between two individuals e.g. distance	Accounting for separation in space, time or degree of genetic relatedness between individuals
Degree on behaviour	Network-behaviour co-dynamic, directed & undirected	Influence of number of interactions on behaviour	Social behaviour carry-overs to non-social contexts e.g. Winner-loser effects
Behaviour on degree	Network-behaviour co-dynamic, directed & undirected	Influence of behaviour level on formation of new ties	Behavioural carry-overs to social contexts e.g. social behaviour being correlated with behaviour in non-social contexts

Data types

We now outline the type of data required to use SAOMs to explore questions such as those outlined above. See Fig. 7.1 for pictorial representation of a SAOM, indicating the breadth of effects that can be specified. For examples of some of these types of data see the data files of the online supporting information.

The starting point is the network data:

- *t* matrices of size *n* x *n*, representing all members of the population (*n*) and their observed social associations at each time point (*t*).

Ties can be directed or undirected; this will influence what network processes can be investigated. Individuals do not need to be able to interact at every time point to be included. If they could not possibly interact at a particular time point (e.g. they had died or left the study area) “structural zeroes” can be entered into the rows and columns for that individual in the association matrix at that time point (Ripley *et al.* 2015). This prevents the lack of interactions involving that individual informing parameter estimates. This is a major advantage of using SAOMs with RSiena; researchers can avoid omitting individuals that were not socially active at every time point (e.g. Frère et al 2010; Aplin et al 2014). Excessive structural zeroes should be avoided however as they can reduce the stability of parameter estimates. “Structural ones” can also be entered, indicating individuals that must interact (e.g. mothers and their offspring), and therefore that these interactions should not influence parameter estimates. As previously discussed, associations between individuals are represented as either existing or not i.e. they are binary, although a small set of different interaction strengths can be entered through the use of multiple networks.

Alongside the network data, various predictor variables can be added:

- *n* constant actor covariates (e.g. sex)
- *n* x *n* matrices of non-changing dyadic covariates (e.g. genetic relatedness)
- *t*-1 changing environmental conditions (e.g. rainfall)
- *t*-1 *n* changing actor covariates (e.g. body condition)
- *t*-1 *n* x *n* matrices of changing dyadic covariates (e.g. spatial proximity)

These covariates can be categorical or continuous. There are *t*-1 values for the changing covariates as SAOMs model the change between *t* and *t*+1. The effect of parameters on the structure of the network at *t* = 1 is not estimated and so covariate values are not required.

Finally, one can model changing traits as response variables:

- matrices of *n* x *t* trait values.

These must be categorical or ordinal data, with a recommended 2-5 categories (Ripley *et al.* 2015). This requirement is not overly restrictive; infection status, whether an individual has acquired a piece of information or not, body condition indices, or the level of some behaviour e.g. degree of risk-taking could all be accommodated within this limitation.

Data requirements

The data requirements for a SAOM through RSiena will be met by many existing animal network or animal behaviour datasets, making the immediate application of the technique viable. The following serves as guidelines, for further details see Snijders *et al.* (2010):

- At least two networks (interactions or associations over different time periods) are required. Three are required if a behavioural change is also modelled alongside a change in network structure (Ripley *et al.* 2015). Modelling many observations (more than 10) relies on the assumption that each effect is constant over time, or an interaction between the effect and time is included in the model.
- The number of individuals should be more than 20, although if a large number of observations are made then fewer may be acceptable. Networks with a large number of individuals require that each individual could theoretically interact with any other individual in the network. This may restrict the application of SAOMs in some animal systems, but controlling for this to some extent is possible with structural zeroes, or by including group membership or spatial information as covariates (see below).

- There is a minimum amount of change required in the network for change to be effectively modelled. Over all observations, a total of 40 changes (ties formed or dissolved) serves as a minimum. However, too high a number of changes per individual would violate the assumption that it is a gradually changing network. Whether too much change has occurred can be evaluated with the Jaccard index (Jaccard 1901). This is the ratio between the total number of ties present in both observations and the sum of: 1) the number of ties present in both observations; 2) the number of ties broken and 3) the number of ties created. A Jaccard index greater than 0.3 is desirable; models can be specified with lower indices but stable estimation may be hard to achieve.

- As mentioned above, missing data in the form of individuals entering and leaving the network over time are acceptable within SAOMs. Missing data in the other traits and covariates is also acceptable, providing that missingness is unbiased. Too great an amount of missing data is however undesirable as it makes estimation less stable (Huisman & Steglich 2008; Ripley *et al.* 2015).

The modelling process

The total range of possible model specifications is daunting. Furthermore, the most complex model may be a poor starting point if it fails to converge or fits the data poorly, giving unreliable parameter estimates and therefore making the testing of any specific terms unwise. Hence the typical (and recommended) approach is to start with a basic model such as the tendency for individuals to form ties with those with whom they share a mutual connection (triadic closure), then add more complex effects (Burk *et al.* 2007; Snijders *et al.* 2010).

Regardless of your modelling philosophy, terms with weak/non-significant effects may have to be removed from models, as large standard errors can lead to poor convergence. See the RSiena manual (Ripley *et al.* 2015), the SIENA website (http://www.stats.ox.ac.uk/~snijders/siena/) or our R code in the online supporting information for how to specify effects and test them in R.

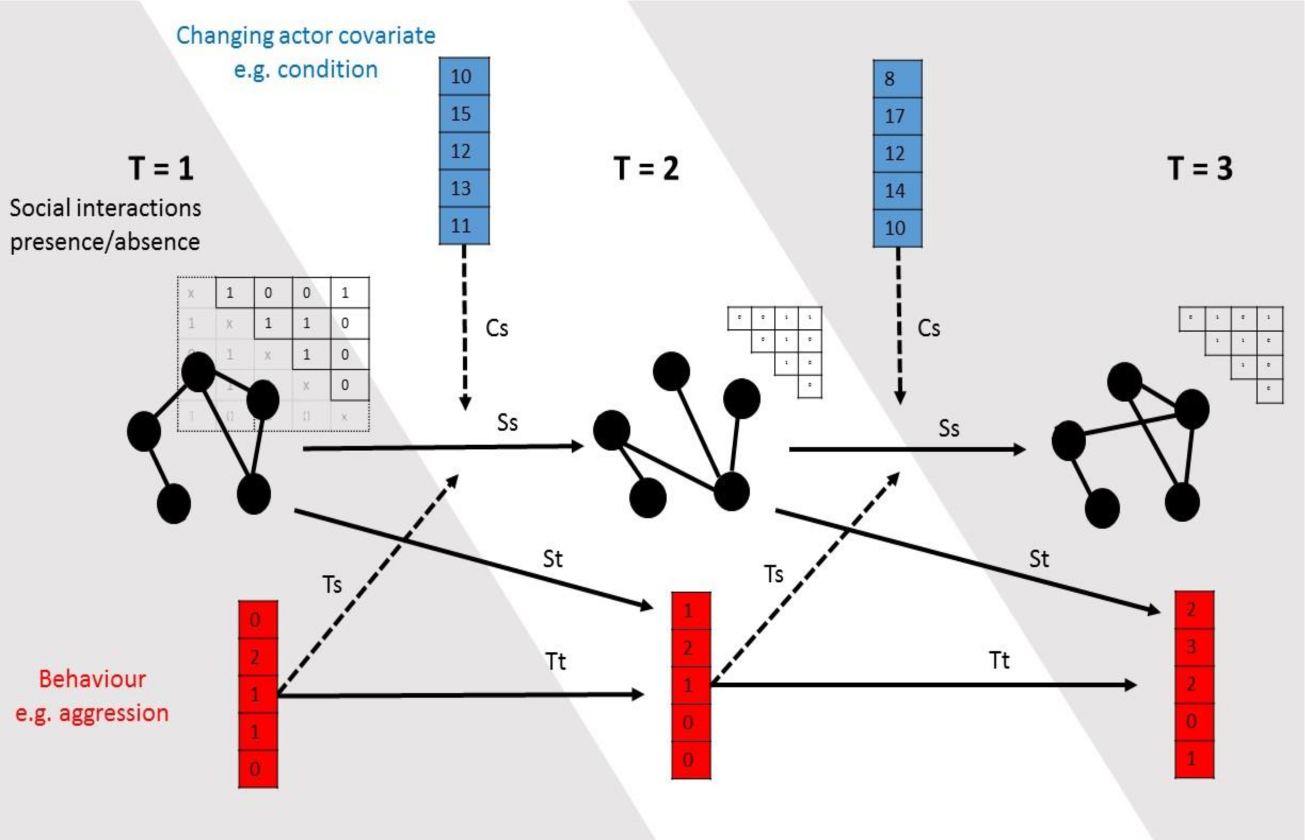

Figure 7.1. Pictorial representation of a toy SAOM, to illustrate the kind of effects that can be modelled. Note that our recommendation of a minimum of 20 individuals still applies. Here there are three time-periods, where five individuals change (or not) their social associations over time. Simultaneously, there is another dependant variable (a trait value, e.g. aggression) changing across each of the three time-periods. Processes depicted model effects of: the social structure at one time point depending on the social structure at previous time points (lines labelled “Ss”); social structure influencing the value of traits at the next time point (lines labelled “St”); the trait at one time point influencing the trait at the next time point (either through a linear or quadratic relationship; lines labelled “Tt”); the trait influencing how the social structure changes from one time point to the next (lines labelled “Ts”) and some changing actor variable (e.g. condition influencing the social structure change from one time point to the next (lines labelled “Cs”)). Here the network is undirected/symmetrical, so only the above-diagonal of the association matrices are shown at time points two and three, but full association matrices would be entered as data for all.

Additionally, for undirected networks, the model type must be set. This states how two individuals become connected. For example, a tie may require agreement within the pair (e.g. in non-coercive mating). In contrast, in some cases a tie would be defined using a forcing model, where one individual forces the connection with the other (e.g. where a fight is motivated by only one contestant). For further information on model types see the RSiena manual (Ripley *et al.* 2015). We now describe the modelling process, with emphasis that it is on goodness-of-fit of the model to the data, rather than statistical significance, which is the aim. Fig. 7.2 is a flow chart illustrating this process. This process is applied in an example, with a guide and full code available online.

Convergence

At each step it must first be determined that the model has converged satisfactorily (model verification). This is assessed by convergence t-ratios (one value per parameter; distinct from a t-value which we outline below) and the maximum convergence ratio (one value for the model; both supplied in the RSiena output). The convergence t-ratio for a parameter is the distance between the observed and simulated values of that parameter. Ideally this would be zero, but absolute scores of less than 0.1 indicates the model is robust enough for the result to be fully interpretable, while less than 0.2 are acceptable when first specifying the model (Ripley *et al.* 2015). The maximum convergence ratio is the maximum t-ratio for convergence for any linear combination of the parameters, and by definition is greater than or equal to the maximum t-ratio for single parameters (Snijders 2015). The distance of estimated model terms from true values is better indicated by the maximum convergence ratio than by the t-ratios in isolation (Snijders 2015). Values below 0.25 are considered acceptable (Ripley *et al.* 2015). In RSiena a repeat simulation run can use starting parameter values from the results of a prior run. Using these more accurate initial values should enable better convergence. Starting values from models lacking some parameters of the new model can also be used, e.g. when adding new effects. We highly recommend using initial parameter estimates from simpler models when adding new effects, as in our experience this consistently leads to better convergence in the new model.

Goodness-of-fit

Once the model has converged, the next stage is to test for goodness-of-fit (GOF; model validation). A model that converges is not necessarily a good model to describe the given data. GOF tests allow the researcher to examine whether a model can simulate networks that are structurally similar to the observed networks. Commonly used tests include estimating the degree distribution (number of unique connections each individual possess), the geodesic distribution (the distance in terms of network links an individual is from others in the network), and the triad census (frequency of sets of three individuals possessing zero, one, two or three connections amongst them; Ripley *et al.* 2015; Ilany *et al.* 2015). The results of GOF tests are plotted to assess how the observed values of network statistics compare to simulated values. These plots can help the researcher by suggesting effects to add. We provide examples of both adequate and inadequate GOF plots in the online supporting information. For instance, if the degree distribution plot shows that the model fails to account for the number of isolates in the network (solitary individuals); one can add the isolates effect to specifically model this tendency. The Mahalanobis distance (MHD; the distance of the mean of the distribution of the simulated data from the observed value; low values desirable) and the associated test are also used to evaluate GOF. Non-significance indicates the simulated values do not differ from the observed values; see Lospinoso (2012) and the RSiena manual (Ripley *et al.* 2015) for further details. Following Ilany et al (2015), an acceptable GOF is when the p-value for each of the MHDs for degree distribution, geodesic distribution, and the triad census are > 0.05. The statistics for a successful GOF should be reported, either in the supplementary materials or in the main text if it relates to a term relevant to a hypothesis. To achieve proper GOF, we strongly recommend first adding structural effects related to network dynamics before adding terms related to individual or dyadic covariates, or network-trait co-dynamics. In our experience, these are much more likely to improve model GOF than other covariates.

Hypothesis testing

Once the model has satisfactorily converged and possesses acceptable GOF, the researcher can start adding effects relevant to particular hypotheses. Each time an effect is added, repeated runs are performed until the model converges. Following this, the GOF of the new model is examined to determine whether the new term has improved or worsened fit. If the term has worsened fit we recommend it should not be retained for further steps, but if they are relevant to hypotheses terms that do not necessarily improve fit can be kept in the model. Terms with large standard errors (> 4) may also have to be fixed at a particular (large) value, as they can prevent satisfactory convergence (Ripley *et al.* 2015).

Once the model of interest, which converges and demonstrates acceptable GOF, has been arrived at, the estimates and standard errors for effects relevant to particular hypotheses can be evaluated. A simple statistical test can also be carried out: the estimate can be divided by its standard error to give a t-value (not to be confused with the t-ratio used to assess convergence); t-values greater than two indicate significance at 95% (Burk *et al.* 2007). Another option for statistical testing is the score-type test (Ripley *et al.* 2015). This test determines whether the GOF is significantly worsened by constraining the value of the parameter to be zero (for more details see Schweinberger 2012). The score-type test separates the estimation and the testing procedures. This is likely to be preferable in ecological datasets when the model will often have many parameters for the amount of data available (Ripley *et al.* 2015). The convergence t-ratios are ignored for any effect being estimated using a score-type test (Ripley *et al.* 2015). If either t- or score-type tests indicate that an effect could be removed, it is still worth visually assessing the change in GOF, and retaining any terms which do appear to contribute to GOF. It is also good practice to assess whether any effects dropped previously contribute to GOF in the final candidate model. It is possible that terms that did not contribute to GOF alone will improve fit when used in conjunction with other parameters.

Alongside convergence and GOF, the model will also calculate correlations between pairs of parameters. Correlations between parameters are quite likely for network effects, therefore values below 0.9 are acceptable (Ripley *et al.* 2015). Values over 0.9 may mean that one of the effects should not be included, although not in every case (see Snijders *et al.* 2010). If two parameters are highly correlated then a model including either of them may achieve good GOF, but will not converge if both are included. In such cases, this should be reported, as it indicates that the two processes the terms represent are linked, which is possibly of biological interest.

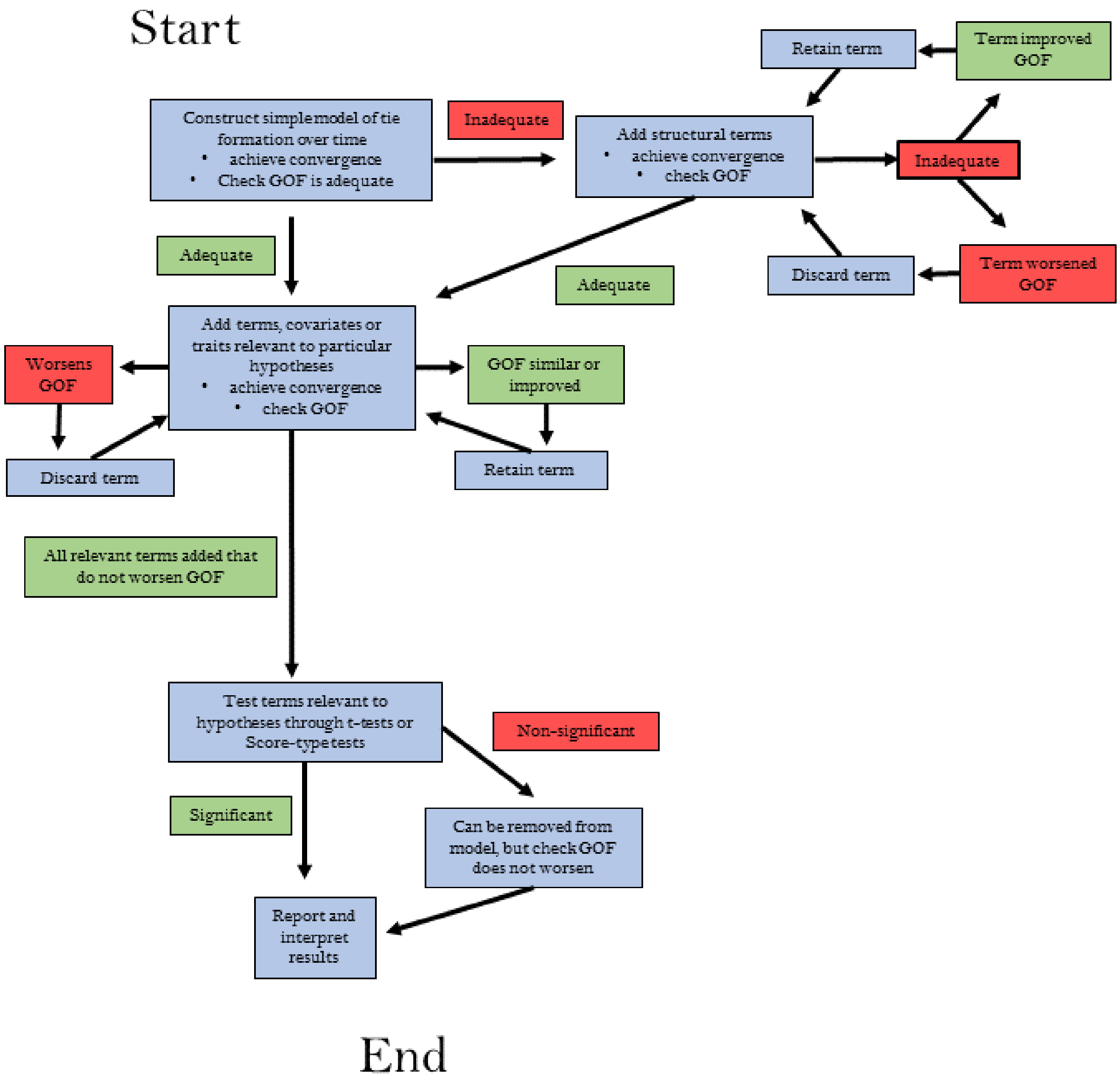

Figure 7.2. A flow chart to illustrate the modelling process. Blue indicates actions, while green and red distinguish between results that might lead to term retention or removal respectively. Note the focus is on achieving an adequate goodness-of-fit (GOF), with the statistical significance of terms only considered at the penultimate step. In some cases following this process will result with

multiple models with adequate GOF. This will typically support the inclusion of particular effects that are present in both models. If two parameters are highly correlated then a model including either of them may achieve good GOF, but will not convergence if both are included.

Note that in some cases multiple different models will give adequate GOF. These typically will have similar terms, supporting the inclusion of these terms as important in the system of study. There is currently no provision for the direct comparison of different models that is analogous to likelihood ratio tests or the comparison of information criteria in RSiena. In general, we recommend that the simplest model that allows the hypotheses of interest to be investigated should be used. If there appear to be several of these then all should be considered as candidate “best” models, and researchers should discuss why differences in model structure may affect parameter estimates.

Using network terms and covariates as controls

Now that we have outlined how SAOMs work and the kind of data they require, we can outline how structural terms and/or covariates can be used as an appropriate null model. If biases are introduced during data collection, structural network parameters can be used to control for their effect whilst hypotheses based on individual traits or behaviours are tested. For example, a criticism of association-based approaches is that they artificially increase the rate of triadic closure (Franks *et al.* 2009). So in models of association-based networks the estimate for triadic closure could be considered to be (at least in part) controlling for this effect rather than being a parameter of interest. There are a wide range of structural terms; which is specified will depend on the likely biases a particular method of data collection introduces.

A similar method can be employed using nodal or dyadic covariates to control for the fact that spatial or temporal factors may have an important influence on the likelihood of two individuals interacting (Frère *et al.* 2010;

Carter *et al.* 2013; Best *et al.* 2014). For example, shared group membership or a spatial relationship such as the distance between home ranges could be entered as a dyadic covariate which accounts for the fact that individuals in the same group or near each other are more likely to interact. This then enables hypotheses relating to factors of particular interest to be examined. This effectively incorporates an appropriate null model in the analysis, as the significance of terms of interest is calculated alongside the influence of these control terms. A similar approach is advocated by Whitehead & James (2015), who suggest calculating “generalized affiliation indices” (GAIs) that represent interactions that occur beyond what is expected based on factors such as spatiotemporal overlap to enter into further network analyses. Such GAIs could be entered into a SAOM, but we recommend using the original association data and the factors that need controlling for within the SAOM.

Summary

In short, SAOMs have great, but as yet unrealised, potential for studying animal social networks. We hope that those interested will consider applying them to their own data, with the R code in the supplementary material serving as a template. Previously, ecologists have used linear models and their extensions (mixed, generalised, animal, non-linear, hierarchical and multivariate linear models) to tackle most problems. We have highlighted one of the other available tools, which can solve some problems that may have required multiple approaches or simply appeared intractable. Additionally, fully appreciating the range of effects that can and have been implemented in SAOMs in other fields should enable ecologists to ask new questions of existing datasets or formulate new questions surrounding social and non-social behaviour. For instance, the extent to which networks represent complex systems with non-linear emergent properties remains yet to be explored (Bradbury & Vehrencamp 2014; Hasenjager & Dugatkin 2015), a topic SAOMs would be suited to analyse due to the variety of effects that can be specified. Further development of SAOMs, for instance through adding information criterion values to models, would further broaden their potential for implementation and interpretation in tackling a host of network-based problems in ecology.

8. Dynamic cricket behaviour and population-level properties

Abstract

Complex social structure, consistent among-individual variation in behaviour and skewed reproductive success are ubiquitous in animal populations, yet overarching explanations for these phenomena are lacking. All of these properties of populations can be linked through social interactions at the individual level. Social interactions among-individuals create a population's social structure, can lead to social niches and so to among-individual differences in behaviour, and dictate mating success and other key parameters. These social interactions can be represented and modelled as a dynamically changing network. We used stochastic actor-orientated models to analyse the change in behaviour in a wild population of crickets under surveillance from a network of video cameras. This method allowed us to attempt to explain the social structure, among-individual differences in activity level and highly skewed reproductive success observed in the cricket population. We find that our models were able to simulate real characteristics of cricket fighting and mating networks with relatively few parameters. This enables us to account for the social structure of the population. However, we found no support for a hypothesis suggesting consistent social niches lead to consistent non-social behaviours. Finally, the skew in total number of connections in the mating network closely mirrors the skew in reproductive success observed in the population, indicating that by effectively modelling the mating network we can account for the reproductive skew in the population. Our results show that one can link population-level parameters down to dynamic individual behaviours and back up to population-level properties, arriving at a holistic understanding of the properties of natural populations.

Key words: dynamic analysis, *Gryllus*, individual-based model, reproductive skew, social network

Introduction

Individuals in dynamic networks

All animals are part of a network of interactions with conspecifics. These are typically competitive, e.g. competition for access to resources or mates, but can also be cooperative e.g. when mating or forming groups for mutual benefit. Interactions such as these influence an individual's fitness and allow it to influence the fitness of others (Formica *et al.* 2012; Royle *et al.* 2012; Wey *et al.* 2013). They therefore can play a key role in ecological and evolutionary processes. Furthermore, these interactions are temporally dynamic, as individuals change interactions partners over time (Blonder & Dornhaus 2011; Blonder *et al.* 2012). This may influence the rate at which individuals encounter potential mates or competitors, the rate of opportunities for pathogen and information transmission, and the opportunities for different social strategies (Pinter-Wollman *et al.* 2013). Networks with properties similar to real-world networks can be simulated by network growth models with few rules (Newman 2002; Ilany & Akcay 2015), indicating that a network's dynamics are fundamentally related to its structure.

Individual-level processes and decisions, such as deciding to leave a nest to forage for food or choosing between male A or male B at a lek, can accumulate to form the population-level properties we observe. For instance, simple rules individuals follow in relation to the movement of fellow group members can result in the apparently complex patterns displayed in murmurations of starlings or synchronised swimming in shoals of fish (Sumpter 2006; Rosenthal *et al.* 2015). Understanding individual-level decisions about interactions with other population members will therefore allow us to explain the structure and properties of whole groups. These individual-level processes however can be influenced by alternative population-level processes to the ones they drive. For instance, decisions about mating opportunities will be influenced by population-level factors such as the relative density of conspecifics and the operational sex ratio (Clutton-Brock *et al.* 1997; Jirotkul 1999; Kokko & Rankin 2006; Oh & Badyaev 2010). Additionally, decisions about behaviours such as foraging will depend on the environmental conditions (Magnhagen & Borcherding 2008; Farwell & McLaughlin 2009; Vankosky & VanLaerhoven 2015). Therefore, in theory, population level processes can be linked down to individual decisions about interactions, and back up the population level again (Fig. 8.1; Farine *et al.* 2015).

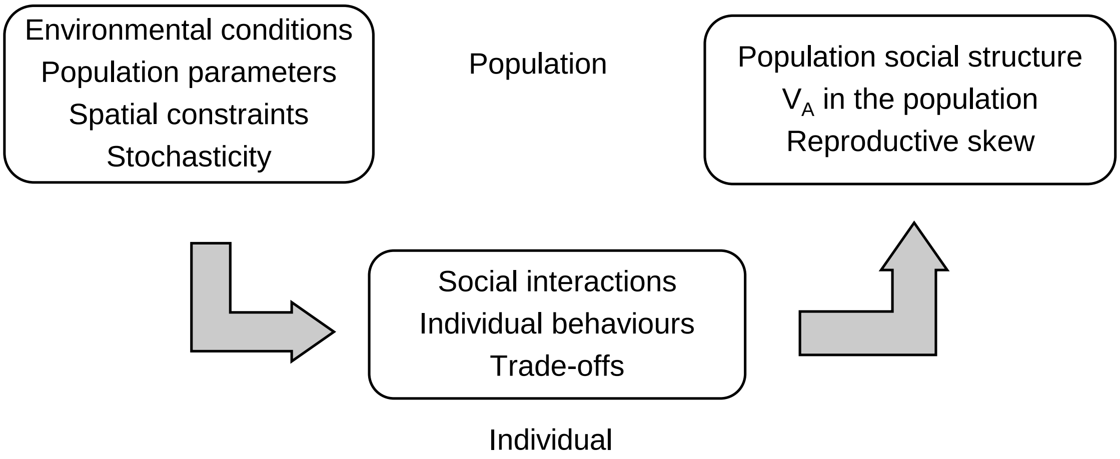

Figure 8.1. Population-level properties such as population size and the prevailing environmental conditions will influence decisions on interaction partners and expression of individual behaviours. These in turn will interact to produce population-level properties such as the observed population social structure, consistent among-individual variation in behaviour (V_A) and the strong skew in reproductive success observed across populations.

Linking individual and population-level properties with SAOMs

As discussed in the previous chapter, stochastic actor-orientated models (SAOMs) allow the modelling of the change in individuals’ social interactions and behaviours over time, as influenced by individual or dyadic effects (Steglich *et al.* 2006; Burk *et al.* 2007; Snijders *et al.* 2010). Which of these individual and dyadic effects are prevalent is dictated by the available interaction partners due to the composition of the population. What is also possible, but was only briefly touched upon in the last chapter, is that these individual behaviours can be influenced by environmental factors (Ilany *et al.* 2015). Therefore, instead of being noise-introducing elements, we can account for environmental variation to create models that better fit our data. This then allows us to model an extensive range of effects, from factors outside the population such as changes in the weather, to individual-level processes such as choice of interaction partners, back to population-level processes such as the spread of information across a group. Fully exploiting the potential of SAOMs therefore allows us a holistic understanding of variation in and among social groups.

We set out to use SAOMs in this manner. We were interested in explaining several population-level properties of a population of wild field crickets, outlined below. *Gryllus campestris* is univoltine and adults are active in the months April – July following overwintering as nymphs in burrows they dig themselves. Once sexually mature, males start calling to attract mates, and both sexes move among burrows to search for mating partners. When encountering a member of the same sex at a burrow they will typically fight, with the loser leaving the burrow (Alexander 1961). Large, small males that sing frequently, long lived and more promiscuous individuals achieve higher lifetime reproductive success (Rodríguez-Muñoz *et al.* 2010).

The first population-level property to explain is that cricket social networks possess structure beyond that expected by chance or due to solely spatially driven associations (chapters 5 & 6; Figs. 8.2 & 8.3). In fact, the vast majority of animal social networks are significantly different from random networks. Network structure influences the spread of disease (Hamede *et al.* 2009) and information (Boogert *et al.* 2014) through a population. It can also dictate the intensity of mate competition (Oh & Badyaev 2010) and the cohesiveness of social groups (Barocas *et al.* 2011). Hence models that can effectively re-create the features of various real-world networks are valuable.

The second population-level property we wanted to investigate was the presence of consistent among-individual variation in behaviour (V_A) in the population (Fisher *et al.* 2015a). This property, also known as animal personality (Dall *et al.* 2004), is widespread across taxa (Bell *et al.* 2009), yet confounds initial expectations that behaviour should cluster around adaptive peaks (Sih *et al.* 2004a). It has been suggested that individuals can achieve greater fitness by inhabiting social niches within populations, exploiting alternative strategies (Bergmüller & Taborsky 2010). This hypothesis then suggests that consistency in social behavioural type will lead to correlated expression of consistent behaviours in non-social contexts (Niemelä & Santostefano 2015). Evidence for this hypothesis has been found in some systems (Laskowski & Pruitt 2014; Carter *et al.* 2014; Modlmeier *et al.* 2014) but not others (Laskowski & Bell 2014). We therefore looked for consistency in social behaviour, and whether this was linked to an individual's activity level, one of the most commonly studied axes of personality (Réale *et al.* 2007). In chapter 4 we were able to explain some V_A in activity through a pace of life syndrome, but our model accounted for less than 50% of the variance in activity, leaving more to be explained.

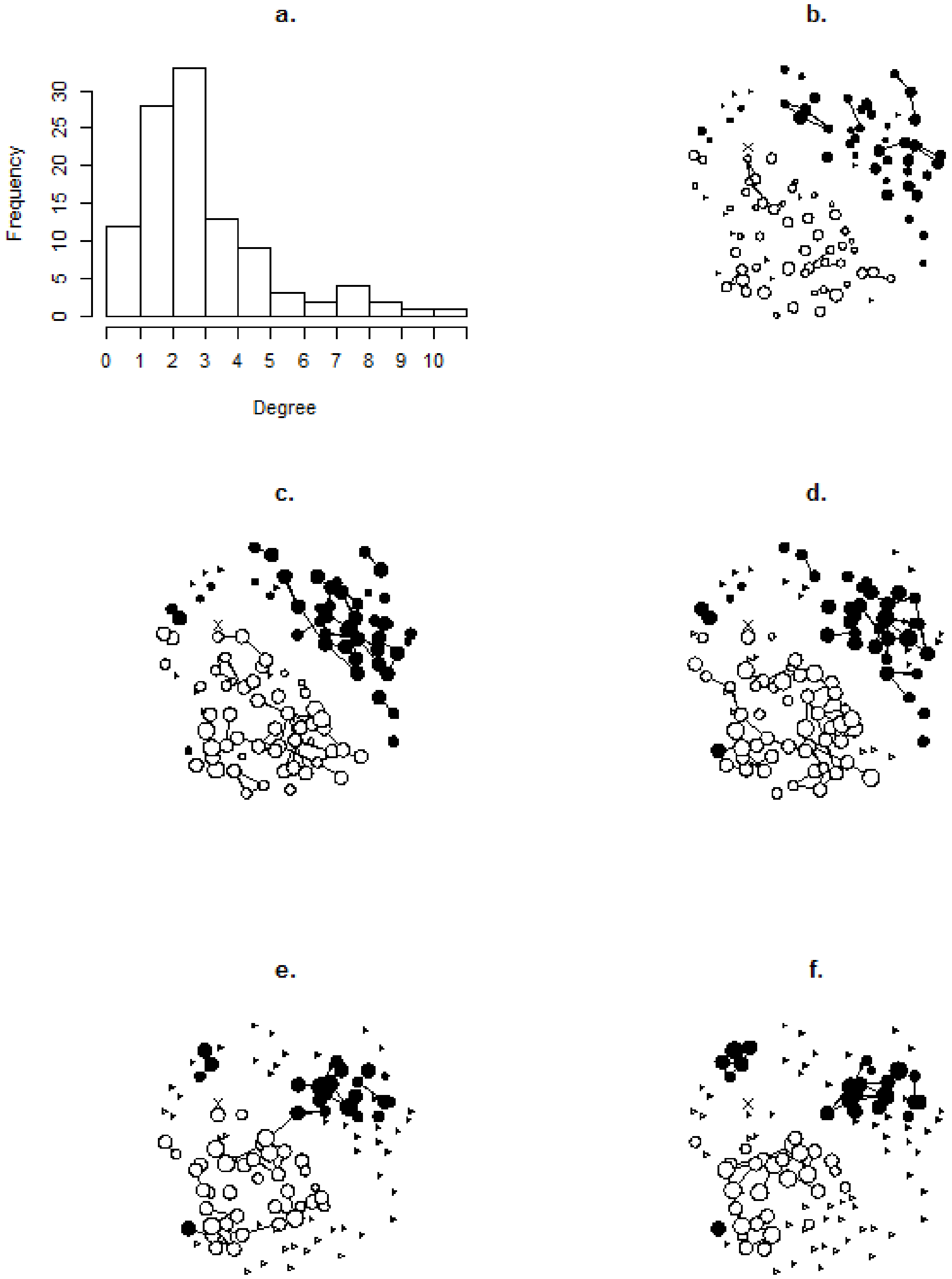

Figure 8.2. The degree distribution of the fighting network (a.), and a network plot for each of the five time periods (b-f.). For the degree distribution all five time points are aggregated to give the frequencies of the total number of different crickets an individual fought in 40 days. For the network plots, males are filled circles, and females open circles. The size of the circular nodes indicates the activity level of the individual (from 1-4) with individuals who were not alive during the time period plotted as a small triangle. The position of an

individual is the same in each plot, using a Fruchterman-Reingold algorithm (Fruchterman & Reingold 1991) based on an aggregation of all five time periods. For illustrative purposes, the “X” indicates a female who fought two other individuals and recorded 3 leaves events (and so an activity level of 2) in the 1st time period, 1 fight and 4 leaves (activity = 2) in the 2nd time period, 0 fights and 9 leaves (activity = 3) in the 3rd time period, 0 fights and 12 leaves (activity = 3) in the 4th time period, and was dead for the 5th time period. Networks plotted using the R package “network” (Butts 2008a).

Finally, the third population-level property to explain was the strong reproductive skew observed in both sexes in this population (Rodríguez-Muñoz *et al.* 2010). In common with many other social and non-social animals (Keller & Reeve 1994; Clutton-Brock *et al.* 1997; Engh 2002; Frentiu & Chenoweth 2008; Ryder *et al.* 2009; Thompson *et al.* 2011) many male and female *G. campestris* achieve very low fitness, while a minority have large numbers of offspring surviving to adulthood in the following generation. In *G. campestris,* reproductive success is strongly influenced by mating success (Rodríguez-Muñoz *et al.* 2010), although post-copulatory processes may have some influence (Bretman & Tregenza 2005; Bretman *et al.* 2009, 2011). The matings in a population can be represented as a network, with connections between individuals formed if they mate (Sih *et al.* 2009; McDonald *et al.* 2013). The degree (number of unique links an individual possesses) distribution of this network shows a similar skew to the observed skew in reproductive success (compare Fig. 8.3a of this chapter with Fig. 1 of Rodríguez-Muñoz *et al.* 2010). Therefore, if we can effectively model the mating network and account for the skew in connections among the population, we are likely to be effectively explaining a large proportion of the skew in reproductive success.

To understand these three properties, we turned to the dynamics of two social networks of the cricket population. First, to see whether cricket social networks possess structure beyond that expected by chance or due to solely spatially driven associations, we investigated the population-level and individual-level factors that contribute to the observed social structure, including spatial proximity. Secondly, to test the hypothesis that consistency in social behaviour leads to consistency in other behaviours, we linked the number of fighting partners to the number of times a cricket left a burrow, a measure of activity. Finally, to account for the strong skew in reproductive success observed in the population, we investigated how the network of matings among crickets changes over time alongside the fighting network, and how these networks are influenced by population- and individual-level processes. We can also interpret the results of this final analysis in the light of the first question: what non-random processes lead to the observed population social structure?

Methods

Study site

The study site is located in a meadow in Northern Spain, see www.wildcrickets.org and Rodríguez-Muñoz *et al.* (2010) for further information. We used data collected in 2013 for this analysis. In the early spring we located each burrow and marked it with a unique identifier. In late April, just before adults start to emerge, we set out 124 cameras at random at those burrows with an active juvenile cricket (nymph). This then allowed us to record the exact moment of emergence for those adults, and all subsequent behaviour at the burrows. We directly monitored burrows that were without cameras daily or every other day, and recorded the life stage and identity of the individual using the burrow. As nymphs do not move among burrows, when there was an untagged adult at a burrow where on the previous days there had been a nymph, we could infer the emergence date for that adult. This allowed us to record accurate emergence dates for the vast majority of the population. Adults mate with members of the opposite sex, fight individuals of typically the same sex and hide from predators at these burrows, so by monitoring these directly we capture the vast majority of relevant cricket behaviour. If we did not observe a cricket’s death, we estimated it as the day after it was last observed. A few days (mean ± standard deviation = 3.76 ± 2.81) after a cricket emerged as an adult, we trapped it (using a custom-built trap, see www.wordpress.com/crickettrapping for more details), and transported it to a laboratory adjacent to the field site. Here we weighed it and fixed a water-proof vinyl tag to its pronotum using cyanoacrylate glue. This allows the identification of individuals, and as far as we are aware does not affect their natural behaviour.

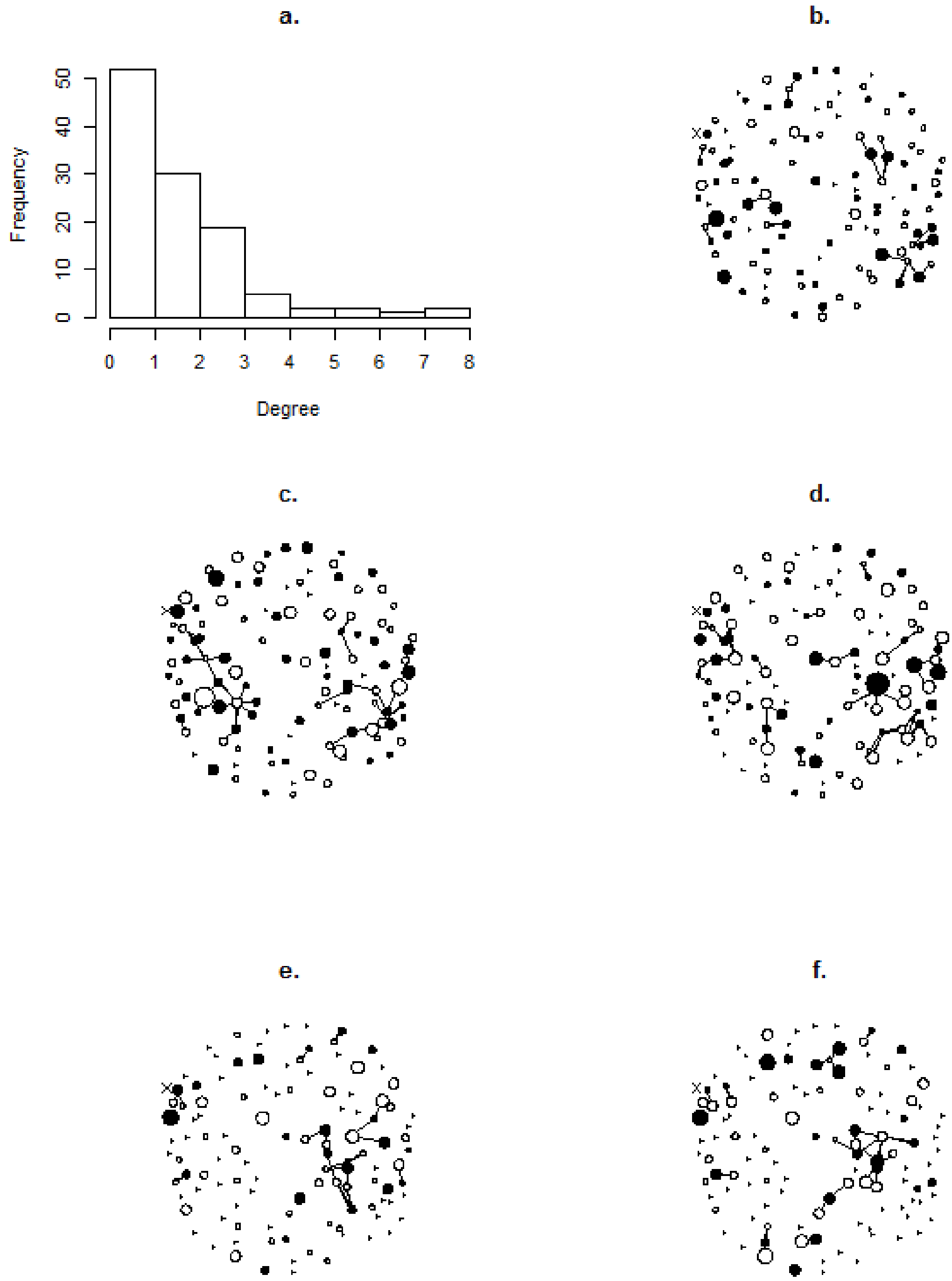

Figure 8.3. The degree distribution of the mating network (a.), and a network plot for each of the five time periods (b-f.). For the degree distribution all five time points are aggregated to give the frequencies of the total number of different crickets an individual mated with over 40 days. For the network plots, males are filled circles, females open circles. The size of the circular nodes indicates the degree in the fighting network of that individual in that time period. Individuals who were not alive in the time period are plotted as small triangles. The position of an individual is the same in each plot, using a Fruchterman-

Reingold algorithm (Fruchterman & Reingold 1991) based on an aggregation of all five time periods. For illustrative purposes, the “X” indicates a male that had no matings and a single fight in the first time period, 1 mating and 3 fights in the 2nd time period, no matings and 1 fight in the 3rd time period, 2 matings and 2 fights in the 4th time period, and 1 mating and no fights in the 5th time period. Networks plotted using the R package “network” (Butts 2008a).

After tagging the crickets, we released them back to the burrow they were trapped from, which we kept blocked in the meantime to prevent other animals, including other crickets, from usurping the burrow. We moved cameras away from burrows that hosted no cricket activity for two days to nearby ones where cricket activity had been directly observed or which showed signs of activity. As the season progresses there become more cameras than live adult crickets. This gives us very good information on behaviours over individuals’ entire adult lifetimes.

Social interactions and activity levels

We implemented our SAOMs in the R package “RSiena” (Ripley *et al.* 2015). For our first question we were interested in the fighting behaviour of individual crickets. We judged two crickets to have fought if there is any kind of aggressive interaction between them, which can be unidirectional. These fights typically occur immediately after a cricket arrives at a burrow at which there is already a member of the same sex. The loser will then leave the burrow. These fights are assumed to be over potential mating partners (Alexander 1961) and to provide access to the safety of a burrow. We split the season into nine eight day time periods, which gives a manageable number of time steps but also allows enough time for interactions to occur to prevent each time period having a low frequency of interactions. To avoid exceptionally sparse networks we removed crickets who only fought a single other individual in a single time period (n = 58). There were 108 tagged crickets who fought in more than one time period or fought more than one individual, giving us networks of 108 individuals. For each time period we created a network, linking individuals if they fought at least once in that time period. If an individual was not alive during a time period we entered “structural zeroes” for all its potential interactions. These indicate that interactions with that individual could not have taken place, preventing the lack of interaction from informing parameter estimates (Ripley *et al.* 2015).

For our second question we entered crickets' activity levels as a behavioural co-variable alongside their fighting interactions. For our measure of individual activity level we recorded the number of "leaves" events each cricket performed in an eight day period. To score a "leaves" event a cricket must leave the burrow and the area around it under observation by a camera, and stay away for more than five minutes. Crickets doing this more frequently per day are more active individuals than those that remain at the burrow. A daily version of this measure is repeatable within-individuals in the wild, and related to a measure of activity in captivity (Fisher *et al.* 2015b). It is recommended in a SAOM using RSiena that behavioural variables are constrained to 2-5 levels (Ripley *et al.* 2015). Therefore, we assigned crickets a score of 1 if they left a burrow 0 times in an eight day period, 2 if they left a burrow 1-5 times, 3 if they left 6-20 times, and a 4 if they performed more than 20 leaves events (up to a maximum of 78). These boundaries were chosen as we feel they represent biologically different degrees of movement, they resulted in similar sample sizes for the first three levels (in total there were 208, 226, 275 and 58 scores of 1, 2, 3 and 4 respectively) and the models with alternative boundaries encountered problems converging.

For our third (and to a lesser extent our first) question, we recorded matings between individuals. We linked crickets in a network if they mated at least once in the eight day period, similar to the fighting network. We added structural zeroes for all potential interactions between individuals of the same sex, as such interactions in that network were impossible. This was input into a SAOM alongside the networks of fighting behaviour, as we expected them to influence each other. We limited both networks to the 113 crickets who mated or fought more than one other crickets or mated or fought in more than one time period, again to prevent exceptionally sparse networks (n = 53). For both networks, if an individual was not alive during a time period we entered structural zeroes for all its potential interactions.

Data analysis

Unless otherwise stated, we used the same method and rationale as outlined in the preceding chapter. We initially had nine time periods. However, in the first two and last two time periods there were not enough social interactions to investigate the processes that influence their change, so we did not use them, leaving the middle five time periods (spanning 20/5/13-28/6/13). Terms are considered significant at the 95% if |estimate / standard error| > 2 (Burk *et al.* 2007; Ripley *et al.* 2015). Bellow we explain the modelling process for each of the networks.

Fighting network

We used a forcing model (model type 2) for this analysis, where one individual dictates whether a tie is created or dissolved (Ripley *et al.* 2015), as for fighting a cricket can simply attack another or leave the area when they both meet. The initial SAOM for fighting behaviour contained rate parameters for each time period and the effects of density (typically negative as networks are generally sparse) and triadic closure (typically positive as individuals interact with those they share a mutual connection with). We tested this for satisfactory goodness-of-fit (GOF) with three network statistics: outdegree distribution (the frequencies of the different numbers of unique connections possessed by crickets in the networks), geodesic distribution (the frequencies of the different shortest path lengths in the networks) and the triad census (the frequencies of each set of three crickets that possessed 0, 1, 2 or 3 links among them). These are chosen as they are commonly calculated network statistics, but their values are not defined by any of the parameters in the model (Ripley *et al.* 2015). The observed network statistics were not different from the network statistics of the set of networks generated by the model fitting process (p = 0.281, 0.399 & 0.994 for the GOF tests for outdegree distribution, geodesic distribution and the triad census respectively). Therefore, we began adding terms of interest. After adding a term we ran the model until it achieved convergence, and assessed the GOF. If it had worsened we removed the newly-added term(s) before continuing, otherwise it/they were retained.

To determine whether crickets have social personality types, we added the effect of "indegree popularity". This effect, when positive, indicates that individuals with many connections tend to have more connections in the next time period, while individuals with few connections have fewer connections in the next time period, suggesting consistency in aggressive behaviour. This model with this term converged, but its GOF was lower than for the simpler model (the Mahalanobis distances, a measure of model fit, increased for all three tests (60.54->61.14, 20.48->22.19 & 10->10.39 for the GOF tests for outdegree distribution, geodesic distribution and the triad census respectively)), so we did not retain in subsequent models.

Secondly, we added the individual covariate of sex, and the parameters for sex affecting the number of interactions an individual has, and for interactions occurring depending on the sex of both individuals. The former term models the tendency for members of one sex to fight more often than members of the other sex, which we expect to have little effect based on previous results (chapter 6). The latter term models the tendency for crickets to predominantly fight members of the same sex as themselves, which we expected to be a strong effect. We next added a changing dyadic covariate of distance, which was the Euclidean distance between each pair of crickets at the start of the time period. This models the probability that crickets nearer each other are more likely to interact than those further away. As a SAOM models the transitions between networks, rather than the structure of the networks themselves, we entered four instead of five measures of distance for the four transitions. We then added the constant covariate of individual mass (g), and its effect on the number of connections and individual acquired, and the interaction between the mass of each individual and its potential associates. We expected heavier crickets to fight more often (Dixon & Cade 1986), and crickets to avoid fighting those of more different weight (Arnott & Elwood 2009). We next added two effects for weather: the total amount of rainfall (cm) and the intensity of solar radiation (Watts/m^2) in each time period. They are recorded by a weather station in the centre of the meadow that takes measurements every ten minutes (Vantage Pro 2, Davis instruments, California). These are predicted to increase and decrease the frequency of social interactions respectively, as they have concurrent effects on movement around burrows (Fisher *et al.* 2015b). Each individual is scored as being exposed to the same amount of rainfall and solar radiation in each time period. This is the final model for the fighting network dynamics.

Activity level

Once we arrived at our final model for cricket fighting behaviour, we added a behavioural co-variable: the activity level of each cricket in each eight day period. For this model we removed the non-significant effect of the interaction between the mass of an individual and the mass of a potential associate, as the effect had a very large standard error (see Table 8.1) which can hinder convergence of the whole model (Ripley *et al.* 2015). Adding the activity co-variable leads to the inclusion of four rate parameters for the change in activity between each time period, as well as the linear and quadratic changes of activity. The first of these estimates the linear change in an individual's activity over time. The second estimates the change in activity level relative to the difference between the cricket's current activity level and its mean activity level. Positive values of the quadratic term indicate divergence of behaviour to extremes, while negative values suggest regression to the mean (Ripley *et al.* 2015). After adding these terms the model failed to converge, so following the RSiena manual we fixed the rate parameters of the change in network ties to the values achieved in the previous model run, rather than estimate them (Ripley *et al.* 2015). Once these terms were fixed, this model converged, so we proceeded as before. We added terms related to the covariance between activity level and the social interactions. We added the term "activity on degree" (AoD) which estimates how an individual's activity level influences the number of connections it gains in the next time step. We also added the effect "degree on activity" (DoA) which estimates the influence of the number of connections an individual has on its change in its activity level in the next time step. The model failed to converge with these new parameters, so we removed the two non-significant effects of weather (see Table 8.1). After this, the model converged satisfactorily and the GOF for all tests remained satisfactory. This was our final model for the co-dynamics of activity and fighting behaviour.

Mating and fighting networks

For this model we entered the five mating networks alongside the five fighting networks. We used a unilateral initiative and reciprocal confirmation model (model type 3; Ripley *et al.* 2015), since for mating, both crickets need to be receptive for it to occur. This model initially includes the effects of density and triadic closure for both networks. We removed the effect of triadic closure from the mating network, as it is impossible in this network. As only males and females interact, it is impossible for an individual to interact with a cricket with whom they share a mutual contact, as they must both be of the same sex. Once this model converged we began adding terms. The GOF for the mating network was not initially satisfactory (p = 0.019, 0.041 & 0.008 for the GOF tests for outdegree distribution, geodesic distribution and the triad census respectively) so we added the effect of degree assortativity for the mating network. If significant and positive, this effect indicates that individuals with many associations preferentially interact with other individuals with many associations. This possibly represents mutual mate choice, something we have found inferential evidence for previously (Fisher *et al.* 2016). This model converged, and achieved satisfactory GOF (p = 0.413, 0.612 & 1.00 for the GOF tests for outdegree distribution, geodesic distribution and the triad census respectively), so we began adding terms of interest. We first added the changing dyadic covariate of distance for both networks, calculated in the same way as previously. We next added the effect of mass for both networks, and the interaction between the mass of two potential associates for the mating network. The latter effect was not added for the fighting network as previous results indicated it was not important (Table 8.1), and we wished to avoid over-parameterising the model. We expected mass to be positively related to mating interactions, but for the interaction to not be important, as individuals of all sizes may prefer larger, presumably more fecund individuals (e.g. Aquiloni & Gherardi 2008; Baldauf *et al.* 2009). We also added the effects of rainfall and solar radiation for the mating network. These were not added for the fighting network as previous results indicated they were not important (Table 8.1). We then added terms relating to the co-evolution between the networks. The first of these was the effect of across-network popularity, where the number of an individual’s connections in one network influences its number of connections in the other network. We expect this to be positive, as individuals engaging in many fights are assumed to be doing to gain access to many mating partners. We actually added two effects here, one for the mating-networks’ effect on the fighting networks, and then the effect in the opposite direction. We finally added the “mutual partner” effect, from the fighting network to the mating network. This models the possibility that two individuals that fight are then more likely to share a mutual connection in the mating network. We have previously found that males who fight are also typically in sperm competition (Fisher *et al.* 2016) so we expect this effect to be positive. This was our final model.

Results

Fighting network

From the final model of fighting we found significant effects for density, triadic closure, the distance between two individuals, an individual's mass and both the main effect of sex and the interaction between the sexes of two potential associates (Table 8.1). Density was strongly negative, indicating that crickets tend not to be connected to all other crickets, and so the network is relatively sparse, like most social networks (Snijders *et al.* 2010). Triadic closure was positive, indicating that the presence of a mutual connection increased the chances of two crickets fighting. This was true even when accounting for the effect of distance between individuals, which negatively influenced their tendency to have interactions. The sex effect was negative, indicating that males fought fewer other individuals than females, while the interaction between the sex of one cricket and the sex of another was strongly positive, as expected since fights are predominantly intra-sex. Heavier crickets fought more unique crickets, again as predicted, but the interaction between the mass of an individual and the mass of its potential fighting partner was not important. The weather variables did not influence the fighting network.

Activity level

Results relating to a cricket's activity level are summarised in Table 8.2. The linear effect of age was positive, while the quadratic effect was negative. Therefore, crickets become more active with age, and tend to return to the mean activity for a given age rather than diverge to extremes. The DoA effect was negative but not quite significant, indicating that crickets that fought more other crickets tended to be less active in the next time point. There was no influence of the AoD effect: an individual's activity level did not affect the number of crickets it fought at the next time step.

Table 8.1. Results for the SAOM for the fighting network. Shown are the effect estimates, standard errors, convergence scores and the t-statistics (estimate / standard error). Effects are considered significant at the 95% level when the absolute t-statistic is greater than two. Such effects (aside from the rate parameters) are highlighted in bold. Rate parameters in a SAOM with only one

dependent network are calculated rather than estimated, so convergence scores are not given here.

Effect name	***Estimate***	***Standard error***	***Convergence***	***t-statistic***
Rate of change (period 1)	3.300	1.130	NA	2.921
Rate of change (period 2)	2.169	0.373	NA	5.811
Rate of change (period 3)	1.040	0.191	NA	5.456
Rate of change (period 4)	1.913	0.456	NA	4.200
Density	**-4.519**	**0.355**	**0.057**	**-12.739**
Triadic closure	**0.861**	**0.217**	**0.024**	**3.959**
Distance	**-0.159**	**0.018**	**-0.075**	**-8.790**
Sex	**-0.414**	**0.183**	**-0.031**	**-2.262**
Sex ego x Sex alter	**6.398**	**1.144**	**0.059**	**5.595**
Mass	**1.991**	**0.892**	**-0.003**	**2.232**
Mass ego x mass alter	-5.214	5.466	-0.005	-0.954
Rainfall	0.007	0.013	0.058	0.592
Solar radiation	< 0.001	< 0.001	-0.025	1.500
Maximum Convergence ratio = 0.118				

Table 8.2. Results for the SAOM with the activity co-variable. This model also contained terms for the change in the fighting network, but as these do not add to the previous results they are not presented here. DoA stands for “degree on activity”, AoD for “activity on degree”. Shown are the effect estimates, standard errors, convergence scores and the t-statistics (estimate / standard error). Effects are considered significant at the 95% level when the absolute t-statistic is greater than two. Such effects (aside from the rate parameters) are highlighted in bold.

Effect name	***Estimate***	***Standard error***	***Convergence***	***t-statistic***
Rate of change (period 1)	2.705	0.644	-0.026	4.200
Rate of change (period 2)	2.500	0.618	0.049	4.047
Rate of change (period 3)	2.233	1.032	-0.011	2.164
Rate of change (period 4)	2.543	0.957	-0.024	2.656
Linear change	**0.477**	**0.219**	**0.070**	**2.178**
Quadratic change	**-0.539**	**0.103**	**-0.045**	**-5.223**
DoA	-0.210	0.140	0.008	-1.502
AoD	-0.226	0.275	-0.035	-0.820
Maximum Convergence Ratio = 0.153				

Mating and fighting

In the final SAOM for mating and fighting networks, all the significant effects from the previous analysis of fighting behaviour were in the same direction as before, although the effects of sex, distance and mass were not significant (Table 8.3). This possibly indicates a lack of power in the analysis. The effect of across network popularity from the mating network to the fighting network was significantly negative, indicating that individuals who mate with many others fight fewer other crickets in the next time period.

For the mating network, density was strongly negative as for the fighting network, again as social networks are typically sparse. The effect of degree assortativity was positive, indicating that promiscuous males mated with promiscuous females. Otherwise no effects were significant, but as we suspect a lack of power in this analysis we will mention the following effects that were close to significance (|estimate / standard error| >1). The effect of distance was negative, while the effect of rain was positive. The “mutual partner” effect was positive, suggesting that crickets who are connected in the fighting network tend to be more likely to share a mutual connection in the mating network. Neither the main effect of mass nor the interaction were important, nor was the effect of solar radiation and the effect of popularity in the fighting network.

Discussion

Overall, using two SAOMs we were able to explain two out of the three population-level properties we identified. We were successfully able to achieve our first goal; to determine whether cricket social networks possess structure beyond that expected by chance or due to solely spatially driven associations. We identified various terms that influenced crickets’ tendencies to have fights or matings.

Table 8.3. Results for the mating and fighting network SAOM used for the third (and to a lesser extent the first) question. Effects are considered significant at the 95% level when the absolute t-statistic is greater than two. Such effects (aside from the rate parameters) are highlighted in bold. The four rate-of-change parameters for the fighting network were fixed rather than freely

estimated, hence their statistics other than the estimate are not provided (see Table 8.1).

Fighting network effects	**Estimate**	**Standard error**	**Convergence**	**t-statistic**
Rate of change (period 1)	3.300	NA	NA	NA
Rate of change (period 2)	2.169	NA	NA	NA
Rate of change (period 3)	1.040	NA	NA	NA
Rate of change (period 4)	1.913	NA	NA	NA
Density	**-2.004**	**0.170**	**-0.067**	**-11.795**
Triadic closure	**0.862**	**0.221**	**-0.026**	**3.907**
Distance	-0.005	0.016	0.072	-0.313
Sex	-0.129	0.135	0.030	-0.955
Sex ego x Sex alter	**3.270**	**0.577**	**-0.076**	**5.672**
Mass	0.997	0.714	0.056	1.396
Popularity in mating network	**-0.637**	**0.291**	**0.027**	**-2.185**
Mating network effects	***Estimate***	***Standard error***	***Convergence***	***t-statistic***
Rate of change (period 1)	5.306	1.490	0.015	3.558
Rate of change (period 2)	3.829	1.018	-0.009	3.761
Rate of change (period 3)	3.280	0.894	0.013	3.669
Rate of change (period 4)	3.664	1.657	0.007	2.212
Density	**-1.605**	**0.118**	**-0.002**	**-13.609**
Degree assortativity	**0.158**	**0.066**	**-0.004**	**2.411**
Distance	-0.019	0.017	0.004	-1.139
Mass	-0.610	0.715	-0.033	-0.853
Mass ego x Mass alter	-1.704	4.520	-0.019	-0.377
Rainfall	0.011	0.007	-0.028	1.454
Solar radiation	< 0.001	< 0.001	0.001	0.343
Popularity in fighting network	-0.026	0.185	-0.033	-0.138
Mating to fighting agreement	1.143	0.838	-0.009	1.364
Maximum Convergence Ratio = 0.146				

However, we found no evidence for the hypothesis that consistent social niches lead to consistent non-social behaviours. In field crickets at least, the pace of life hypothesis is a better explanation for the presence of personality (see chapter 4) than the social niche hypothesis. As we were able to simulate realistic mating networks, we were also able to achieve our third aim of providing a potential explanation for the skew in mating success, and so likely reproductive success, in the population. We now deal with each of our results in more detail.

Non-random structure of the fighting network

Our first finding was that the effect of indegree popularity decreased the GOF for the fighting network. This suggests that crickets do not have distinct social personality types (Carter *et al.* 2014; Aplin *et al.* 2015b), with the tendency to fight varying strongly within-individuals. This has implications for our second question (see below).

We found that males fought less than females. This does not necessarily mean that females are more aggressive; in this species, while both sexes engage in active mate searching (Hissmann 1990), typically it is females that move between burrows, while males sit and sing to attract them. Females are then more likely to encounter another female as they are moving among burrows, and so be involved in an aggressive interaction. Fighting amongst males does not decrease the intensity of sperm competition between them (Fisher *et al.* 2016), and since fights have inevitable energetic costs and carry the risk of injury, male fights may not bring sufficient sexually selected benefits to drive more frequent combat.

The effect of spatial distance was significant and negative, as expected. In many species individuals will associate more with those close to them, so controlling for spatial proximity when attempting to detect genuinely socially driven associations is important (Whitehead & James 2015). However, the relationship is likely to be bidirectional for many species, with space use influencing who you interact with and animals moving based on the results or potential consequences of social interactions (Cantor *et al.* 2012). This makes simply “controlling” for space use problematic when space use itself may be an expression of social behaviour.

Heavier crickets fought more different individuals, although the interaction between the mass of an individual and its potential associates was not important. This may suggest that fighting is a condition dependent strategy (Luttbeg & Sih 2010) or that heavier individuals employ a different social strategy that involves attempting to dominate their rivals (Hack 1997; Brown *et al.* 2006). This seems to be part of a separate suite of related traits to the pace of life syndrome identified in chapter 4, as activity was not related to mass (chapter 4). Why these separate axes of variation in the form of behavioural syndromes exist, and whether they are adaptive is an interesting question (Sih *et al.* 2004a,b).

Finally, we found no link between the weather variables and frequency of fighting behaviour. We consider it unlikely that rain and solar radiation do not influence cricket social interactions, as crickets' activity levels on a given day are influenced by the amount of rain and solar radiation (Fisher *et al.* 2015b). Instead, we suspect that the eight day periods we selected were too coarse a scale to detect these fine-scale behavioural responses. Ilany *et al.* (2015) found that wetter years lead to more sparse spotted hyena (*Crocuta crocuta*) social networks using a SAOM, so relationships between environmental and network characteristics can be detected with this approach in some systems.

No consistent social niches, so no link to consistent activity levels

We initially found that crickets were not consistent in their degree of fighting. This would then explain why we found no link with the fighting behaviour and the consistency of activity levels: the fighting behaviour itself is not consistent. We therefore find no support for the hypothesis that consistent social niches are a driver for consistent behaviours in non-social contexts such as activity level in *G. campestris*.

Instead, we found that crickets become more active with age, as found previously using linear-modelling based approaches (Fisher *et al.* 2015a,b). This helps to confirm the reliability of SAOMs for investigating variations in behavioural traits. We also found that crickets did not diverge in their activity levels over time, as the quadratic effect was negative. We have previously found conflicting results, with random regression suggesting an increase in V_A in older crickets, but an alternative approach suggesting no clear pattern (Fisher *et al.* 2015a). This result then appears to support the idea that crickets do not change with age differently, but rather remain equally different over time. We also found that those fighting many other crickets tended (although not significantly) to be less active in the next time step. Contests are typically energetically costly (Briffa & Elwood 2005), so being involved in many fights may have reduced the energy levels of the crickets, meaning they were unable to move much in the next time step.

Non-random structure and strong skew in the mating network

After adding the term of degree assortativity, we were successfully able to simulate the mating network, including a highly skewed pattern of mating success. Reproductive skew is ubiquitous in natural populations (Keller & Reeve 1994; Clutton-Brock *et al.* 1997; Engh 2002; Frentiu & Chenoweth 2008; Ryder *et al.* 2009; Rodríguez-Muñoz *et al.* 2010; Thompson *et al.* 2011) and helps provide the variation in fitness that is necessary for evolution. We would be very interested to know to what extent other mating systems can be modelled in this manner, and whether the processes of degree assortativity is as important in other mating systems as it is in the crickets.

Lifetime reproductive success is correlated with number of mating partners in this species (Rodríguez-Muñoz *et al.* 2010). Therefore, assortment by promiscuity may indicate mutual mate choice or assortment by “quality” (Aquiloni & Gherardi 2008; Baldauf *et al.* 2009), which could increase the variance in reproductive success in the population if high-fecundity individuals pair. However, as males with many mating partners mate with more promiscuous females, they face increased sperm competition for each ovum of females they mate with. This will reduce the variance in reproductive success among-males (Sih *et al.* 2009). Both the main effect of mass and the interaction between the mass of an individual and the mass of its potential mating partners did not relate to links in the mating network, suggesting mating partner choice is not based on mass. Instead, chemical cues such as cuticular hydrocarbons are likely to be important in mediating partner choice between closely related species (Tyler *et al.* 2015), so may play a role here.

Only degree assortativity was needed to get a satisfactory GOF for the mating network, perhaps suggesting the mating system is quite simple and stochasticity plays an important role in determining its structure. This would be troubling given the amount of effort that is devoted to understanding patterns of mate choice and sexual selection in the wild. However, there is the potential for a lot of different behavioural processes to be contained within the effect of degree assortativity, such as the trait(s) crickets are using for mate choice and the processes that generate variation in these traits that cannot be exploited by “cheats”. Additionally, we have only modelled the choice of mating partners, not the frequency of mating with a particular partner in an eight day period, as we were constrained to use binary networks. Therefore, there is likely variation in preference among mating partners that we are ignoring, which could have large fitness effects as frequency of copulation is likely related to share of paternity (Parker 1970; Simmons 1987).

We found that spatial distance did not significantly influence the mating network. This surprising result could stem from a number of sources. A lack of power as suggested earlier may have prevented us from detecting a true result. Alternatively, this may reflect the fact that there are many crickets near each other that do not mate. In this population more related individuals are generally found closer to each other (Bretman *et al.* 2011) so not being more likely to mate with closer individuals could be a form of inbreeding avoidance (although Bretman *et al.* (2011) did not find any evidence for inbreeding avoidance). In general if the choice of mates for an individual in a population is not limited to its neighbours, simple models for population-level processes such as partner choice or sexual disease transmission that do not explicitly account for spatial constraints may be more accurate than thought (Patterson *et al.* 2008). The weather variables were also not important, but we hesitate to make conclusions about this if this stems from looking at too coarse a scale as suggested above.

Individuals with more mating partners had less fighting partners at the next time step. This seems in contrast to previous results that the involvement in fighting and sperm competition is positively correlated (Fisher *et al.* 2016). However, these results are compatible if we consider the dynamic nature of the new result. Crickets over their lifetimes may show positive correlations between involvement in different types of competition, perhaps due to links to “quality” or differences in lifespan, but at any given time they may not be able do both (perhaps due to energetic constraints), creating a negative relationship between adjacent time steps. Furthermore, crickets that shared a mutual connection in the mating network were more likely to fight. This seems a direct response to the threat of sperm competition, as we have found previously (Fisher *et al.* 2016). Crickets have flexible mating systems where they are involved in pre- and post-copulatory competition (Buzatto *et al.* 2014), so they are adapted to both physical contests and sperm competition, but may be limited by time or resources to simultaneously engage in both.

Conclusions

We used a dynamic individual-based modelling approach to understand the social interactions and activity levels of individual crickets. By allowing population-level factors to influence individual-level decision making, we have effectively modelled the population-level properties of a population in the wild. We were able to address two out of the three population-level properties we had identified as requiring explanation. The cricket fighting social network is structured as it is due to crickets being near each other, and those connected by a third individual through mating or fighting, being more likely to fight. Furthermore, heavier crickets fought more, and individuals predominantly fought members of the same sex. However, individuals did not display much consistency in their fighting tendencies, and fighting behaviour was not significantly related to consistency in activity level. The structure of the mating network was largely governed by positive assortment by popularity. This, along with stochastic processes, produces networks with a skewed degree distribution that mirrors the observed skew in reproductive success in the population. We hope this stimulates others to use approaches such as this to gain more holistic understanding of complex animal social systems.

9. General discussion

My thesis has addressed a range of questions focusing on the individual behaviours and social interactions of a population of wild field crickets. I used a unique study system with an unprecedented degree of scrutiny of the lives of individual wild insects. This has allowed me to assess the stability of among-individual variation in behaviour (V_A) across adult lifespans, the consistency of V_A between the laboratory and the field and test theories for the maintenance of V_A over generations. I have also assessed the factors that drive the structure of the cricket social network, whether it is stable over evolutionary time and the role it plays in sexual selection.

I will now discuss the overarching topics that my thesis addressed. I have attempted to draw some general conclusions, and suggest studies or approaches that might build on what I have done.

Personality

One of my initial findings, using a random regression approach, was that V_A shows a U-shaped change with age, increasing strongly in older crickets (chapter 2). However, this finding was not replicated when the data were examined using alternative analytical approaches: Firstly in the same chapter, I found that the estimated repeatability of traits at different time points did not differ (chapter 2). Secondly, analysis using a stochastic actor-orientated model indicated that individuals' activity levels regressed to the mean rather than diverged to extremes (chapter 8). The increase in V_A predicted by the random regression was based on the divergence of individual reaction norms caused by the presence of a small amount of among-individual variance in change of behaviour with age. However, the amount of this variance in slopes was in fact very low, so I think that the likely significance of the increase in later life would be small. Therefore, the most likely answer appears to be that the degree of V_A does not show any predictable pattern of change over the lifetime of crickets, implying that additive genetic variation, and so heritability, also do not change.

There then remains the question of why any V_A persists in the population. One hypothesis, that individuals inhabit social niches which then leads to consistencies in non-social behaviours, is rejected for *Gryllus campestris*. I found that individuals did not have consistent social phenotypes, and that in any case their activity level was not strongly linked to their number of opponents in fights (chapter 8). Instead, a cricket's activity level appears linked to its life-history strategy in a pace of life syndrome (chapter 4). Our model for activity in chapter 4 successfully explained some of the long-term consistency of individuals through trade-offs between mating rate and lifespan. There was still some V_A and considerable within-individual variation outstanding however. Potentially there are direct drivers of these, such as differences in parasite burden (Barber & Dingemanse 2010) or differences in genetic "quality" (Rowe & Houle 1996). Alternatively, more stochastic processes may cause within-individual variation and contribute to initial among-individual differences which are then amplified by life-history strategy variation.

Alongside the within-individual variation in activity identified in chapter 4, in chapter 3 I found quite low V_A for each behaviour in the wild. This indicates that there is more variation among measurements of single individual across different monitoring points than there is variation among different individuals. This was despite modelling fine-scale weather variation, which had a significant influence on cricket behaviour (Fisher *et al.* 2015b). There is therefore still a large amount of work to be done in understanding how and why individuals show so much variation in behaviour over time in their quickness to emerge from a burrow after a disturbance, and their patterns of movement around the meadow (chapter 3). Recent developments in linear modelling allow us to explicitly model within-individual variation (Cleasby *et al.* 2014), which should prove useful in this area. Event-based models, capable of accounting for past experiences and current variables in a continuous time-process (Patison *et al.* 2015; Tranmer *et al.* 2015), might also provide more insights into variation in individual behaviour.

Finally, I measured a repeatable trait in the laboratory (shyness) which turned out to be not even slightly related to a superficially similar trait in the field (chapter 3). It has been suggested that unnatural stimuli will produce responses that are unrelated to aspects of natural behaviour (Niemelä & Dingemanse 2014), although I would expect a cricket to respond to a novel stimulus with a behaviour from within its original repertoire rather than something outside that.

Furthermore, shyness in the laboratory was significantly influenced by traits of individual crickets such as age. Therefore, I expect that my laboratory shyness assay measured some aspect of individual “personality” that does relate to the natural phenotype of the crickets, but what it actually most closely represents in terms of individual behaviour (perhaps susceptibility to stress?) remains opaque.

Social interactions

Throughout the chapters on social interactions, I found that tools developed for social network analysis (SNA) were useful for answering questions from behavioural and evolutionary biology in a non-social species. The use of SNA in the study of animal behaviour is growing (Farine & Whitehead 2015), although it is typically limited to animals that are considered “social” i.e. they live, move, feed or reproduce in groups. This need not be the case however, investigating any kind of competitive interactions or patterns of mating in a population can be tackled using SNA methods.

In chapter 6, I demonstrated that the general structure of the social network of crickets is conserved across generations, despite the fact that complete turnover of individuals with no overlap between generations occurs. This therefore indicates that crickets could be adapted to the properties of their social environment. In chapter 5, I showed how this social environment is related both within-individuals and between pairs of males for both pre- and post-copulatory competition. The evolutionary stability of the networks then may allow particular individuals to be heavily involved in both networks, and so both types of competition (chapter 5). Possibly this suggests that “good gene” effects in sexually selected traits are present in *G. campestris*, especially as species with stronger mating skews show stronger such effects (Møller & Alatalo 1999), although Rodriguez-Munoz *et al.* (2008) found no evidence for good genes in the sister species *G. bimculatus*. While I suspect lifespan is a trait key to this positive correlation (with longer-lived individuals being better connected in both networks), the analysis in chapter 8 indicated that mass could also be important. Heavier crickets are the ones fighting most other individuals (chapter 8), perhaps using their size to exert a degree of dominance over their rivals.

This dominance does not appear to extend to the mating arena however, with mass not being related to connections in the mating network (chapter 8), and males with high mating success possibly losing some paternity as the females they mate with also have a high number of mating partners (chapter 5). In *G. campestris*, female choice of males seems to be the dominant force in sexual selection (Rodríguez-Muñoz *et al.* 2010), and males may have no way to coerce females into mating (Rodríguez-Muñoz *et al.* 2011). Alternatively, it could be this very act of mate guarding that mediates the creation of apparently successful and unsuccessful males. Males that do not mate guard may gain extra copulations with different females, but endure increased sperm competition, while males that do mate guard may have fewer different partners, but high exclusivity with the guarded female (Sih *et al.* 2009). Among-individual consistency in mate guarding would reveal whether such alternative strategies exist.

Finally, I found that individuals tend to fight those they share a mutual (antagonistic) association with, those they share a mating partner with and those that are closer to them (chapters 5, 6 and 8). All of these effects will likely create a situation where crickets tend to fight any cricket of the same sex they encounter in their local environment, as they are likely to be direct competitors. Fights in *G. campestris* rarely lead to injury or death (Alexander 1961); in other species where fighting carries a similarly low risk we might expect this pattern to be common. In species where fighting in more dangerous, individuals may show more clear avoidance behaviour, or settle contests through ritualised displays without direct physical contact (Maynard Smith 1974).

Mating behaviour and general conclusions

I found that crickets show clear variation in behaviour along two distinct axes. On the first axis, heavier crickets fought more frequently than lighter crickets (chapter 8), while on the second axis, more active crickets achieved a greater mating success in the short term, but ultimately died sooner, than less active crickets (chapter 4). Interestingly, both these axes of variation seem to have flat relationships with overall mating success, with fighting not being effective for gaining mating partners or preventing females from remating (chapters 5 and 8), and the trade-off between mating rate and lifespan being sufficient to create a flat mating success curve for activity (chapter 4). A possible explanation for the presence of variation in these traits in the population therefore is that selection is working from both directions, creating no single optimum. This explanation is attractively simple, and given the ubiquity of trade-offs between traits across taxa I would not be surprised if it was very common.

In fact, the only factor that helped me to predict the mating network was a pattern of assortativity by popularity. Females with many connections tended to pair with males with many connections (chapters 5 and 8). With only this term (alongside the default terms), a stochastic actor-orientated model was able to accurately re-create the cricket mating network. Presumably there are some traits that drive this popularity in the mating network for both sexes. In males, their singing ability is an obvious candidate for creating differences in popularity among-males. For females a candidate trait is less obvious; indicators of fecundity that we cannot perceive, such as a chemical signal like the cuticular hydrocarbon profile may be important, as more obvious physical aspects such as mass or condition are not related to the number of mating partners (chapter 8) or activity level (chapter 4).

I found we could accurately simulate the mating network using a stochastic model with few terms. This suggests that stochastic processes may be important in determining mating success in the wild. I have also suggested that stochastic processes could lead to the initial differences among-individuals that are built on by divergent life-history strategies. These both suggest that stochastic processes play an important role in determining the events in an individual’s life and its fitness. How important stochastic processes are for long-term ecological and evolutionary processes such as speciation and population size change is actively debated (Palstra & Ruzzante 2008; Lenormand *et al.* 2009). I suggest that such processes may well have a great, influence on the behaviour of individuals. Alternatively, apparently variable or random behaviour may instead be rooted in adaptively structured brain circuits which operate in a non-linear manner to produce unpredictable behaviour (Maye *et al.* 2007). Finding and using statistical tools that can effectively differentiate between systems where stochasticity plays a strong role, and those where complex, non-linear dynamics may in fact mask order will enable us to investigate this (Bradbury & Vehrencamp 2014).

Appendix

Table S1. Fixed effects for the multivariate mixed-model of shyness, activity and exploration from chapter two. Given are the posterior distribution modes (PDM) and 95% credible intervals (CRIs) of the variance, covariance or correlation estimated. Correlations and fixed effects are considered significant if the 95% CRIs do not cross zero (highlighted in bold).

	Effect name	***PDM***	***Lower 95% CRI***	***Upper 95% CRI***	***pMCMC***
Fixed effects - Shyness	Age	-0.017	-0.032	0.001	0.067
	Mass	-0.194	-0.936	0.546	0.560
	Temperature	**-0.159**	**-0.269**	**-0.039**	**0.010**
	Sex	-0.181	-0.410	0.003	0.059
	Test	-0.014	-0.135	0.082	0.707
	Maximum age	0.003	-0.006	0.012	0.482
	Year	-0.214	-0.428	0.070	0.138
Fixed effects - Activity	**Age**	**0.010**	**0.003**	**0.019**	**0.003**
	Mass	-0.093	-0.413	0.364	0.938
	Temperature	**0.141**	**0.089**	**0.199**	**< 0.001**
	Sex	**-0.121**	**-0.227**	**-0.020**	**0.019**
	Test	0.019	-0.031	0.073	0.461
	Maximum age	0.001	-0.003	0.006	0.661
	Year	**-0.586**	**-0.699**	**-0.458**	**< 0.001**
Fixed effects - Exploration	Age	0.007	-0.021	0.038	0.607
	Mass	0.291	-1.010	1.594	0.702
	Temperature	**0.450**	**0.232**	**0.649**	**< 0.001**
	Sex	-0.068	-0.484	0.246	0.516
	Test	-0.015	-0.229	0.162	0.765
	Maximum age	-0.002	-0.015	0.017	0.906
	Year	**0.540**	**0.073**	**0.973**	**0.022**

Figures S1-3. Plots of the full (left box in each panel) and reduced (right box in each panel) simulations and their predictive distances (y axis) for chapter 6. The predictive distance is the difference between the simulated values and the real value from the network. S1 is for mean path length, S2 for degree correlation and S3 for clustering coefficient. See Methods of chapter 6 for details on how these were calculated and see Results of chapter 6 for which comparisons are statistically significant.

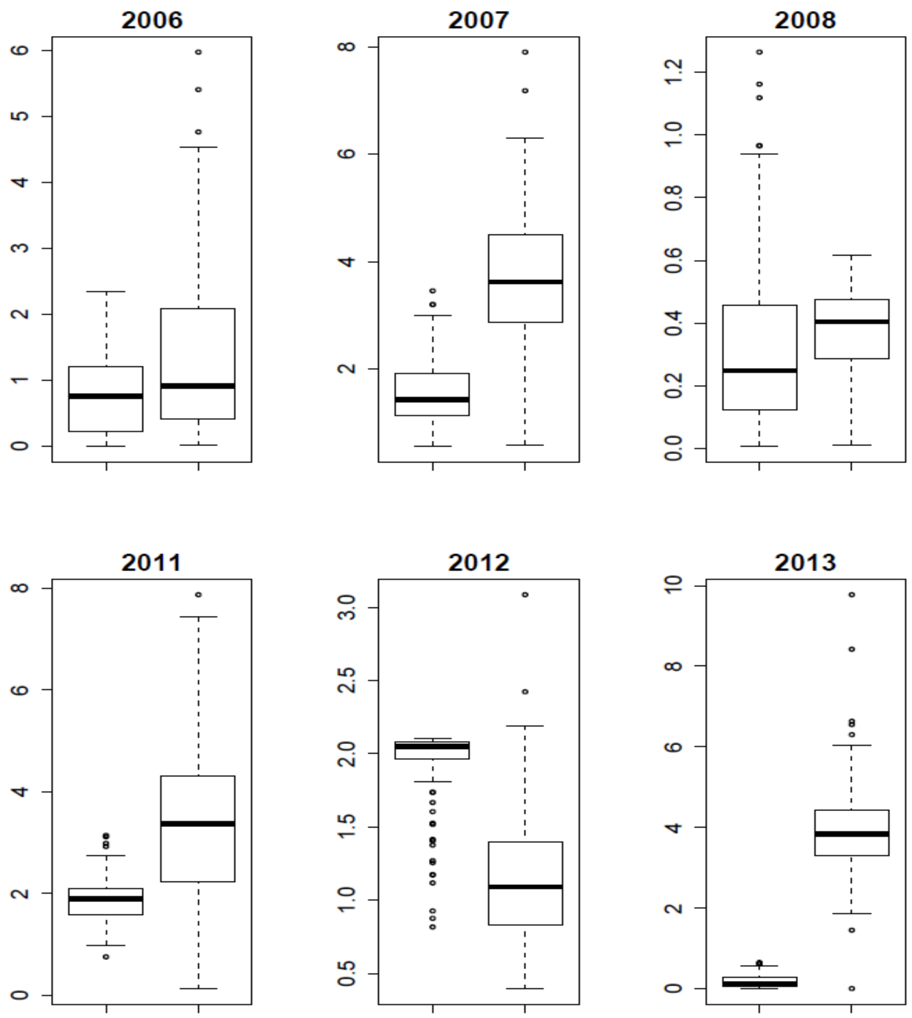

Figure S1. Mean path length

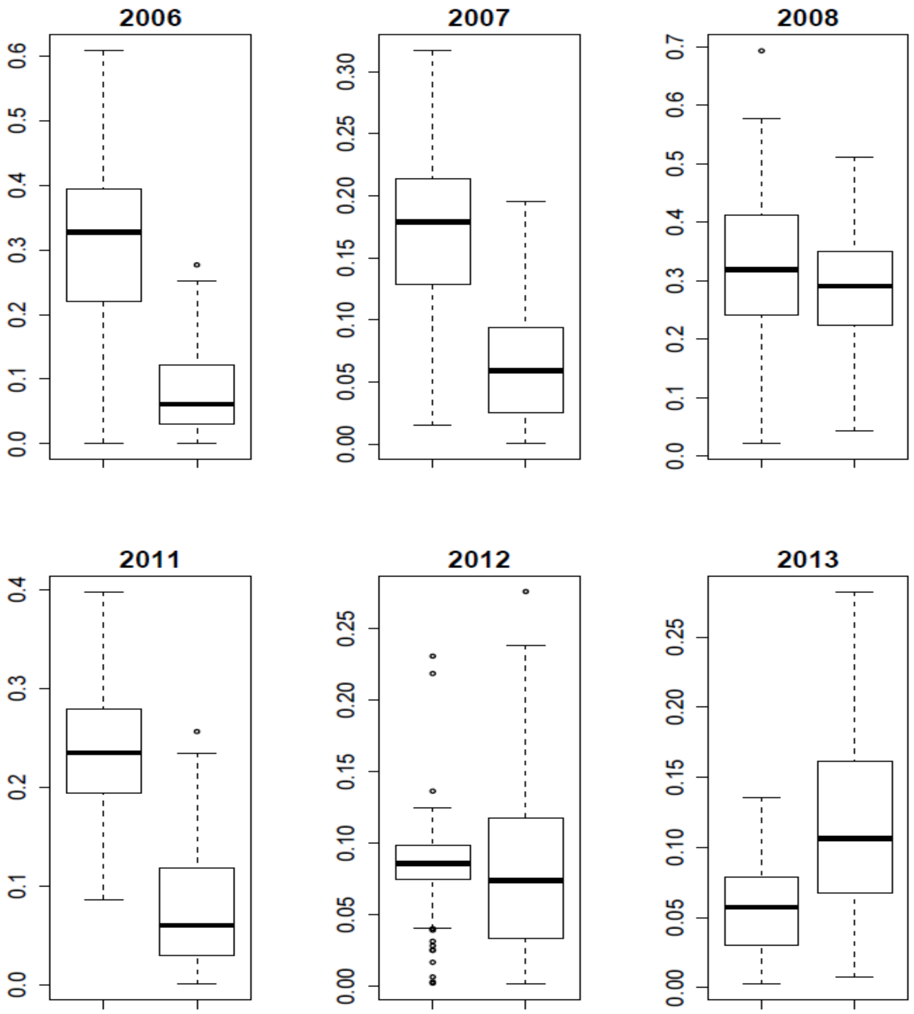

Figure S2. Degree correlation

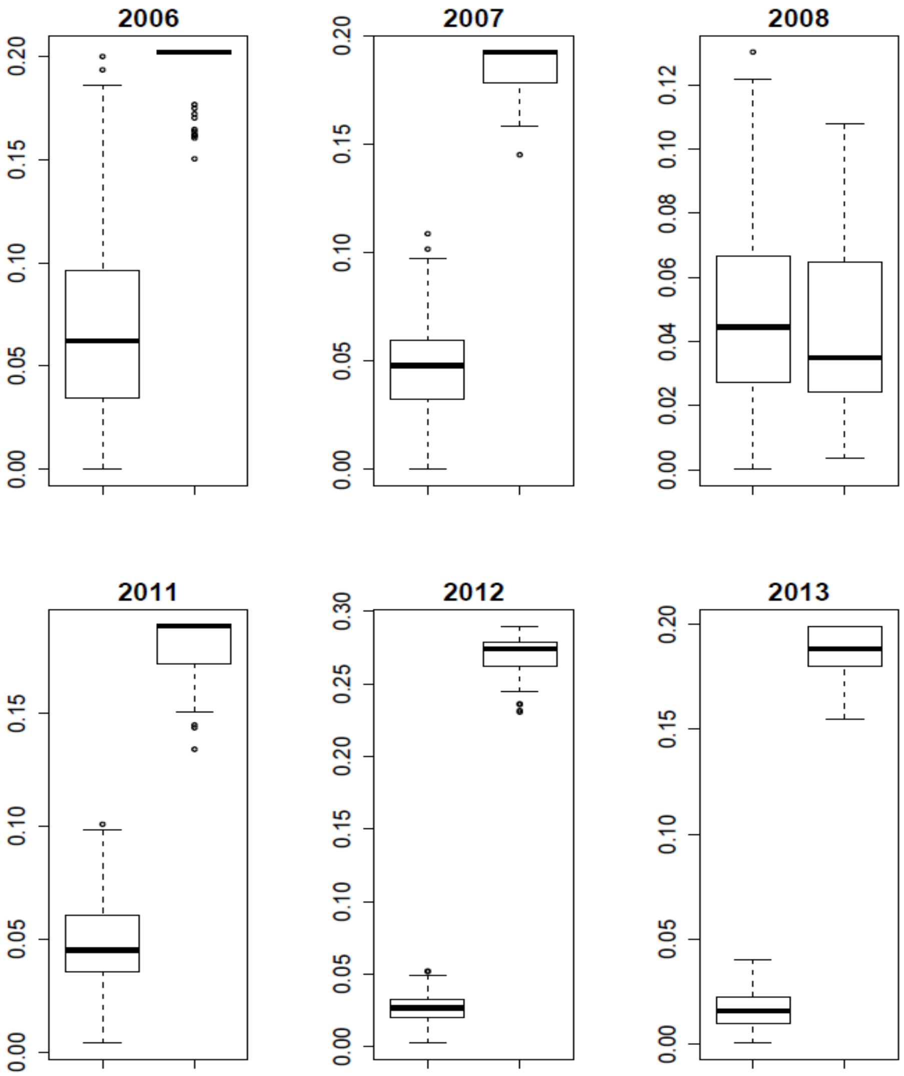

Figure S3. Clustering coefficient

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“The great thing is to last and get your work done and see and hear and learn and understand; and write when there is something that you know; and not before; and not too damned much after. Let those who want to save the world if you can to see it clear and as a whole. Then any part you make will represent the whole if it’s made truly. The thing to do is work and learn to make it.”

- Ernest Hemingway, Death in the Afternoon