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Uncertainty and the evolution of altruism

Theory and fieldwork in the paper wasps of Central and South America

Patrick Kennedy

Supervised by Dr Seirian Sumner and Professor Andrew Radford

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy in the Faculty of Life Sciences.

*“Many problems of insect social life are at best seen darkly.
The study of living wasps in the tropics will undoubtedly
throw a great deal of light onto these problems.”*

– Émile Roubaud, 1916 (translated: Starr, 1996)

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University of Bristol Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others is indicated as such. Any views expressed in the dissertation are those of the author.



GENERAL ABSTRACT

The evolution of altruism (costly self-sacrifice in the service of others) has fascinated biologists since the origins of evolutionary biology. Why should selection favour altruism over self-interest? Nowhere is the problem more striking than in the social insects, where large numbers of non-reproductive workers raise the offspring of reproductive queens. For over fifty years, the dominant explanation for altruism has been ‘inclusive fitness’ theory and an associated principle known as ‘Hamilton’s rule’, which emphasises the role of relatedness: altruists help carriers of shared genes. In this thesis, I explore two outstanding problems in the evolution of altruism and inclusive fitness theory. First, does altruism evolve differently in unpredictable environments? Second, what explains the evolution of altruism by Neotropical *Polistes* wasps to foreign queens, a situation in which ‘drifting’ workers paradoxically divert help to distant relatives? To answer the first question, I show that altruism in unpredictable environments can be favoured without any effects on the expected reproductive success of recipients – and, in principle, can evolve even if both altruist and recipient suffer a reduction in expected reproductive success. Instead, altruists can confer volatility-suppressing benefits on recipients, stabilising their otherwise uncertain reproduction. This extends ‘bet-hedging’ theory to social behaviour, and implies a stochastic version of Hamilton’s rule that differs from the interpretation of Hamilton’s rule commonly used empirically. To answer the second question, I use field experiments in the paper wasp *Polistes canadensis* in French Guiana and Panama, and *Polistes satan* in Brazil. Using a combination of radio-tagging, queen removals, recognition tests, and a longitudinal study of brood development, I explore various hypotheses for ‘drifting’. I argue that two recently published hypotheses for cooperative ‘drifting’ in *Polistes* may be unlikely to provide a general explanation for paradoxical altruism. Using longitudinal data, I show strong diminishing returns to cooperation in free-living colonies, which may represent an adaptive context in which altruism to more distantly-related recipients can evolve. Finally, I discuss the tension between adaptive and neutral explanations of subtle social traits.

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*"In her paper universe she had built an order
slavish to her will, while we, with keen eyes
and ordinary preoccupations, suspected nothing."
– from The Paper Wasp by Teresa Cader*

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DATA CHAPTER CONTRIBUTIONS

Dr Seirian Sumner and Professor Andrew Radford supervised all chapters.

Chapter 3: Analytical results derived by PK, with advice from Dr Andrew Gardner and Dr Andrew Higginson. Simulation results were made jointly in collaboration with Dr Andrew Higginson. Paper written in collaboration with Dr Andrew Higginson, Prof Andrew Radford, and Dr Seirian Sumner.

Chapter 4: Results derived by PK.

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Introduction

I | Introduction to social evolution

1.1 Chapter Summary

A foundational principle in evolutionary biology is that organisms act like rational agents with coherent agendas. In this widely-held view, natural selection shapes all organisms to follow a single objective: maximise your 'inclusive fitness'. First proposed by W. D. Hamilton in 1964, inclusive fitness is a measure of an individual's Darwinian success that considers social as well as non-social behaviour. Inclusive fitness theory is used throughout this thesis, together with a principle (known as Hamilton's rule) that is implied by the logic of inclusive fitness theory. However, the validity of the theory has recently been challenged by high-profile criticism on several fronts. In this chapter, I introduce inclusive fitness and Hamilton's rule, consider the ongoing debate about their utility, and justify the use of Hamiltonian logic in the subsequent chapters.

"There is no universal design principle." (Allen, Nowak, et al., 2013)

"The most salient feature of organisms is adaptation, the seeming goal-directedness that makes organisms different from merely physical entities." (Queller and Strassmann, 2009)

1.2 Introduction

The aim of this thesis is to explore two connected questions. First, does cooperation evolve differently in unpredictable environments? Second, what explains the evolution of cooperative 'drifting' in *Polistes* paper wasps, in which individuals help multiple colonies? At present, the prevailing hypothesis for drifting in *Polistes* invokes a strategy known as 'evolutionary bet-hedging' in the face of extreme unpredictable risks (Sumner *et al.*, 2007). Both questions concern stochasticity (unpredictable fluctuation in either the environment or population size) and social behaviour. Stochasticity has been widely discussed in non-social contexts for decades (Gillespie, 1975; Starrfelt and Kokko, 2012; Yasui

and Garcia-Gonzalez, 2016). However, the influence of stochasticity on social behaviour remains little studied (Cockburn and Russell, 2011), despite recent speculation that major empirical links exist between social behaviour and stochastic environments (Jetz and Rubenstein, 2011; Rubenstein, 2011; Cornwallis *et al.*, 2017; Guindre-Parker and Rubenstein, 2018).

To explore the two main questions in this thesis, I turn to inclusive fitness theory (Hamilton, 1964a; Birch, 2017). W. D. Hamilton's 'inclusive fitness' quantifies an individual's total success at propagating copies of its own alleles into the future (Hamilton, 1964a; Abbot *et al.*, 2011; Gardner *et al.*, 2011). Before Hamilton (1964a), 'fitness' (the measure by which we judge an organism's Darwinian success) was typically understood as simple reproductive success: absolute or relative number of surviving offspring. However, organisms influence the reproductive success of others, increasing or decreasing the total offspring production of social partners. Hamilton (1964a) realised that a fully causal measure of fitness would include these social effects. Relatives share alleles through common descent. Accordingly, organisms increasing the reproductive success of relatives – or decreasing the reproductive success of non-relatives – may help convey copies of their own alleles into the future. All else being equal, the value of others as vehicles for shared alleles is their relatedness (r) to oneself: closer relatives (higher r) carry a higher proportion of shared alleles.

In general, an interaction may increase a social partner's reproductive success by the amount B . The total value of the interaction in terms of production of related offspring carrying copies of the focal individual's alleles is then rB . If the interaction incurs a cost C to the focal individual's reproductive success, it is favoured by selection only if $rB > C$. This principle – known as 'Hamilton's rule' (Hamilton, 1964a; Gardner *et al.*, 2011) – is the basis of the fields of behavioural ecology and social evolution, and is widely invoked as an explanation for 'altruism' (paying a cost C to confer a benefit B on a social partner; West *et al.*, 2007). The sum of fitness effects $rB - C$ from all interactions over the organism's life is then its 'inclusive fitness' – 'inclusive' because it accommodates social as well as non-social effects.

Despite their foundational roles in social evolution (Gardner *et al.*, 2011), Hamilton's rule and inclusive fitness have recently been criticised on theoretical grounds (Nowak, Tarnita and Wilson, 2010; Allen, Nowak and Wilson, 2013; Nowak *et al.*, 2017; van Veelen *et al.*, 2017). Radically, Doebeli *et al.* (2017) have suggested abandoning the concept of fitness altogether (whether 'inclusive' or not). Following these critiques, the predictive power of inclusive fitness theory is currently controversial (Birch, 2017). By extension, these critics have called into question the fields of behavioural ecology and social evolution, leading to a strong defence (Abbot *et al.*, 2011; Gardner *et al.*, 2011) and an ongoing debate (de Vladar and Szathmary, 2017).

Inclusive fitness and Hamilton's rule are used throughout this thesis. The assumption underlying all subsequent chapters is that organisms act solely to maximise their inclusive fitness – an assumption that is routine in behavioural ecology yet subject to strong criticism from population genetics and game theory. In this chapter, I introduce and justify this assumption by briefly describing the current state of the debate. In Part 1, I consider the extent to which inclusive fitness is the ultimate 'objective' of individual organisms (Grafen, 1999; Gardner, 2009; West and Gardner, 2013; Rousset, 2015), and evaluate criticisms of this position (Allen, Nowak, *et al.*, 2013; Akçay, 2015; Akçay and Van Cleve, 2016; Birch, 2017). In Part 2, I consider objections to Hamilton's rule as an explanation for social behaviour (van Veelen *et al.*, 2017) and argue that it remains valid despite these criticisms.

1.3 Part 1: Inclusive fitness

Over 150 years after first publication of *The Origin of Species*, evolutionary biologists are divided on one of the simplest of questions (Birch, 2017): what are organisms trying to do? Most biologists advocate an explicitly 'goal-directed' view of behaviour (Gardner, 2009; West and Gardner, 2013; Grafen, 2014b). In this view, all organisms are shaped by natural selection to strive after the same objective, a single quantity known as 'inclusive fitness'. However, a minority are sceptical that any universal agenda exists (Nowak, Tarnita and Wilson, 2010; Lehmann *et al.*, 2015), inclusive fitness or otherwise. As put by Allen *et al.* (2013), '*there is no universal design principle.*'

Inclusive fitness theory has much in common with economics (Archetti *et al.*, 2011). Like economic utility, inclusive fitness allows the benefits and costs of phenotypes to be quantified with a single currency. This naturally leads to a view of animals and plants – or their genes (Dawkins, 1976; Gardner and Welch, 2011) – as agents: natural selection generates seemingly-rational decision-makers optimising a single utility function with the convincing illusion of conscious planning. This view of organisms has various names, including the 'intentional stance' (Dennett, 2010), the 'individual-as-maximising-agent analogy' (Grafen, 1999), the 'universal design principle' (Allen, Nowak, *et al.*, 2013), 'as-if intentionality' (Searle, 1991), the 'agential perspective' (Godfrey-Smith, 2009; Okasha, 2018a), 'design thinking' (Birch, 2017), and 'Darwinian paranoia', the view that biology is the study of 'little agents with agendas' rather than just the dynamics of allele frequency change (Godfrey-Smith, 2009).

Two groups oppose this tradition: (1) a group of population geneticists (Cavalli-Sforza and Feldman, 1978; Schwartz, 2002; Ewens, 2014), for whom detailed models have conclusively shown that selection does not maximise any universal quantity (Grodwohl, 2017); and (2) a new group of game theorists who find inclusive fitness conceptually confused and empirically underwhelming (Nowak, Tarnita and Wilson, 2010; Van Veelen *et al.*, 2010; Allen, Nowak, *et al.*, 2013). In place of inclusive fitness theory,

this second group proposes ‘evolutionary dynamics’, a view of populations that emphasises variation in population structure and is devoid of fitness-maximisation arguments at the level of individual organisms (Allen and Nowak, 2016).

1.3.1 What does maximisation mean?

“Anyone who believes a thermostat has a belief about the temperature must be crazy!”
(Dennett, 2006, paraphrasing criticism of the agential perspective)

Before Hamilton (1964a), hypotheses of social evolution were focussed on either individual self-interest or imprecisely-defined forms of group-level benefit (Wynne-Edwards, 1962). To perform field studies that make logical sense, it is crucial to define explicitly what we expect organisms to act as if maximising: what is the currency by which individuals should be judged in the struggle for existence?

Part of the controversy over behavioural ecology is attributable to different interpretations of the word ‘maximisation’ by different groups (Birch, 2016a). In population genetics, maximisation is largely seen as occurring only under very special conditions. The view that selection seeks to maximise the average fitness in the population became unfashionable after Moran (1963) criticised the ‘adaptive landscape’ view associated with Wright (1967). Given epistasis or frequency-dependence, population average fitness can actually decline through the generations (Moran, 1963; Turner, 1969). However, population-level maximisation is not the sense in which behavioural ecologists use the term, and the semantic confusion between behavioural ecologists and population geneticists has long been problematic. Behavioural ecologists pay little attention to the protests of population geneticists when invoking fitness maximisation, because the two fields often talk past one another (Grafen, 2009a).

Amongst population geneticists, scepticism towards maximisation is often associated with the failure of either Lyapunov or gradient functions to describe selection in anything other than the simplest of idealised populations (Grafen, 2009a). When maximisation is defined according to either of these functions, we are asking whether the *population*, rather than individual organisms, has a maximising tendency. Under this definition, maximisation occurs when (1) the space of possible gene frequencies is overlaid by a set of real numbers corresponding to fitness and (2) evolution heads to the fitness maximum by never allowing a fitness function to decrease in value (Lyapunov function) or tracks the maximally-steep route upwards (gradient function). The population ‘strives’ to optimise gene frequencies to secure the highest value of the fitness set. By contrast, behavioural ecologists see fitness maximisation as something occurring in the lives of individuals (as opposed to the population’s allele

frequency): like rational actors in economics, each *individual* strives to optimise its own phenotype under constraints (Grafen, 1999).

The individual maximisation view invokes three things – an instrument, a maximand, and constraints (Grafen, 2008, 2009b):

$$x \max u(x) \quad \text{subject to} \quad x \in \mathbf{x} \quad (1.1)$$

A strategy choice (x) that the agent can vary (the ‘instrument’) generates values of the fitness ‘maximand’ $u(x)$, such that x should be chosen to generate the highest possible value of $u(x)$, subject to the ‘constraint’ that x can only be chosen from a set of possible strategies \mathbf{x} . The crucial criterion for showing that individuals target a universal maximand $u(x)$ is that it should be possible always to predict the result of selection simply by asking which phenotype x achieves the highest value of $u(x)$: in other words, when we run the evolutionarily process (whether by simulation or analytically), we should find that a population fixed for phenotype x is robust from invasion by any mutant phenotype (Lehmann *et al.*, 2015).

The most explicit attempt to justify inclusive fitness as a universal maximand is the ‘Formal Darwinism’ project led by Alan Grafen (Gardner and Grafen, 2009; Grafen, 2009b; Batty *et al.*, 2014; Crewe *et al.*, 2018). To reach the right maximand, the Formal Darwinism project is founded on four proposed links between selection and organism-level optimisation (Grafen, 2006b). Informally, these can be summarised as the following two statements.

1. A necessary and sufficient condition for the population to be at an equilibrium is that everyone is playing an optimum strategy (where an ‘equilibrium’ is when there is no expected change due to selection).
2. Selection happens when individuals optimise their objective functions with different degrees of success. The resulting change in allele frequency is given by the selection covariance of the Price equation when the right fitness function covaries with breeding value. (‘Breeding value’ is a numerical value that can be placed on the individual to represent its specific combinations of alleles. In the simplest case, where individuals are asexual and haploid and differ at only one bi-allelic locus of interest, the breeding values might, for instance, be set at 0 and 1.)

The Price equation is the most general statement of evolution (Price, 1970; Gardner, 2008). In words, it says that the change over time in average breeding value \bar{G} is equal to (1) the change due to selection (the ‘selection covariance’) plus (2) the change due to transmission bias (such as distortion of meiosis):

$$\Delta \bar{G} = \underbrace{\mathbb{C}_i \left[\frac{w_i}{\bar{w}}, G_i \right]}_{\text{Selection covariance}} + \underbrace{\mathbb{E}_i \left[\frac{w_i}{\bar{w}} \Delta G_i \right]}_{\text{Transmission bias}} \quad (1.2)$$

Here, i denotes the i th individual, w_i denotes the absolute fitness (number of surviving adult offspring) of the i th individual, and \bar{w} denotes the average of w_i across all individuals in the population. $\mathbb{C}_i[\cdot]$ and $\mathbb{E}_i[\cdot]$ denote covariances and expectations over i respectively. Because we are generally just interested in the optimising tendency of selection, in practice we focus only on the selection covariance, and ignore the change due to transmission bias (but see Ewens, 2014). A quantity covarying with breeding value G_i in the selection covariance is typically called a ‘target of selection’.

In the Price equation as it is normally written (as above), the target of selection is the i th individual’s relative fitness ($\frac{w_i}{\bar{w}}$). Intuitively, if individuals carrying a focal allele (and therefore sharing the same breeding value) tend to have a higher relative fitness than all other individuals, the covariance between breeding value and relative fitness will be positive, and selection increases the frequency of the allele in the population. Accordingly, we only need to know two pieces of information about each individual: (a) its genotype (*i.e.*, which alleles it carries; G_i); and (b) its relative fitness ($\frac{w_i}{\bar{w}}$). However, when individuals act socially, a fraction of each individual’s relative fitness will not be due to its own behaviour, but rather to the behaviour of others. The causal connection between genotype and relative fitness is broken. To identify a true maximand, we need to restore the causal connection by finding a target of selection which *is* under the organism’s private control.

Various rearrangements of the Price equation are possible (Okasha, 2006). Ideally, we want to rearrange the selection covariance to obtain a target of selection that means we need only two pieces of information about each individual i : (a) its genotype (G_i); and (b) its causal effects on its own relative fitness plus its causal effects on the relative fitness of others. The second of these would be individual i ’s inclusive fitness. Allowing for social behaviour (and an uncertain environment), one target of selection is the expectation of $\frac{I_i}{\bar{w}}$, where I_i is the sum of additive fitness effects on recipients weighted by relatedness (Grafen, 2006b). If environmental states (denoted $\pi \in \Pi$) occur with frequencies d_π , the target of selection is then as follows:

$$\mathbb{E}_\pi \left[\frac{I_i}{\bar{w}} \right] = \sum_{\pi=1}^{\Pi} d_\pi \frac{b_{i,\pi} + \sum_{j=1}^J r_j b_{j,\pi}}{\bar{w}_\pi} \quad (1.3)$$

This is the covariate in the first bracket of Equation 6 in Grafen (2006b) expressed in the notation of this thesis, where $j \neq i$ denotes i ’s social partner and $b_{j,\pi}$ denotes the additive effect on absolute fitness conferred by individual i on recipient j , related by r_j , in environmental state π . Equation 1.3 is

called ‘expected relative inclusive fitness’ by Grafen (2006b), and – because all the fitness effects are now under one individual’s control – it is a strong candidate for the organism’s private maximand.

Expected relative inclusive fitness (Equation 1.3) is the expectation of absolute ‘inclusive fitness’ over \bar{w} . Because the proposed maximand is a relative fitness concept (and therefore subject to frequency dependence), some authors are sceptical that it can be clearly maximised by organisms, because it is ‘*cognitively implausible*’ (Huneman and Martens, 2017) for organisms to adjust their behaviour to match population-wide frequencies. However, no cognitive capacity is needed for an individual maximand to exist: ‘as if’ maximands can exist for daffodils as much as they can for chimpanzees. More generally, psychological ‘maximands’ are only relevant as proximate and short-term devices for pursuing the real (evolutionary) maximand, and it is important to keep the distinction clear.

1.3.1.a *Where the maximand argument is heading*

Most of the series of papers that comprise the Formal Darwinism project take a function of additive effects on expected relative fitness as the target of selection (leading to Equation 1.3). Recently, however, Crewe *et al.* (2017) develop the approach of Grafen (2006a) and express fitness purely in terms of reproductive value, which offers an alternative perspective on fitness under stochasticity. Informally, reproductive value measures expected contribution to the gene pool of the population in the distant future (elderly grandmothers and young eunuchs, as classes of individuals in the population, have very low reproductive values). Likewise, reproducing in a famine has a higher reproductive value than reproducing in a bonanza: in poor years, an individual who reproduces more than the (unusually low) population average secures a higher proportion of the total gene pool than if the same number of offspring were produced in a good year (when the relative distance between its own success and the population average is lower). Offspring in different years then carry different reproductive values. A similar approach to stochasticity is taken by Lehmann and Rousset (2014). This context-dependence is easily generalised to spatial as well as temporal fluctuations.

Expressed in terms of the expected change in population average p -value (ploidy-weighted breeding values for a trait of interest), the selection covariance of Equation 1.2 appears as Crewe *et al.*’s (2017) Equation 14 (in my notation here):

$$\mathbb{E}_\pi[\Delta\bar{p}] = \mathbb{C}[p, \mathbb{E}_\pi[\mathcal{F}]] \quad (1.4)$$

Here, \mathcal{F} denotes the additional share of reproductive value enjoyed by an actor i above the reproductive value v_{x_i} of its class x_i , as a proportion of class reproductive value ($\frac{W_i - v_{x_i}}{v_{x_i}}$). Classes may

be defined by sex, status, location, age, and so on. Crewe *et al.* (2017) have not yet extended this argument to social behaviour, but it seems likely that future claims of inclusive fitness maximands will replace the target of selection in Equation 1.3 by the sum of social and non-social effects on reproductive value.

1.3.2 Challenges to the argument from the Price equation

Several assumptions limit the generality of the argument from the Price equation to the inclusive fitness maximand. First, Grafen (2006b) restricts the scope of Formal Darwinism to ‘universal strategic equivalence’: all organisms are confronted with the same proximate optimisation problem. Second, the inclusive fitness maximand remains undefined for demographic stochasticity in small or subdivided populations: there is no established maximand for metapopulations of small demes with local competition. To see this, note that Grafen (2006b) assumes no single individual having an appreciable effect on \bar{w} : ‘*it is like a central limit theorem assumption, that no individual should be very important, even in just one situation*’ (Grafen, 2006b). Third, the maximand assumes that fitness effects are additive (Akçay and Van Cleve, 2016; Allen and Nowak, 2016; Birch, 2017), where individuals interacting socially are not more than the sum of their parts (I return to this contentious assumption below).

A fourth proposed limitation concerns the definition of ‘equilibrium’ (Okasha and Paternotte, 2014; Birch, 2016a). In simple cases, an equilibrium is unambiguous: at equilibrium, allele frequencies cannot change because no phenotype has a higher fitness than the one that dominates the population. Maximisation and equilibria are naturally linked: the best solution to a given problem is an equilibrium, because there is no incentive for any individual to change its strategy (Creedy, 1994). However, various authors have objected to the way in which equilibria are defined by the Formal Darwinism project. This objection largely focuses on heterozygote advantage (Okasha and Paternotte, 2014; Birch, 2016a), which leads to the stable persistence of imperfect phenotypes at equilibrium: carriers of the fittest phenotype (*i.e.*, the heterozygotes) inevitably produce offspring with suboptimal phenotypes (*i.e.*, the homozygotes). In this case, genetic constraints lead to an equilibrium populated by organisms that seem to be acting irrationally (failing to maximise their inclusive fitness). How, then, can we say that selection inevitably leads to inclusive fitness maximisers?

In the view of critics of Formal Darwinism, the problem here is that Grafen’s (2006b) definition of equilibria conveniently excludes these scenarios in which genetic constraint leads to irrational organisms (Okasha and Paternotte, 2014; Birch, 2016a). In Formal Darwinism, these apparent equilibria are not true equilibria because there is still ‘scope for selection’ (Grafen, 2006b). Informally, scope for selection means that individuals with different alleles are responsible for the production of different

numbers of offspring (Grafen, 2006b). Critics of Formal Darwinism argue that this provides no guarantee that selection will produce a world populated by inclusive fitness maximisers, leaving ‘considerable distance’ (Okasha and Paternotte, 2014) between inclusive fitness theory and the assumptions of behavioural ecologists doing fieldwork. Heterozygote advantage and other forms of genetic constraint may be common empirically (Sellis *et al.*, 2011). Practically, then, biologists must instead commit the ‘phenotypic gambit’ (Grafen, 1984) – the optimistic assumption that unknown genetic constraints do not lead to otherwise unknowable equilibria.

There may also be a (less severe) problem with linking maximisation and equilibria in general, which is that equilibria are typically defined by zero expected change in allele frequencies ($\mathbb{E}_{\pi}[\Delta\bar{G}] = 0$) over stochasticity (states $\pi \in \Pi$). Taken to extremes, zero expected change can occur in highly unstable situations that nobody would consider to be real equilibria. Consider a diallelic population currently at 50:50 allele frequencies. Let the environment switch equally at random between two states: in state 1, allele *A* carriers fail to reproduce; in state 2, allele *B* carriers fail to reproduce. In any single generation, $\mathbb{E}_{\pi}[\Delta\bar{G}] = 0$, even though it is guaranteed that one allele will immediately fixate. This is an artificial situation, but can be made realistic by considering smaller step changes in allele frequency. Now, a chance correlated run of one state over several generations will take the population to fixation (see Lande, 2007). For a stable equilibrium, then, we also need $\mathbb{V}_{\pi}[\Delta\bar{G}] \approx 0$. If selection is optimising, it is optimising in the average (expected) sense – even if the single allele-frequency change that corresponds to this average sense is not actually possible in a fluctuating environment.

1.3.2.a *Does it matter if relatedness is not fixed?*

Relatedness (*r*) is generally interpreted as the degree to which individuals with similar genotypes (measured by breeding values) assort in the population (Foster *et al.*, 2006; Bourke, 2011). This is captured as the regression of the partner’s breeding value G_j on the actor’s breeding value G_i :

$$r = \frac{\mathbb{C}(G_j, G_i)}{\mathbb{V}(G_i)} \quad (1.5)$$

For some authors, there is a potential problem with the standard view of *r* as the regression of partner breeding value on focal breeding value (Okasha, 2018a), which is that relatedness can change over the course of selection:

“...the value of *r* may change as the population evolves. Thus, in a full evolutionary analysis, *r* needs to be treated as a dynamic variable, not a fixed parameter...” (Okasha, 2018b)

Okasha argues that, as a result, r cannot be part of the organism's maximand. There are at least three different ways to answer this objection:

1. We do not need to worry about changes in r , as r is not a dynamic variable when the population is at equilibrium – and this is where we should invoke individual maximisation;
2. We should restrict the generality of the claim that organisms maximise a single quantity to those populations where assortment between social partners is frequency-independent (and so r is a constant). This argument suggests that r is unlikely to be frequency-dependent in most cases, so it is an essentially fixed parameter of the population;
3. Over the generations, selection may pull in different directions due to frequency-dependence. In any one generation, the individual maximand at the level of organisms can be defined as the optimum 'end goal' desired by selection; it is just that what 'selection' considers the optimum end goal changes through time.

Accordingly, dynamic r does not necessarily challenge inclusive fitness as a maximand. A separate issue is whether it challenges the usefulness of Hamilton's rule (which I return to in Part 2).

1.3.2.b *The additivity assumption and δ -weak selection*

The 'additivity problem' challenges the generality of inclusive fitness theory. In a non-additive (*i.e.*, synergistic) scenario, it is unclear which fitness effects to allocate to which individual. Crucially, a true inclusive fitness maximand has to be under the control of the actor – but what is this quantity when multiple individuals have to interact together to produce a result? This issue is of particular relevance to this thesis, because I argue in Chapter 6 that the production of offspring in *Polistes canadensis* colonies is a diminishing (*i.e.*, nonlinear) function of the worker-to-brood ratio: *P. canadensis* colonies suffer from negative synergistic effects. In other words, a group of individuals is not simply the sum of its parts.

Fortunately, the problem can be eliminated by committing to certain assumptions, such as δ -weak selection and small-effect mutations, which are widely believed to justify the inclusive fitness maximand view '*regardless of the complexity and strategic nature of the social interaction*' (Lehmann *et al.*, 2015). Recently, Birch (2017) has suggested that the commitment to δ -weak selection is not a coincidence for inclusive fitness theory, given the extent to which R. A. Fisher influenced W. D. Hamilton. Fisher's geometric view of adaptation argues that adaptive mutations have infinitesimal fitness effects (Fisher, 1930): selection scrutinises new mutations that differ only slightly (phenotypically) from a resident genotype, to the degree δ . Accordingly, an interaction will generate negligible fitness effects that are

proportional to δ^2 : the first-order terms describing the effect of a social interaction are additive (Rousset, 2013). This gradualism justifies a maximand view in which the quantity under the agent's control is the additional fitness increment above that produced by the wild-type.

Criticism of the necessity of assuming weak selection is not new. Hamilton himself dismissed weak selection criticisms as biologically irrelevant in 1996:

"...it made me tense to see my eldest child challenged but usually I became relaxed soon again after noticing some misunderstanding or that my critic was studying cases I had not claimed to cover and, as biological reality, didn't believe in. Usually they were the cases with strong selection and/or unconditional gene expression." (Hamilton, 1996)

Although Allen and Nowak (2016) concede that δ -weak selection eliminates the additivity problem, they resist this argument as a general way to rescue the agential perspective, claiming instead that small-effect mutations *'are not the general case of evolution'* and *'single mutations can have dramatic phenotypic effects'*. Nonetheless, outside the inclusive fitness controversy it is routinely assumed that selection is weak (Lande, 1981; Nagylaki, 1993; Akashi, 1995; Wayne and Simonsen, 1998; Lu and Wu, 2005; Akashi, Osada and Ohta, 2012; but see Endler, 1986). Even if there is a wide gulf between two phenotypes, it is often possible to evolve from one to the other via a gentle series of infinitesimal step-changes. For instance, the evolution of social nesting from solitary nesting can occur via a series of small steps, if each step simply increases the probability of social nesting by an infinitesimal degree. Selection is powerful over eons, and often weak within generations. This immense gradualism means we are rarely in a world where fitness non-additivity invalidates the maximand view. Invoking δ -weak selection also eliminates the problem with equilibria under stochasticity (see above): now, $\mathbb{E}_\pi[\Delta\bar{G}] = 0$ does represent a stable equilibrium (in the sense that $\mathbb{V}_\pi[\Delta\bar{G}] \approx 0$).

Conceding that we need weak selection is, however, a step back from the ambitions of Formal Darwinism to establish a 'universal' and axiomatic maximand. Instead, the appeal to δ -weak selection justifies a pragmatic approach in which the maximand view is generally though not universally correct. There are two issues:

1. Having to assume δ -weak selection means that the maximand view is (partly) an empirical hypothesis: it is possible to find a population in which δ -weak selection is violated and social fitness effects are sufficiently synergistic to leave the inclusive fitness maximand undefined.
2. When population size is sufficiently small – in bottlenecked populations or structured populations consisting of miniature demes – genetic drift may dominate the outcome when selection is weak. In this case, individual maximisation would be the hypothetical result of the

selective component of allele frequency change were it not for displacement of the population by random walks.

A second answer to the additivity problem is to argue that inclusive fitness is simply an imperfect way of expressing something that genuinely is universal: genes are the ultimate units of selection, possessing true universal maximands, and individuals are only temporary agents of the genes (Dawkins, 1976; Bourke, 2014b). Under this view, the additivity problem vanishes, a position taken by Lehmann *et al.* (2015).

To sidestep the additivity problem entirely, a surprising suggestion has recently been proposed by Fromhage and Jennions (2018). A persistent misunderstanding of inclusive fitness is that it is the sum of the organism's own reproductive success and its (relatedness-weighted) effect on the reproductive success of others. This mistake – which is perpetuated in a number of textbooks – errs by counting offspring twice: a single offspring contributes to the inclusive fitness of multiple individuals (Grafen, 1982). Fromhage and Jennions (2018), however, suggest that this view is actually the more legitimate. If inclusive fitness is an accounting device for modellers, Fromhage and Jennions (2018) are clearly wrong: we will attribute single offspring to multiple actors. If inclusive fitness is an individual maximand, however, Fromhage and Jennions (2018) suggest a simple solution to the additivity problem: if both individuals i and j are required to work together to produce an offspring x , then the private maximands of i and j can both claim x . It is currently unclear whether this would lead to a genuine maximand, defined as a maximisation problem that we could solve to identify the phenotype that would dominate at an uninvadable equilibrium; the problem of double counting may make this seem unlikely.

1.3.2.c *Are organisms single agents at all?*

Individuals may be inclusive-fitness-maximising agents, but where did individuals come from? What was being maximised during the evolution of individuality? Do individuals lose their individuality when part of cohesive groups? In this thesis, I treat individual wasps in primitively eusocial colonies as inclusive fitness maximisers, but – given the potential for selection at a between-group level in social groups (Pruitt and Goodnight, 2014; Pruitt *et al.*, 2017) – is this justified?

Gardner and Grafen (2009) argue that a group-level maximand exists for groups whose members are (a) clonal or (b) subject to mechanisms that completely suppress the ability of group members to pursue self-interested strategies. If we accept the logic of the Formal Darwinism project, Gardner and Grafen (2009) justify this claim using the multilevel Price equation (Gardner and Grafen, 2009; Gardner, 2015c). Here, I write this equation in terms of variances in genetic value at a group and within-group level:

$$\Delta \bar{G} = \underbrace{\frac{\beta_{\bar{w}_d, \bar{G}_d}}{\bar{w}} \text{Var}[\bar{G}_d]}_{\text{Between-group selection}} + \mathbb{E}_d \left[\underbrace{\frac{\beta_{w_{id}, G_{id}}}{\bar{w}} \text{Var}[G_{id}]}_{\text{Within-group selection}} \right] \quad (1.6)$$

When there is no variance in genetic value within groups (*i.e.*, groups are clonal: $\text{Var}[G_{id}] = 0$) or there is no scope for differential fitness within groups (*i.e.*, $\frac{\beta_{w_{id}, G_{id}}}{\bar{w}} = 0$), within-group selection is zero (Gardner and Grafen, 2009). All that matters now is between-group selection. Individuals i are no longer fitness maximisers, and groups d of individuals i have now become individuals d in their own right. This upwards shift in individuality is often termed an ‘evolutionary transition in individuality’ (ETI; Clarke, 2016). Gardner and Grafen’s (2009) argument loosely corresponds to the criterion emphasised by Boomsma and Gawne (2018) for identifying whether a social insect colony has become a ‘superorganism’ (an individual organism in its own right): in Boomsma and Gawne (2018), an evolutionarily irreversible transition to a developmental separation between a reproductive germline (queens and males) and an obligately-nonreproductive ‘soma’ (sterile workers) is necessary for a social insect colony to be a ‘superorganism’. This makes intuitive sense, because obligate sterility sets $\frac{\beta_{w_{id}, G_{id}}}{\bar{w}} = 0$ within the colony (differences in fitness are eliminated). Accordingly, individual workers i in colonies d dissolve as individual organisms: the new organism is the colony d , captured by the first term of Equation 1.6.

Some authors are reluctant to surrender group-level adaptation when the second term is low but nonzero. Cancer, for instance, is often seen as a case of within-group selection (Michod, 1997; Goodnight, 2015): does this invalidate the organism (a group d of cells i) as an individual inclusive fitness maximiser? Simple eusocial wasps are structured into breeders and non-obligate non-breeders, a glimmer of a potential future superorganism: does the possibility of selection occurring at a whole-colony level invalidate individual wasps (individuals i in colony d) as individual inclusive fitness maximisers? The level at which we identify fitness maximisers is just one level in a hierarchy: there may also be nonzero selection covariances occurring at lower and higher levels, at least in the sense that the multilevel Price equation would partition a proportion of allele frequency change to selection at different levels.

When both between-group and within-group terms are nonzero, it is generally thought that we should emphasise individuals i rather than groups d as inclusive fitness maximisers. Supporting this view, Gardner and Grafen (2009) argue that the concept of a ‘superorganism continuum’¹ commits a semantic mistake, confusing the terms ‘group-level selection’ and ‘group-level adaptation’ (Gardner,

¹ In which a spectrum, rather than a sharp threshold, defines ‘superorganismality’ (Reeve and Holldobler, 2007).

2015a). Group-level selection occurs whenever the between-group term in the multilevel Price equation is positive; group-level adaptation is much stricter and requires that groups are inclusive fitness maximisers in their own right. Group-level adaptation only occurs when the between-group term in the multilevel Price equation captures the entirety of selection.

Significantly, some cases of apparently unambiguous within-group selection turn out not to threaten the agential perspective on closer inspection. Above, I pointed to cancer as a phenomenon that is often interpreted as within-group selection (Goodnight, 2015). If selection pulls in different directions within the organism, the organism is no longer an individual whose lower-level units have fitness interests in full alignment. Cancer appears to undermine the individuality of the organism, and therefore reduces its agential status; the implication is that cancer compromises inclusive fitness maximisation by splitting the individual into two agents with contradictory agendas (tumour versus non-tumour). However, Gardner resists this conclusion for (nontransmissible) cancer, on the grounds that alleles in cancer cells have no chance of being inherited by the long-term future population (they will die with the organism), and so a cancer cell's reproductive value is zero (Gardner, 2015b).

The general principle here is that classes of lower-level units with reproductive values of zero cannot lead to the dissolution of the higher-level unit as an inclusive fitness maximising agent. In a class-structured population (in which individuals in different classes have different reproductive values), the multilevel Price equation can be written by summing over classes $k \in K$. Each class is weighted by its class-specific reproductive value c_k . Writing Gardner's (2015c) Equation 7 in the notation above:

$$\Delta \bar{G} = \sum_{k=1}^K c_k \left(\underbrace{\frac{\beta \bar{w}_{k,d}}{\bar{w}_k} \bar{G}_{k,d} \mathbb{V}_d[\bar{G}_{k,d}]}_{\text{Between-group selection}} \right) + \sum_{k=1}^K c_k \left(\underbrace{\mathbb{E}_d \left[\frac{\beta w_{k,id}}{\bar{w}_k} G_{k,id} \mathbb{V}_i[G_{k,id}] \right]}_{\text{Within-group selection}} \right) \quad (1.7)$$

Here, relative fitness $\frac{w_i}{\bar{w}}$ (found by taking the i th individual's absolute fitness relative to the whole-population average absolute fitness \bar{w}) has been replaced by class-specific relative fitness: the i th individual's absolute fitness relative to the population average absolute fitness \bar{w}_k for the class k to which it belongs. For individual i in group d belonging to class k , absolute fitness is here denoted $w_{k,id}$, and its relative fitness is therefore $\frac{w_{k,id}}{\bar{w}_k}$. Although the proliferation of cancer within the body is clearly a short-term evolutionary process (Nesse, 2017), $c_k = 0$ for a nontransmissible cancer cell. The relevant within-group selection term drops from the multilevel Price equation (Gardner, 2015c; Shpak and Lu, 2016). This view leads to the surprising conclusion that – at least in an evolutionary sense – somatic cells undermining the rest of the body do not compromise the integrity of the organism as a

unified agent striving to maximise inclusive fitness². Significantly, a parallel argument was made by Hamilton (1964b) at the superorganismal level, where it is tempting to see worker cloning as a form of selfish superorganismal cancer, compromising the integrity of the superorganism as a unified agent striving to maximise superorganismal fitness:

*“Female-to-female parthenogenesis by workers does occur sporadically in honeybees... In the South African race, *Apis mellifera capensis* Esch., it seems that worker eggs always develop into females. But whether this is explicable as a selfish trait is rather doubtful. To be such the laying-workers would have to try to get their eggs cared for in queen cells.”* (Hamilton, 1964b)

1.3.2.d ***Do alleles have their own inclusive fitnesses?***

In the previous section, I argued that purely somatic ‘defection’ is not really defection at all, and the organism retains its optimisation agenda as an inclusive fitness maximiser (Gardner, 2015c). The same is not true when conflict occurs in the germline. Now, the lower-level units (alleles) have positive reproductive values, and the organism (or superorganism) can be partially fractured into entities with contradictory interests. In general, alleles in the same organism may enjoy aligned fitness interests: inheritance is (normally) fair (Leigh, 1977), so every allele has an equal chance of being passed on to the organism’s offspring. However, the genome is a temporary collaboration between alleles, and opportunities to exploit the collective are taken when they arise – including undermining the normal laws of Mendelian segregation to ensure the selfish allele enters a disproportionately large proportion of the gametes (Burt and Trivers, 2006; Helanterä, 2006). In short, aspects of the organism’s phenotype can be hijacked to serve a minority of the genome (Haig, 2014a, 2014b); where, then, is the coherent inclusive fitness maximiser amongst this intragenomic strife?

One solution is to broaden our concept of inclusive fitness in the context of intragenomic conflict. We could picture the ‘inclusive fitness’ of specific alleles whose interests diverge. This view has recently been championed by Gardner and Úbeda (2017). At first glance, the Gardner-Úbeda perspective appears to be the gene’s-eye-view familiar from *The Selfish Gene* (i.e., each allele is a self-interested agent; Dawkins, 1976). However, Gardner and Úbeda (2017) have in mind a more direct analogy between allele behaviour and inclusive fitness maximisation by individual organisms:

“Whereas Dawkins defines the ‘selfish gene’ as a distributed agent that comprises every copy of a particular allele in an evolving lineage, we define the gene as a single, physical scrap of nucleic acid... A consequence of our definition is that – just like whole organisms – inclusive-

² Unless, of course, cancer is transmissible or enters the germline, in which case $c_k > 0$.

fitness-maximising genes may behave altruistically, spitefully and mutually beneficially, rather than purely selfishly.” (Gardner and Úbeda, 2017)

If alleles have their own inclusive fitnesses, does inclusive fitness still exist at the level of the individual organism? This is a live question. After Haig (2014b) suggested that intragenomic conflict should be incorporated into organismal fitness maximisation arguments, Grafen (2014a) acknowledged that assuming unity of purpose within the genome could ‘*potentially represent serious problems for the formal Darwinism project*’ (Grafen, 2014a). It remains to be seen whether a simple maximand argument can be made that captures the degree of fitness alignment in the underlying alleles.

1.4 Part 2: Hamilton’s rule

Hamilton’s rule ($rB > C$) is the central equation of social evolution (Hamilton, 1964a; Gardner *et al.*, 2011; Queller, 2011; Smith, 2014): any behaviour is selected if the benefits B accruing to a beneficiary, multiplied by the relatedness r between beneficiary and actor, exceed the cost C paid by an actor (Bourke, 2014a). It is possible to accept the universality of Hamilton’s rule without accepting the universality of inclusive fitness as the organism’s maximand; in essence, this is because fitness effects in Hamilton’s rule are defined as regression slopes across the whole population rather than fitness changes to specific individuals. In other words, the regression slope fits a least-squares line through the scatter of all individuals’ fitnesses (on the y-axis) and the breeding values associated with each relevant actor (on the x-axis). The slope of the line therefore represents a population-wide quantity, a measure of the association between breeding value and fitness across all individuals, rather than a quantity associated with any specific individual. I use Hamilton’s rule extensively in Chapters 3, 4, and 6 of this thesis. In this section, therefore, I address the generality of Hamilton’s rule, and discuss recent criticism.

The following five statements are all part of the textbook interpretation of Hamilton’s rule:

1. Hamilton’s rule is a falsifiable prediction, which can be – and often is – tested empirically.
2. Sufficiently increasing r , decreasing C , or increasing B increases the scope for cooperation.
3. B and C capture the causal influences of the actor on its partner and itself.
4. r denotes the degree of genealogical kinship (common sense ‘relatedness’) between social partners.
5. B and C are simple effects (or average effects) on the partners’ numbers of offspring.

Strictly, however, none of these statements are entirely correct, although they may be reasonable approximations. Taking each claim in turn:

1. In its general form, Hamilton's rule is not falsifiable: it is a mathematical necessity (like $1 + 1 = 2$) and is therefore true *a priori* for any bout of selection. In this sense, it is not possible to 'test' empirically whether it is correct (van Veelen *et al.*, 2017).
2. In principle, increasing r or B can select *against* cooperation, and increasing C can select in its favour. This seeming paradox arises because the specifics of population structure in any given case can make r , B , and C tightly co-dependent. Changes made to one parameter may then be necessarily accompanied by counter-acting or over-compensating changes elsewhere in Hamilton's rule (shifting the sign to $rB < C$), so individual parameters cannot make guaranteed predictions in isolation.
3. B and C can still be nonzero when the actor has no causal effect on itself or its partner.
4. Nonzero relatedness r can arise in the absence of genealogical kinship. Regression 'relatedness' r measures the extent of simple assortment between strategies in interactions. This may or may not be caused by common ancestry (Frank, 1998). Hamilton's rule makes sense – with $r \neq 0$ – even if familial kin never interact.
5. B and C are not effects on absolute numbers of offspring. Instead, they are effects on the expectation of relative fitness, averaged over all states of the environment that may occur.

Points 1–3 are used as criticisms of Hamilton's rule (Nowak, Tarnita and Wilson, 2010; Allen, Nowak, *et al.*, 2013; Nowak *et al.*, 2017; van Veelen *et al.*, 2017). In this section, I unpack criticisms based on these points in turn, and discuss whether they pose genuine problems for social evolution. I explore the surprising implications of point 5 in Chapter 3.

1.4.1.a **Criticism 1: Hamilton's rule is a tautology**

Perhaps the most striking irony about the controversy arises in the debate over the generality of Hamilton's rule. The strongest critics of Hamilton's rule are the same authors who argue the most emphatically that Hamilton's rule is *always* true, in *all* conditions, at *all* times, for *all* adaptation. This may sound like a paradox, but the point made by these critics is that a theory that explains everything explains nothing at all.

A shift has taken place in the last decade of controversy over Hamilton's rule. The initial critique by Nowak, Tarnita, and Wilson (2010) strongly criticised the form of Hamilton's rule now known as 'HRA' ('Hamilton's rule additive'), a tractable but not assumption-free approach (assumptions of HRA include additive interactions and weak selection). Since 2010, most defences of Hamilton's rule have emphasised the superior generality of a different form of the rule, now known as 'HRG' ('Hamilton's rule general'). First introduced by Queller (1992) and championed by Gardner *et al.* (2011), HRG

redefines benefits and costs as regression slopes, rather than simple increments in fitness, and is ‘as general as the genetical theory of natural selection itself’ (Abbot *et al.*, 2011). Accordingly, the debate has refocused on HRG. In 2010, critics argued that Hamilton’s rule ‘almost never holds’ (Nowak, Tarnita and Wilson, 2010). In 2017, the same school of critics wrote that Hamilton’s rule ‘always holds’ and ‘always indicates the direction of selection correctly’ (van Veelen *et al.*, 2017). There is no contradiction here, and both criticisms are consistent: the debate has simply shifted from HRA to HRG.

HRG fits the linear least-squares multiple regression through the fitness values (Figure 1.1). This does not mean that it assumes that the underlying relationship between breeding value and fitness is linear (additive) across the population. Rather, HRG is true under all conditions, and the goodness-of-fit scores around the B and C slopes are free to take any values (a regression slope is still a regression slope whether the goodness-of-fit R^2 is 1 or 0.001). An additive regression slope can be fitted to the data, even if this means generating highly autocorrelated residuals (reflecting a curved underlying relationship). Remarkably, this implies that the simple additive slope is sufficient to capture the action of selection even when the true exact relationship between genetic value and expected relative fitness is some complicated polynomial.

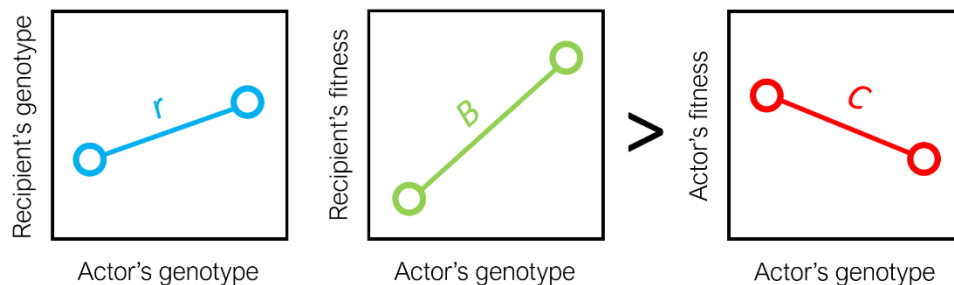


Figure 1.1 | r , B , and C in the ‘HRG’ version of Hamilton’s rule are regression slopes fitted to the whole population. Each one uses the actor’s genotype as the predictor.

Recent challenges to inclusive fitness theory have argued that the Price equation and HRG are tautologies, and are therefore uninformative. On one level, this criticism is correct: HRG is, in an important sense, ‘uninformative’. It adds no more information than we already have about the system (Doebeli *et al.*, 2017). However, this is not necessarily fatal to Hamilton’s rule: $rB > C$ is still useful conceptually. By analogy, the number 1,729 and the sentence ‘the smallest number expressible as the sum of two cubes in two different ways’ (Hardy, 1940) would be indistinguishable to a computer that sees all logical connections instantly. To a human observer, the fact that these two expressions converge on the same numerical value is not obvious. Equivalently, a computer would see $rB > C$ as

an uninteresting restatement of the fact that $\Delta\bar{G} > 0$ (average breeding value is increasing under selection), yet $rB > C$ repackages this fact in a form that carries intuitive weight for human observers. It makes clear the necessary relationships underlying the response to selection. In short, the value of Hamilton's rule is not in adding new information, but in packaging that information intuitively (Birch, 2016b). Because it provides no new information, there is no falsifiable content in Hamilton's rule: it is true by definition.

Not all critics of inclusive fitness arguments from the Price equation are troubled by its apparently tautological nature. Ewens (2014), for instance, likens the Price equation to an ANOVA as a potential means of partitioning variance, and Van Veelen *et al.* (2017) acknowledge that the tautologous nature of HRG does not mean that kin selection itself is questionable. Despite how the controversy is often represented as a debate over the importance of kin selection, the main issue is not with kin selection as a mechanism but rather with Hamilton's rule as a description of the process.

Accepting that HRG is *a priori* true leads to a strange conclusion. If Hamilton's rule is true by definition, it does not make sense to try to test it empirically (van Veelen *et al.*, 2017), just as we do not try to test $1 + 1 = 2$ by doing experiments. What, then, are behavioural ecologists doing when they set out to 'test' Hamilton's rule? The answer is that – with one bacterial exception (Chuang *et al.*, 2010) – field tests using Hamilton's rule do not aim to 'test' the unfalsifiable regression version (HRG), but rather to test the looser proposition that simple effects on recipient reproductive success, weighted by relatedness, are enough to justify observed costs to the actor's reproductive success (Bourke, 2014a). The 'true' benefits and costs may be complicated and inaccessible functions of population structure (Gardner *et al.*, 2011), but uncovering these is not the aim of the experiment: instead, the question is whether the simple fitness increments are enough, in themselves, to justify altruism. If the answer is 'no', then we know from HRG that more complex benefit and cost terms may provide the solution. Accordingly, additional factors can be tested experimentally.

1.4.1.b ***Criticism 2: co-dependence of regression parameters***

The second of the points in the list forms the basis for an argument that HRG is predictively impotent – and, more seriously, likely to lead to spurious general predictions (van Veelen *et al.*, 2017). Perhaps the most fundamental prediction in social evolution is that higher grades of sociality should be associated with higher values of r . This prediction is routinely tested empirically (Green *et al.*, 2016). Yet is it justified by Hamilton's rule?

The common-sense answer is that r , B , and C will be rarely interwoven in such a way that increasing r automatically decreases B or increases C . This is, however, a testable hypothesis that remains to be confirmed. Resolving whether co-dependence genuinely leads to an increase in relatedness leading to *less* cooperation in anything other than a negligible subset of population structures remains an outstanding question. One fruitful avenue for analysing population structure is provided by ‘games on graphs’, which reinterpret social evolution in terms of interactions on networks (Ohtsuki *et al.*, 2006; Nowak and Roch, 2007; Allen *et al.*, 2016). Because millions of permutations of population structure can be generated computationally and tested (see Allen *et al.*, 2016, for a powerful demonstration), games on graphs should offer a tractable framework in which to address the extent to which the co-dependence of regression parameters does genuinely lead to flawed predictions.

1.4.1.c **Criticism 3: B and C are not necessarily causal effects**

Critics of HRG argue that it obscures causal relations (Okasha and Martens, 2016). Strictly speaking, this is also correct. The most forceful argument against Hamilton’s rule as a causal hypothesis is made by Allen *et al.* (2013), who note that there is no requirement that regression slopes describe causal effects. To illustrate the point, Allen *et al.* (2013) propose an example in which individuals with a so-called ‘hanger-on’ genotype (with breeding value G_i) associate socially with high-fitness partners but have no causal effect on the partner’s fitness. In this case, the ‘benefit’ term B is artificially positive for the interaction because – if we simply survey the population – individuals have a higher fitness w_j when associated with partners possessing the focal breeding value G_i (*i.e.*, $\beta_{w_j, G_i} > 0$). The ‘benefit’ term has no causal meaning.

However, it is worth returning to Price’s original justification for covariance-based logic in evolution:

“...at any step in constructing hypotheses about evolution through natural selection – for example, about... why parrots mimic, why dolphins play – one can... consider whether the slope really would be appreciably non-zero under the assumptions of the theory.” (Price, 1970)

Although rarely expressed this way, the Price equation provides a plausibility meter for adaptive hypotheses. Any hypothesised combination of fitness effects, by definition, must conform to the Price equation (and its rearrangement, Hamilton’s rule); otherwise, it is logically inconsistent as an argument for $\Delta\bar{G} > 0$. Claims of mistaken causality misconstrue the ‘plausibility meter’ role provided by HRG: as in any experimental study, causality must be determined empirically.

In this sense, the causality criticism is partly a straw-man. Allen *et al.* (2013) write:

“Variants of this hanger-on behaviour may occur in many biological systems. A bird may choose to join the nest of a high-fitness pair, with the goal of eventually inheriting the nest. Similarly, a social wasp may be more likely to stay at its parents’ nest if the parent has high fitness, also with the goal of eventual inheritance. Applying the regression method to these situations would lead one to mistake purely self-interested behaviors for cooperation.” (Allen, Nowak, *et al.*, 2013)

This is correct, but partly beside the point: Hamilton’s rule is not used in this way empirically. In fact, the regression method has essentially never been applied, with no empirical context, directly to real-world empirical systems (a point that forms part of Allen and coauthors’ criticism elsewhere; van Veelen *et al.*, 2017). A rare example is Chuang *et al.* (2010), who face considerable predictive difficulties. A behavioural ecologist observing birds joining nests starts by hypothesising fitness effects (*does the joiner increase the residents’ fitnesses?*) and then aims to identify the direction of causation by manipulation (*if I remove the joiner experimentally, what happens to the residents’ fitnesses?*) or observation (*do I observe the joiner performing behaviours that increase the recipients’ fitnesses?*). They then ask if the effects they have identified are sufficient to explain an adaptation of interest (*does any causal effect on the residents’ fitnesses, weighted by relatedness, justify any costs paid by the joiner?*). The aim empirically is always to describe causation, and social evolution is no different: if you start by empirically identifying additive fitness effects caused by a given behaviour, Hamilton’s rule will be a fully causal description, and that is – appropriately – how it is used by empiricists.

A second defence against the causality criticism is to argue that Hamilton’s rule is just a useful device for planning an investigation: it conveniently splits selection into three separate components. In effect, Hamilton’s rule provides a road-map for how to approach a puzzling behaviour:

“Hamilton’s rule tells researchers on the ground where to look first. Then they can move beyond it and construct a more precise model that includes ecological parameters relevant to the particular case.” (Jonathan Birch, quoted in Cepelewicz, 2018)

This abstract quality makes Hamilton’s rule appealing to empiricists (broadly, what parameters should we be studying?) and occasionally frustrating to mathematicians (specifically, what parameters are important?).

1.5 Conclusion

As an ‘*accounting method*’ for modellers (Nowak, Tarnita and Wilson, 2010), inclusive fitness theory may well be justifiable in principle but unnecessary in practice. As put by Allen *et al.* (2013), ‘*there is no*

problem in evolutionary biology that requires an analysis based on inclusive fitness'. I agree with this claim. Inclusive fitness may be an overcomplicated approach in many cases. It is perhaps better employed in these situations as a '*universal language*' (Gardner *et al.*, 2011) after the results are known, allowing us to place seemingly disconnected findings in a common framework (Birch, 2017).

However, inclusive fitness serves a more profound role in biology (Gardner, 2009): it is the only remaining candidate for the quantity pursued by all organisms (Bourke, 2011). In this sense, it seeks to answer an empirical question that is considered irrelevant by some biologists and fundamental by others. Similarly, the disagreement between different camps over Hamilton's rule (Part 2 above) is largely due to different aims. Critics want to know how specific traits evolve (Nowak, Tarnita and Wilson, 2010); supporters also want to know, at a fundamental and abstract level, how the action of selection works (Gardner, 2010; West and Gardner, 2013; Taylor and Maciejewski, 2014). Nonetheless, for most biologists, it is critically important to understand the generality of any proposed universal principle of organismal design. In a practical sense, formalising the intentional stance is vital empirically: without a fitness concept, it is impossible to know what to measure.

There are, at present, a series of open questions in inclusive fitness theory. Answering each will be crucial to establishing the roles of maximand arguments and Hamilton's rule in the future of social evolution. These include the following general questions:

1. What is the effect of population structure on cooperation (Nowak, Tarnita and Antal, 2010), and can different categories of population structure be captured simply within Hamilton's rule?
2. Is there a general solution to the non-additivity problem that holds even in the absence of weak selection?
3. What are the conditions under which a group-level analogue of inclusive fitness can evolve?
4. What happens to inclusive fitness theory in stochastic populations? As observed by Nowak, Tarnita, and Wilson (2010), '*the stochastic element of evolution, which leads to a distribution of possible outcomes rather than a single optimum, is not a part of inclusive fitness theory.*'

I take up the last of these questions theoretically in this thesis (Chapters 3 and 4): what happens to Hamilton's rule – and altruistic behaviour – in populations subject to environmental and demographic fluctuations? In Chapters 5–7, I explore 'drifting' behaviour empirically in Neotropical *Polistes* paper wasps, which poses an outstanding paradox to inclusive fitness theory (Hamilton, 1964b; Sumner *et al.*, 2007). In the next chapter, I introduce drifting behaviour in the social insects.

Chapter 2

2 | Drifting and eusociality

2.1 Chapter Summary

Social insect colonies are often seen as ‘fortresses’ – impenetrable, self-contained, and mutually aggressive. However, recent studies have revealed surprisingly high levels of ‘drifting’ behaviour, in which individuals move – temporarily or permanently – to foreign colonies. In Chapters 5–7, I explore drifting in Neotropical *Polistes* paper wasps. In this chapter, I introduce drifting in general, and define five general categories of adaptive drifting: parasitic ‘egg-dumping’, kleptoparasitism, social cancer, nest inheritance, and indirect fitness. Because drifting can offer an alternative route to maximising inclusive fitness, I argue that a focus on drifting may be valuable in understanding the origins and evolution of eusociality.

2.2 What is drifting?

Six years before *The Origin of Species*, Reverend Lorenzo Langstroth of Massachusetts complained that ‘*arrant rogues*’ amongst his honeybees were stealing honey from other colonies (Langstroth, 1853). ‘*Some branches of morals in my little friends,*’ he wrote, ‘*need very close watching.*’ Recently, ‘*very close watching*’ has revealed 56% of paper wasp workers (*Polistes canadensis*; Sumner *et al.*, 2007) and 59% of nest-leaving bumblebees (*Bombus terrestris*; Blacher *et al.*, 2013) visiting foreign colonies, a behaviour known as ‘drifting’. In this thesis, I define drifting broadly as movement of individuals (or a subset of the colony) to foreign conspecific colonies for reasons other than mating. Drifters can be further categorised as either temporary drifters (Sumner *et al.*, 2007) or permanent drifters (*e.g.*, a fraction of bees in Blacher *et al.*, 2013). In this chapter, I introduce the known extent of drifting behaviour in the social insects (*Table 2.1*).

Seemingly accidental drifting has long been known in managed honeybee apiaries (*Apis mellifera*; Free, 1956, 1958), where up to 42% of nest-members may be non-natal drifters (Pfeiffer and Crailsheim, 1998). However, there is increasing evidence that drifting can serve an adaptive function for drifters (Lopez-Vaamonde *et al.*, 2004; Birmingham *et al.*, 2004; Härtel *et al.*, 2006; Sumner *et al.*, 2007; Blacher

et al., 2013). Here, I categorise adaptive drifting into five general categories: (1) ‘egg-dumping’, (2) nest-inheritance, (3) kleptoparasitism, (4) social cancer, and (5) indirect fitness. In principle, drifters may be motivated by more than one factor. I define and describe each in turn, with illustrative examples:

1. Egg dumping

Egg-dumping drifters attempt to parasitise foreign colonies by laying eggs (*e.g.*, Birmingham *et al.*, 2004). Egg-dumping rates vary widely across species and studies, for which there is currently little explanation. The best-studied cases occur in bumblebees (*Bombus* spp.), where colonies can face approximately fifteen infiltration attempts per week from presumed egg-dumpers, of which fewer than one may succeed (Zanette *et al.*, 2014). In one study of *B. terrestris*, 58.9% of nest-leaving bumblebees drifted, of which 32.5% were observed egg-dumping (Blacher *et al.*, 2013). In *B. deuteronymus*, drifters produced 19% of male offspring (Takahashi *et al.*, 2010). However, in a separate population, O’Connor *et al.* (2013) concluded that egg-laying by drifting workers occurs at a low level in wild *B. terrestris* (detecting only six drifters in 14 colonies), finding some evidence of egg-dumping by foreign queens. Remarkably, in contrast to *Bombus*, there is only a single claimed case of egg-dumping in ants, inferred from allozymes in a British population of *Leptothorax albipennis* (Pearson, Raybould and Clarke, 1997; see Armitage *et al.*, 2010 for a second potential case, in *Atta sextans*). Similarly, despite apparently optimal conditions for egg dumping (high density nesting and minimal non-nestmate aggression), the stingless bee *Tetragonilla collina* shows surprisingly low levels of drifting (Leonhardt *et al.*, 2011).

Queenright superorganismal³ colonies are generally protected from egg-dumping drifters as a by-product of the policing of worker-laid nestmate eggs (Beekman and Oldroyd, 2008). Worker policing may remove the need for a specialist ‘first line’ of colony defence targeting foreign drifters (Nanork *et al.*, 2007; but see Couvillon *et al.*, 2008). Indeed, when colonies of the Asian honeybee *Apis florea* were made queenless experimentally, the percentage of foreigners in the workforce rose from 2% to 4.5%,

³ As in Chapter 1, I follow Boomsma and Gawne (2018) in defining a ‘superorganism’ as a social group with irreversibly-committed adult reproductive castes (a ‘germline’ and a ‘soma’), which represent a qualitatively distinct form of social organisation to non-superorganismal species, in which adults retain caste flexibility. (Note, however, that even in most superorganismal Hymenoptera taxa, workers are able to lay unfertilised eggs, which develop as males.) Superorganismal species include the vespine wasps, *Macrotermes* termites, stingless bees, bumblebees, and the vast majority of ants. A small minority of ants (such as *Dinoponera quadriceps*) have secondarily reverted to castelessness, but can be considered derived superorganisms. Non-superorganismal social insects lack irreversible caste differentiation, and include the ‘simple’ social wasps (*e.g.*, *Polistes*, *Liostenogaster*, *Ropalidia*, *Belonogaster*) and the drywood and dampwood termites (*e.g.*, *Cryptotermes*).

and foreigners produced 22.5% of pupae (Nanork *et al.*, 2005). Significantly, the predominant sources of *A. florea* egg-dumping drifters are other queenless colonies (Chapman *et al.*, 2009): queenlessness lowers the opportunity cost to a drifter (in lost indirect fitness) from abandoning investment in the home nest, whilst egg-dumping in unrelated nests averts local resource competition with related nestmates on the queenless natal nest (Chapman *et al.*, 2009). Amongst advanced eusocial wasps, egg-dumping has been experimentally shown in *Vespula vulgaris* (Oliveira *et al.*, 2016), where, again, it is likely to be restricted to queenless nests in which normal mechanisms of worker policing break down.

Simple physical constraints may explain much of this interspecific variation. It is presumably easier to deposit an egg in a small and accessible simple social wasp colony, with no covering envelope, than it is to dump an egg in a large *Atta* colony with a narrow, closely-guarded entrance. Indeed, *A. florea* shows higher levels of drifting than *Apis cerana* and *A. mellifera*, and various authors have explained the difference by noting that *A. florea* has unusually accessible combs that can be less effectively guarded (Nanork *et al.*, 2005; Oliveira *et al.*, 2016). There may also be broad biogeographical gradients. Hypothetically, egg-dumping drifting may fall with latitude: Packer (1986) proposed that egg-dumping drifters in *Halictus ligatus* are more likely to find colonies in the right developmental stage in the aseasonal tropics, where multivoltinism is common.

2. Nest inheritance

Nest-inheritance drifters attempt to inherit or usurp the queen position (*e.g.*, Klahn, 1988). Drifting for nest inheritance is well known amongst foundress and pre-emergence colonies in the non-superorganismal wasps, where drifters are generally known as ‘joiners’. In *Ropalidia marginata*, for instance, 32.1% (217/676) of wasps joined from foreign nests (Shakarad and Gadagkar, 1995). Post-emergence queen supersedesures also offer opportunities for nest-inheriting drifters: in an RFID study of an apiary population of the stingless bee *Melipona scutellaris*, (Van Oystaeyen *et al.*, 2013), 37.5% (3/8) of queen successors were drifter queens. Nest inheritance by drifters is also suspected in post-emergence colonies in *B. hypnorum*: Paxton *et al.* (2001) detected between 5% and 28% of workers as possessing ‘alien’ genotypes, and favour an interpretation in which these workers are the offspring of a previous (usurped) queen (egg-dumping was considered unlikely, as the ‘alien’ workers did not show genotypes typical of neighbour colonies in the laboratory set-up).

Nest-inheritance drifting has been studied extensively in *Polistes* wasps. High rates of foundress drifting are associated with high brood mortality in *P. versicolor* and *P. ferreri* (Tannure and Nascimento, 1999). In *P. fuscatus*, Klahn (1988) found that 19.6% of lone foundresses were displaced by drifters (dropping to 2.2% in foundress associations). In principle, subordinates may work for non-natal nests in

order to join a queue for hopeful nest inheritance (a 'pay-to-stay' mechanism; Field and Cant, 2007). Recently, direct manipulations in *P. dominula* have revealed that pre-emergence nests exist in a 'market', where the price of help is determined by supply-and-demand (Grinsted and Field, 2017). In this case, when dominants are forced into higher competition to recruit subordinates by experimentally providing subordinates with outside options, subordinates invest less in helping effort. The interpretation is that subordinates are indeed 'paying to stay', and need pay less when subordinates are more in demand at a whole population scale (Grinsted and Field, 2017).

3. Kleptoparasitism

Kleptoparasitic drifters steal resources from conspecific colonies for their home colony (Couvillon *et al.*, 2008), such as food thieving by the Japanese harvester ant (*Messor aciculatus*; Yamaguchi, 1995). In honeybees, the threat from kleptoparasitic drifters ('robber bees') can be sufficiently extreme that colonies can collapse from the depletion of honey (Langstroth, 1853; Free, 1954; Couvillon *et al.*, 2008). This has led to sophisticated strategies by colony guards, optimising their number and acceptance thresholds in real time to deal with fluctuations in the threat from drifters (Couvillon *et al.*, 2008). More strikingly, the Neotropical 'thief ant' *Ectatomma ruidum* possesses a kleptoparasitic worker caste, which specialises in drifting to conspecific nests to steal food items (Jandt *et al.*, 2015; McGlynn *et al.*, 2015).

Kleptoparasitic drifters can steal more than food. In *Parishnogaster mellyi*, 'marauding' drifters attempt to take nest material (Hansell, 1982). In the 'slave-making' ants, pupae are abducted from foreign colonies and reared as 'slave' workers (D'Ettorre and Heinze, 2001); under the broad definition, I consider this raiding to be a form of temporary 'drifting'. Although victims of interspecific slave-making are now known to 'rebel' by killing host pupae (Achenbach and Foitzik, 2009), there is currently no evidence for slave rebellion against conspecific drifters. Remarkably, however, drifting itself can provide an opportunity for the remaining members of the victim colony to respond. In fire ant (*Solenopsis invicta*) colonies that have lost a bout of mutual brood abduction, mass drifting of workers from the victim to the abductor colony can ensue. Following this exodus, if the victim queen succeeds in burrowing into the abductor nest she appears to have a one-fifth chance of wresting control of the colony, aided by her drifted workers (Tschinkel, 2006) – a strategy of turning kleptoparasitism victimhood into successful nest inheritance.

4. Social cancer

The most extreme form of exploitative drifting – ‘social cancer’ (Dobata *et al.*, 2011) – is found in superorganismal species. Normally, intraspecific parasitism is a secondary avenue to direct fitness. However, in the South African fynbos honeybee subspecies *A. m. capensis*, ‘workers’ drift to colonies of the related subspecies *A. m. scutellata* and parthenogenetically produce clonal diploid offspring (by fusing maternal pronuclei; Cole-Clark *et al.*, 2017). The proliferation of parasitic *A. m. capensis* in South Africa is a recent phenomenon following the anthropogenic introduction of *A. m. capensis* outside the Cape. The result has been an epidemic of colony death amongst managed colonies in northern South Africa (Beekman and Oldroyd, 2008). *A. m. capensis* clones show remarkable adaptive behaviour to maximise virulence, including dominating *A. m. scutellata* by producing queen-like pheromones (Okosum *et al.*, 2017).

Parasitic *A. m. capensis* drifters also target nests of their own subspecies (Härtel *et al.*, 2006): Jordan *et al.* (2008) found that 38% of new queens in *A. m. capensis* were the clonal progeny of these subspecific parasites. It has been suggested that each *A. m. capensis* colony may specialise in either worker policing or drifting, but not both, giving rise to frequency-dependence that maintains a stable polymorphism (Sumner and Keller, 2008). A colony with high levels of policing of worker-laid eggs would successfully eliminate these foreign infiltrators but also pay the opportunity cost of not being able to emit clonal drifters itself (Sumner and Keller, 2008); conversely, colonies with low levels of worker policing gain the chance to parasitise foreign colonies, but are at higher risk of subversion.

As a superorganismal analogue of transmissible cancer (Wenseleers and Van Oystaeyen, 2011), the between-colony metastasis of *A. m. capensis* drifters allows them to evade the evolutionary dead-end that meets non-transmissible cancer lineages, permitting the evolution of a lethal parasitism strategy (akin to a parasitoid life history) that does not require the preservation of the host. Similar drifting ‘social cancers’ are known in two ants, *Pristomyrmex punctatus* and *Platythyrea punctata* (Wenseleers and Van Oystaeyen, 2011). Transmissible cancer is sometimes characterised as a form of instantaneous speciation (Ujvari *et al.*, 2016); the same argument has been advanced for drifting social cancers (Neumann and Moritz, 2002). It is unclear why transmissible social cancers have never been found in non-superorganismal social insects (such as the simple eusocial wasps), especially as the wide taxonomic appearance of female parthenogenesis in solitary and social wasps (Rabeling and Kronauer, 2013) implies that the evolution of female cloning is held back by relatively limited physiological constraints.

5. Indirect fitness

Indirect fitness drifters provide helping effort to non-natal colonies in order to maximise their indirect fitness (Sumner *et al.*, 2007): for this category of drifter, a higher indirect fitness is achieved by drifting than by not drifting. It is important to note that observing drifters cooperating with foreign nests does not necessarily imply an indirect fitness motive. Nest-inheritance drifters, for instance, might provide helping effort to non-natal colonies as part of a nest inheritance strategy, either by ‘paying to stay’ (Grinsted and Field, 2017) or by increasing the group’s productivity in order to increase the size of any future nest inheritance payoff (‘group augmentation’; Kokko *et al.*, 2001). Likewise, numerous authors have interpreted apparent helping effort on non-natal colonies as accidental (and often associated with navigational errors in managed apiaries; Free, 1956; Free and Spencer-Booth, 1958; Smith and Loope, 2016). In principle, however, drifting could maximise indirect fitness if help can be directed to relatives in high need of assistance (Hamilton, 1964b; Sumner *et al.*, 2007; Lengronne, 2013) or if drifting promotes reciprocal help from non-relatives for the drifter’s closely-related natal colony (a scenario recently proposed by Nonacs, 2017). In Chapter 6, I explore these hypotheses for cooperative drifting in detail.

Surprisingly, the literature abounds with examples of foreign-colony helping behaviour, whether interpreted by authors to be accidental or not (*e.g.*, *Lasioglossum duplex*: Sakagami and Hayashida, 1968; *Vespula atropilosa* and *V. pennsylvanica*: Akre *et al.*, 1976; *Lasioglossum versatum*: Michener, 1966; *Polistes jadwigae*: Tsuchida and Itô, 1987; *Polistes canadensis*: Sumner *et al.*, 2007). A study of twenty bumblebee colonies in a managed apiary (using RFID tags) revealed that 52% of workers spent the majority of their foraging effort working for foreign colonies (Gill *et al.*, 2012), apparently due to navigational errors in a small environment. At present, whether drifters observed cooperating in natural colonies are doing so by adaptation or by accident is an open question. This is illustrated well by the ‘supercolonial’ ants (Helanterä *et al.*, 2009; Moffett, 2012; Ellis *et al.*, 2016; Nonacs, 2017) – species in which the normal aggression between superorganismal colonies has been completely replaced by peaceful and seemingly cooperative traffic of drifting workers and resources. Relatedness within ant supercolonies is typically extremely low (Helanterä *et al.*, 2009). Anthropogenic and ecological accidents have been proposed to explain high rates of apparently irrational cooperation: ant supercolonies may be products of extreme population bottlenecks purging recognition loci, eliminating the potential for nepotism, and leading to indiscriminate cooperation with non-relatives on neighbour colonies (Tsutsui *et al.*, 2000; but see Giraud *et al.*, 2002). This hypothesis might explain both natural and human-mediated invasive supercolonies (Helanterä *et al.*, 2009). Nonetheless, the ultimate explanation for ant supercoloniality remains unclear.

The current ambiguity over whether cooperative drifting is driven by indirect fitness or accident is associated with scepticism that conferring help on neighbour colonies can be evolutionarily stable in the long term. Unless some degree of cryptic assortment with relatives can occur within ant supercolonies (e.g., Holzer *et al.*, 2009), worker phenotypes will no longer be visible to selection and should gradually degrade, potentially leading supercolonies to collapse over evolutionary time (Helanterä *et al.*, 2009) and revert to classic aggression towards non-nestmates ('multicoloniality'). In summary, the existence of cooperative drifters poses an outstanding paradox to inclusive fitness theory (Giraud *et al.*, 2002), especially in non-superorganismal wasps (Sumner *et al.*, 2007; see below) and superorganismal ants (Lester and Gruber, 2012): it is not clear whether drifters cooperating with foreign colonies do so by accident or adaptation, and – if the latter – it is not clear what the adaptive purpose might be (Lengronne, 2013).

2.3 Worker drifting in *Polistes*: an unsolved problem

Alongside the supercolonial ants, *Polistes* wasps (non-superorganismal paper wasps) are current candidates for indirect fitness drifting (Sumner *et al.*, 2007; Lengronne, 2013; Nonacs, 2017), and are the focus of Chapters 5–7 in this thesis. Seemingly non-reproductive workers cooperating with close neighbour colonies have been repeatedly documented in *Polistes*, beginning with *P. gallicus* in Europe by Deleurance (1952) and *P. canadensis* and *P. versicolor* in Brazil by Hamilton (1964b). Observing drifting in Neotropical *Polistes*, Hamilton (1964b) remarked that the 'transference of workers' between conspecific nests was an 'anomaly' to inclusive fitness theory (which he introduced in the same paper): workers appear to divert help to less-related recipients. Later, Kasuya (1981) detected apparently cooperative drifting in post-emergence *P. chinensis* in Japan: drifters acted 'as if they were genuine workers born in these nests'. Tsuchida and Itô (1987) detected 52.2% (12/23) of marked wasps drifting between a pair of post-emergence nests in *P. jadvigae*, also in Japan. Page *et al.* (1989) documented 'polydomous' (multiple nest) colonies of *P. fuscatus*, spread between up to nine nests, which may be intermingled with nests of other colonies. Newly-eclosed adults disperse across these polydomous networks, and a proportion provide resources to multiple nests. Pickering (1980) detected over 10% of individuals drifting in a large sample of 10,000 paint-marked *P. canadensis* workers over a three-year study in Panama.

The remarkable extent of worker drifting at a whole-population scale that can occur in *Polistes* has, however, only recently become clear. Using radio-frequency identification (RFID) tagging, Sumner *et al.* (2007) found 56.1% (88/157 detected wasps) of *P. canadensis* workers trafficking between colonies in an aggregation of 33 nests, also in Panama; in a similar study, Lengronne (2013) found 30.8% of

Panamanian *P. canadensis* drifting (255/831 detected wasps across eight aggregations). Explaining these large amounts of nonreproductive drifting in *Polistes* by inclusive fitness theory has proven difficult: nonreproductive drifters in *P. canadensis*, for instance, pay an approximately two-fold cost in relatedness to the recipients of their altruism (from $r = 0.52$ on natal nests to $r = 0.23$ on foreign nests; Sumner *et al.*, 2007).

These apparently paradoxical cases of high levels of nest drifting between post-emergence colonies (which I explore in Chapters 5–7) are potentially more difficult to explain than the existence of satellite foundress nests (created late in the season in the temperate zone) assisted by drifters emitted from a strong post-emergence main nest (*e.g.*, *P. exclamans* in Texas; Strassmann, 1981). Here, small foundress colonies with immediate brood-rearing needs can be given an instant boost in productivity by diverting sister workers from their large, saturated, post-emergence parent nests. This hypothesis is reviewed favourably by Page *et al.* (1989). Strassmann (1981) points to the fact that satellite formation also successfully partitions related brood into separate nests, so that loss of any single nest to natural enemies does not destroy the family group's entire productivity⁴. After predation of the main nest, the workforce can simply switch to the small satellites, where indirect fitness opportunities are still available. Satellites may provide back-up opportunities – with at least some positive return to inclusive fitness for workers – in the case of catastrophe elsewhere. Indirect fitness may also be relevant for drifting by foundresses: Seppä *et al.* (2012) document a high degree of movement by foundresses in *P. carolina* in Texas, switching to helping sisters on other foundress nests, potentially doing so when the indirect fitness returns elsewhere exceed the likely direct fitness returns on the home nest.

2.4 Are drifters specialists or opportunists?

A key unanswered question (Amsalem *et al.*, 2015) is the extent to which drifters are specialists (as opposed to accidental drifters who may then opportunistically attempt to capitalise on entering a foreign colony). In Western honeybees (*A. mellifera*), individuals that accidentally drift do not activate their ovaries (Smith and Loope, 2016). By contrast, *A. m. capensis* 'social cancer' eggs successfully escape cannibalism (Martin *et al.*, 2002), potentially by adopting chemical camouflage to resemble the eggs of the *A. m. scutellata* queen. Likewise, some lines of evidence suggest that bumblebee drifters may be specialists: the successful evasion of egg cannibalism in foreign colonies suggest that drifter bumblebees may be capable of egg-camouflaging (Amsalem *et al.*, 2015). Bumblebee drifters not only appear to target colonies with large pollen reserves and a stronger workforce to be parasitized but also

⁴ A similar motivation is given for the existence of multiple combs within the same colony in the Amazonian range of *P. canadensis* by Jeanne (1979).

preferentially invade during colony phases when the risk of losing eggs to worker policing is low (Birmingham *et al.*, 2004). However, these results may also be explained as passive effects of changeable acceptance thresholds: colonies receiving a strong influx of returning nestmate foragers (and hence having larger pollen reserves) may reduce their rates of per-individual inspection. Nonetheless, in principle, specialist drifting allows parasitic effort to be carefully targeted to colonies likely to yield the highest return (similar to nest ‘prospecting’ by avian brood parasites; Pöysä, 2006).

2.5 Should colonies ever accept drifters?

It is easier to understand why colony members should accept non-reproductive, cooperative drifters (Sumner *et al.*, 2007; Lengronne, 2013). In bumblebees, for instance, sterile non-nestmates are admitted by guard bees, despite seemingly being identified as foreign (Blacher, Boreggio, *et al.*, 2013). However, should colonies ever accept drifters who are motivated by direct fitness?

In some cases, colony members may deliberately accept unrelated drifters whose ultimate motivation may be maximising their own direct fitness (although different colony members may have different preferences; see Cronin and Field, 2007). First, even if non-nestmates are undesirable, the optimum amount of effort to invest in excluding non-nestmates depends on the costs of exploitation (Reeve, 1989): in *A. mellifera*, queenright colonies willingly accept all foreign arrivals when the cost of tolerance is reduced sufficiently (due to improved colony state; Downs and Ratnieks, 2000). Second, even hopeful nest-inheritors may be valuable for their helping effort. Vulnerable pre-emergence colonies and small post-emergence colonies may require additional help (Pfennig, 1990; Grinsted and Field, 2017), and the partial risk of usurpation by the additional helpers may be an acceptable price. Indeed, in *Mischocyttarus mexicanus* (a non-superorganismal wasp), pre-emergence colonies become increasingly likely to reject non-nestmates as the colony ages, presumably because the resident foundress has less need of drifters as her own pupae approach eclosion as workers (Mora-Kepfer, 2013). Intriguingly, Arathi *et al.* (1997) argue that young non-nestmates are preferentially recruited by *Ropalidia marginata* (a non-superorganismal wasp) over older non-nestmates because it is more profitable to accept young, behaviourally-multipotent workers. Nonetheless, Arathi *et al.*'s (1997) results might also be explained by young workers lacking clear markers of colony identity.

Strikingly, orphaned workers on mature post-emergence colonies may permit nest inheritance by foreign drifters in order to obtain a temporary emergency queen: experimental removal of queens in one colony of *Protopolybia exigua* and one colony of *Metapolybia docilis* (non-superorganismal epiponines) resulted in a shift from xenophobic aggression to a willingness to accept foreign queens (Chavarria-Pizarro *et al.*, 2018). Among the epiponines, surplus queens are regularly evicted by

nestmate workers, and may subsequently drift. Accepting an unrelated drifter queen may provide an interim solution for workers until a previously-rejected nestmate queen (who has not been evicted) can re-take the queenship and restore high relatedness (Chavarría-Pizarro *et al.*, 2018).

There are paradoxical cases in which colonies appear to acquiesce to parasitism. In the social clonal aphid *Pemphigus obesinymphae*, for instance, clones make little attempt to resist infiltration by a specialist ‘intruder’ caste of drifters (Foster, 2002; Abbot and Chhatre, 2007), who appear to exploit the host resources. One possibility is that the cost of parasitic drifters is low at the tail end of the season (Foster, 2002), such that there is little selective pressure to resist depredations – a eusocial version of ‘selection shadow’ hypotheses for the evolutionary accumulation of senescent traits after reproductive maturity. Available evidence, however, suggests that drifters appear before this eusocial menopause (Grogan *et al.*, 2010). An alternative possibility is that resistance is simply too costly. The act of challenging foreign parasites may be prohibitively expensive for the host colony. If true, it may be in a drifter’s interests to escalate the cost of challenges beyond what is tolerable for hosts by raising the threat of aggressive contests. The potential payoff from a single success for the drifter’s genotype is sufficiently large that high rates of failure generated by aggressive confrontation may be tolerable. Such ‘brinkmanship’ behaviour – deliberately raising the risk of mutual harm (Schelling, 1980) – requires a credible signal of commitment to carry out a hypothetical threat. Intriguingly, bumblebee drifters show high levels of aggression in host colonies (Lopez-Vaamonde *et al.*, 2004), which is difficult to explain if drifter parasites are secretive egg-layers. Alternatively, elevated aggression may allow parasitic drifters to achieve integration by ‘bluffing’ their dominance status in simple eusocial colonies.

Last, experiments in *Pterotermes occidentis* (a non-superorganismal drywood termite) show that, surprisingly, lone non-nestmates are not rejected but instead enjoy high levels of grooming by host termites (Cooney *et al.*, 2016). Cooney *et al.* (2016) interpret these results as either a mechanism for hosts to ensure uniformity of cuticular hydrocarbons (to permit the successful integration of drifters to the colony) or a means of removing incoming pathogens.

2.6 Outstanding questions

In this chapter, I have briefly surveyed the known extent of drifting in the social insects. Drifting may be both surprisingly widespread and associated with diverse and sophisticated adaptations. One-hundred-and-sixty-five years after Reverend Langstroth first detected an ‘*unmistakable air of roguery*’ (Langstroth, 1853, p. 307) associated with social insect drifters, a renewed focus on these surprising colony members may be valuable for understanding the origin and elaboration of eusocial traits.

In Chapters 5–7, I focus on the unsolved problem of drifting in *Polistes*, following the demonstration that extreme levels of apparently cooperative drifting can occur in the Neotropical species *Polistes canadensis* (Sumner *et al.*, 2007; Lengronne, 2013). I focus on three key questions:

1. Is drifting part of a specialist set of behaviours?
2. Can inclusive fitness explain drifting?
3. Can colonies reliably identify drifters?

In Chapter 5, I use RFID-tagging and queen removal in *P. canadensis* in French Guiana, in order to test whether drifters and non-drifters differ behaviourally. In Chapter 6, I collect longitudinal data on brood development in *P. canadensis* in Panama, in order to quantify the extent of diminishing returns for workers (Michener, 1964): can diverting cooperation to a less related neighbour increase indirect fitness? Last, in Chapter 7, I use RFID-tagging to ask whether (and to what extent) drifting exists in the relatively little-studied paper wasp *P. satan* in Brazil, and use a combination of recognition and acceptance tests to ask whether host colonies possess non-nestmate discrimination in the face of drifting.

Table 2.1 | Accounts of drifting

Interpretation	Species	Study	Type	Rates	Method
Egg-dumping and reproductive parasitism	<i>Bombus terrestris</i>	Zanette <i>et al.</i> (2014)	Natural	3% of workers in 8 colonies	Microsatellites
		O'Connor <i>et al.</i> (2013)	Natural	4 of 14 colonies contained 6 drifters	Microsatellites
		Blacher, Yagound, <i>et al.</i> (2013)	Managed	58.9% of 373 nest-leaving bees drifted (33% of 665 tagged bees)	Colour-tags and video monitoring
		Lopez-Vaamonde <i>et al.</i> (2004)	Natural	100% (32/32) of colonies emitted and received drifters. Drifters produced 28.1% (61/121) of adult males in queenless colonies	Microsatellites; paint-marked
	<i>Bombus occidentalis</i>	Birmingham and Winston (2004)	Managed	0.3–34.8% of bees drifted (12 colonies)	Colour-tags
	<i>Bombus impatiens</i>	Birmingham and Winston (2004)	Managed	0.1–12.2% (32 colonies)	Colour-tags
	<i>Bombus deuteronymus</i>	Takahashi <i>et al.</i> (2010)	Natural	27% (3/11) of colonies contained foreign drifters, producing 19% of males	Microsatellites
	<i>Lasioglossum calceatum</i>	Davison and Field (2018)	Field transplant	At least one successful drifter-produced female	Microsatellites
	<i>Lasioglossum malachurum</i>	Paxton <i>et al.</i> (2002)	Natural	Foreign pupae in 2/18 nests	Microsatellites
	<i>Halictus scabiosae</i>	Brand and Chapuisat (2016)	Natural	46% (12/26) of foundresses produced offspring in multiple nests	Microsatellites
<i>Liostenogaster flavolineate</i>	Cronin and Field (2007)	Natural	87% of hour-long observations contained 1 or more drifter	Paint-marked	
<i>Vespa vulgaris</i>	Oliveira <i>et al.</i> (2016)	Managed	1.13% (109/9,659) of wasps drifted to queenright colonies; 1.2% (116/9,569) to queenless colonies	Paint-marked	

Social cancer	<i>Pristomyrmex punctatus</i>	Dobata <i>et al.</i> (2011)	Natural	Transmissible social cancer has persisted for 200 to 9200 generations	Microsatellites
	<i>Apis mellifera capensis</i>	Härtel <i>et al.</i> (2006)	Managed	6.41% of worker-laid offspring in same subspecies are parasitic	Microsatellites
Kleptoparasitism	<i>Pemphigus obesinymphae</i> (gall aphid)	Abbot <i>et al.</i> (2001)	Natural	50% of 72 galls were intruded (5 days of observation)	Paint-marking
	<i>Ectataomma ruidum</i>	Jandt <i>et al.</i> (2015)	Natural	Specialist intruder caste; percentage unrecorded	Individuals followed visually
	<i>Xylocopa pubescens</i>	Hogendoorn and Velthuis (1993)	Natural	Pollen theft; percentage unrecorded	X-ray radiography
	<i>Polistes chinensis</i>	Kasuya <i>et al.</i> (1980)	Natural	Foundresses cannibalise foreign larvae	Paint-marked
	<i>Polistes jadwigae</i>	Kasuya <i>et al.</i> (1980)	Natural	Foundresses cannibalise foreign larvae	Paint-marked
	<i>Mischocyttarus mexicanus</i>	Clouse (1995)	Natural	Visual account of foundress cannibalising foreign larva	Non-marked
Nest-inheritance	<i>Liostenogaster flavolineata</i>	Strassmann <i>et al.</i> (1994)	Natural	26% (10/39) females drifted	Paint-marked
	<i>Mischocyttarus mexicanus</i>	Clouse (1995)	Natural	6/51 foundress nests usurped	Paint-marked
	<i>Polistes fuscatus</i>	Klahn (1988)	Natural	19.6% of long foundresses displaced by drifters	Paint-marked
	<i>Polistes carolina</i>	Seppä <i>et al.</i> (2012)	Natural	87.5% (91/125) 'behavioural choices' by 104 foundresses involved moving to or visiting a new non-abandoned nest	Paint-marked

	<i>Halictus scabiosae</i>	Ulrich <i>et al.</i> (2009)	Natural	16% of 112 nests contained likely drifters	Microsatellites
	<i>Melipona scutellaris</i>	Van Oystaeyen <i>et al.</i> (2013)	Managed	37.5% (3/8) of queen successors were drifter queens	RFID
	<i>Bombus hypnorum</i>	Paxton <i>et al.</i> (2001)	Natural	5–28% of workers in 6/11 colonies were not offspring of the current queen, interpreted as offspring of a previous queen	Microsatellites
Cooperation, potentially for indirect fitness	<i>Polistes canadensis</i>	Pickering (1980)	Natural	10% of approximately 10,000 wasps drifted	Paint-marking
		Sumner <i>et al.</i> (2007)	Natural	56% (88/157) of radio-detected wasps drifted	RFID
		Lengronne (2013)	Natural	30.8% (255/831) drifted	RFID
	<i>Polistes jadwigae</i>	Tsuchida and Ito (1987)	Natural	52.2% (12/23) of workers from two focal nests drifted	Paint-marking
	<i>Polistes chinensis</i>	Kasuya (1980)	Natural	10 observed drifters	Paint-marking
	<i>Linepithema humile</i>	Giraud <i>et al.</i> (2002)	Natural	No aggression across the Mediterranean	Aggression assays
	<i>Formica yessensis</i>	Higashi (1976)	Natural	Observations of queens, workers, and brood transported between nests	Paint-marked
Possible parasite manipulation	<i>Apis mellifera</i>	Parasitism by <i>Nosema ceranae</i> increases frequency of drifting by drifters (Bordier <i>et al.</i> , 2017)	Managed	9.37% ± 2.31 of bees normally drift	Optical counters
Unknown	<i>Halictus scabiosae</i>	Ulrich <i>et al.</i> (2009)	Natural	16% of 122 colonies contained drifters. Possibly reducing resource competition with kin in the natal nest before hibernation	Microsatellites
	<i>Lasioglossum versatum</i>	Michener (1966)	Natural	32.9% (81/246) of nest entries were foreign	Paint-marked

	<i>Lasioglossum duplex</i>	Sakagami and Hayashida (1968)	Natural	19% (12/63) of marked bees	Paint-marked
	<i>Parishnogaster mellyi</i>	Yamane <i>et al.</i> (1978)	Natural	Unrecorded	Presumed paint-marked
	<i>Xylocopa virginica</i>	Peso and Richards (2010)	Natural	70.1% (46/65) females switched nests in one season	Paint-marked
Accident	<i>Vespula atropilosa</i>	Akre <i>et al.</i> (1976)	Managed	2 workers observed performing worker tasks in a neighbour colony	Paint-marked
	<i>Scaptotrigona postica</i>	Paxton (2000)	Managed	2.2% (4/184) workers	Microsatellites
	<i>Bombus terrestris</i>	Gill <i>et al.</i> (2012)	Managed	52% of foragers spent most of their foraging effort working for foreign colonies (see Gill <i>et al.</i> , 2012, Supplementary Material)	RFID

Chapter 3

3 | A stochastic generalisation of Hamilton's rule

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Appendices A-C can be found at the end of this thesis.

3.1 Chapter Summary

The evolution of altruism – costly self-sacrifice in the service of others – has puzzled biologists since *The Origin of Species*. For half a century, attempts to understand altruism have been built on the insight that altruists may help relatives to have extra offspring in order to spread shared genes. This theory – known as inclusive fitness – is founded on a simple inequality termed ‘Hamilton’s rule’. However, explanations of altruism have typically ignored the stochasticity of natural environments, which will not necessarily favour genotypes that produce the greatest average reproductive success. Moreover, empirical data across many taxa reveal associations between altruism and environmental stochasticity, a pattern not predicted by standard interpretations of Hamilton’s rule. Here, we derive Hamilton’s rule with explicit stochasticity, leading to novel predictions about the evolution of altruism. We show that altruists can increase the long-term success of their genotype by reducing the variability in the number of offspring produced by relatives. Consequently, costly altruism can evolve even if it has a net negative effect on the average reproductive success of related recipients. The selective pressure on volatility-suppressing altruism is proportional to the coefficient of variation in population fitness, and is therefore diminished by its own success. Our results formalise the hitherto elusive link between bet-hedging and altruism, and reveal missing fitness effects in the evolution of animal societies.

“While selection on bet-hedging can shape any life-history character, the evolution of a helping strategy has not received explicit attention.” (Cockburn and Russell, 2011)

3.2 Altruistic bet-hedging

The widespread phenomenon of organisms paying costs to help others (altruism) is a long-standing paradox in biology (Hamilton, 1964a; Gardner *et al.*, 2011). Recently, variance-averse investment in stochastic environments (bet-hedging) has been suggested as an explanation for a number of major puzzles in the evolution of altruism, including: (i) the origins of sociality in birds (Rubenstein, 2011; Griesser *et al.*, 2017; Shen *et al.*, 2017), insects (Stevens *et al.*, 2007) and rodents (Ebensperger *et al.*, 2014); (ii) the altitudinal distribution of eusocial species (Kocher *et al.*, 2014); and (iii) the evolution of cooperation between eusocial insect colonies (Sumner *et al.*, 2007). The global distribution of animal societies is linked to environmental stochasticity (Cockburn and Russell, 2011). In birds (Jetz and Rubenstein, 2011; Griesser *et al.*, 2017), mammals (Lukas and Clutton-Brock, 2017), bees (Kocher *et al.*, 2014) and wasps (Sheehan *et al.*, 2015), cooperation is more common in unpredictable or harsh environments. However, the effects of stochasticity have largely been omitted from social evolutionary theory. There are a handful of notable exceptions: for instance, Grafen (2006b) argues that selection will maximise expected inclusive fitness under uncertainty, Uitdehaag (2011) shows that mutualism between nonrelatives could counteract kin selection by dampening stochasticity, and Lehmann & Rousset (2014) explore stochastic effects on reproductive value. However, despite speculation (Koenig *et al.*, 2016; Shen *et al.*, 2017), the proposed link between bet-hedging and altruism (Rubenstein, 2011) has remained elusive (Cockburn and Russell, 2011). We resolve this link by presenting a stochastic generalisation of Hamilton's rule ('stochastic Hamilton's rule'), which predicts when organisms should pay a cost to influence the variance in their relatives' reproductive success.

We allow environmental state π to fluctuate among the possible states Π ; 'stochasticity' is the condition that states are unpredictable. We follow the established method of capturing fitness effects as regression slopes (Gardner *et al.*, 2011). Both the fitnesses w_x of individual organisms and the average fitness \bar{w} in the population may vary among the states Π . We denote the k th central moment of \bar{w} as $\langle\langle^k \bar{w}\rangle\rangle$. The joint distribution of the fitness of individual x (w_x) and \bar{w} across states Π is captured by their mixed moments (covariance $k=1$, coskewness $k=2$, cokurtosis $k=3$, etc.; *Appendix A1*). Altruists may alter not only the expected number of offspring (mean, $k=0$), but may reduce the variation in offspring number (variance, $k=1$) or increase the likelihood of large numbers of offspring (skew, $k=2$). We denote the actor's effect on the recipient's expected number of offspring as the benefit b_μ , the effect of the actor on its own expected number of offspring as the cost c_μ , and relatedness as r . Likewise, we denote the actor's effect on the k th mixed moment defining the recipient's reproductive success as b_k , and the actor's effect on the k th mixed moment of its own reproductive success as c_k . The stochastic Hamilton's rule is therefore:

$$r \left(b_{\mu} + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_{\pi}[\bar{w}]^k} (\ll^k \bar{w} \gg b_{\mu} + b_k) \right) > c_{\mu} + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_{\pi}[\bar{w}]^k} (\ll^k \bar{w} \gg c_{\mu} + c_k) \quad (3.1)$$

Empirical tests of Hamilton’s rule have looked for benefits and costs constituting effects on the average reproductive success of recipients and actors, using the form $rb_{\mu} > c_{\mu}$ (henceforth, ‘means-based Hamilton’s rule’; Bourke, 2014). However, Inequality 3.1 reveals that b_{μ} is a single component of a spectrum of potential benefits of altruism. Conclusions based on mean reproductive success (b_{μ} and c_{μ}) overlook effects on the variance of the distribution from which a recipient samples its reproductive success.

Non-social bet-hedging has been analysed extensively (Starrfelt and Kokko, 2012), and is typically described in terms of costs and benefits: the cost is a reduction in mean reproductive success, whilst the benefit is a reduction in the variance of reproductive success (Starrfelt and Kokko, 2012). Following speculation that these benefits and costs could be accrued by different partners (Stevens *et al.*, 2007; Rubenstein, 2011) – actors pay costs whilst recipient derive benefits (*Figure 3.1a*) – we refer to decoupled benefits and costs as ‘altruistic bet-hedging’. We let b_{σ} and c_{σ} denote, respectively, the effects on the recipient and actor’s standard deviation (‘volatility’) in reproductive success (weighted by its correlation with population average reproductive success \bar{w} ; for details see *Table 3.1* at the end of this chapter). We introduce the ‘stochasticity coefficient’ v as the coefficient of variation in \bar{w} across environmental conditions ($v = \frac{\sigma_{\pi}[\bar{w}]}{\mathbb{E}_{\pi}[\bar{w}]}$; *Figure 3.1b*). Where the actor can affect both the mean and the volatility (but not higher moments) of the recipient’s reproductive success, Inequality 3.1 simplifies (*Appendix A2*) to:

$$r(b_{\mu} + vb_{\sigma}) > c_{\mu} + vc_{\sigma} \quad (3.2)$$

Reducing the (\bar{w} -correlated) volatility in the recipient’s number of offspring ($b_{\sigma} > 0$) confers on recipients greater *relative* fitness in poor environmental states: extra offspring are disproportionately valuable when competitors produce few offspring (Grafen, 2000), underscoring the principle that the ultimate currency for benefits and costs under stochasticity is the expectation of relative fitness (Gardner *et al.*, 2011). It is straightforward to derive the established non-social bet-hedging model (Starrfelt and Kokko, 2012) by setting $r=0$ (*Appendix A3*).

Formally, we define altruistic bet-hedging as a reduction in a recipient’s reproductive volatility (positive b_{σ}) that overcomes an otherwise-deleterious cost to the actor’s mean fecundity (positive c_{μ}). Strong benefits can arise when b_{μ} and b_{σ} are both positive. Reductions in the actor’s own reproductive volatility ($c_{\sigma} < 0$) diminish total costs (*Figure 3.2a,b*). Moreover, when $b_{\sigma} > c_{\sigma}$, increasing stochasticity reduces the minimum relatedness (r) required for altruism to evolve (*Figure 3.2c*). Fluctuations in

relatedness (r) alter selection only if they correlate with strong fluctuations in population average reproductive success (\bar{w}) (see *Appendix A4*).

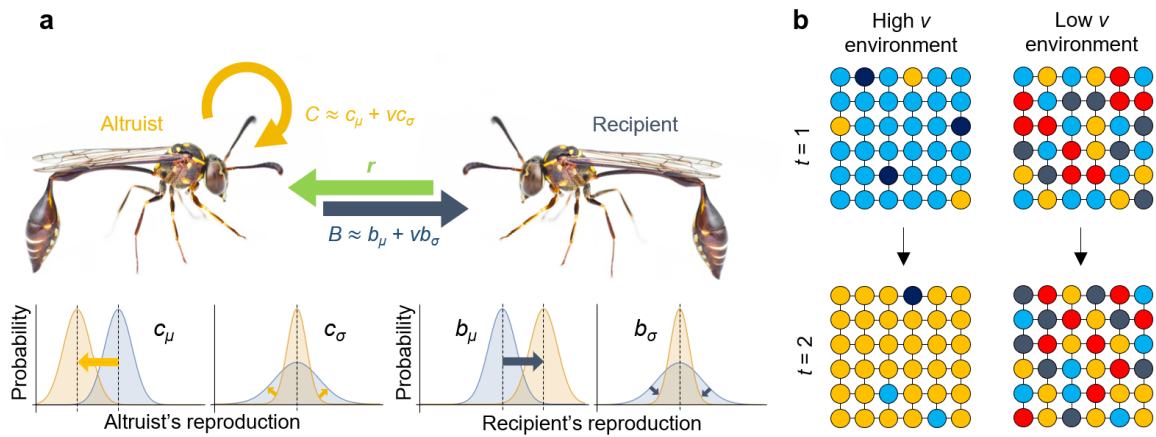


Figure 3.1 | Environmental stochasticity has been missing from models of social evolution. In the non-stochastic application of Hamilton's rule ($rb_\mu > c_\mu$) to real-world organisms (Bourke, 2014), recipients gain an increase in average reproductive success ($b_\mu > 0$) whereas actors suffer a decrease in average reproductive success ($c_\mu > 0$). **(a)** We derive an explicitly stochastic Hamilton's rule: $r(b_\mu + vb_\sigma) > c_\mu + vc_\sigma$. This shows that benefits can also arise by reducing the volatility of the reproductive success of the recipient ($b_\sigma > 0$), which depends on the magnitude of environmental stochasticity (v). An increase in the reproductive volatility of the actor ($c_\sigma > 0$) imposes a cost on the actor. Each effect represents a transformation of a probability distribution for reproductive success (bottom). Total benefits and costs (B and C) are measured in expected relative fitness (Gardner *et al.*, 2011). **(b)** Environmental stochasticity (v) is highest when spatial patches fluctuate in sync: for instance, if drought affects a randomly chosen patch Z , it should be likely that it also affects a randomly chosen patch Y (*Appendix A6*). Here, following Starrfelt and Kokko (2012), we represent patches in a lattice connected by dispersal. Colours denote environmental condition on patches at sequential time points t . See *Appendix A. Image of wasp reproduced with permission from Z. Soh.*

We note four predictions of the stochastic Hamilton's rule that differ from standard expectations:

1. Selection can favour altruism ($C > 0$) with zero increase to the recipient's mean fecundity ($b_\mu = 0$). Such a seemingly paradoxical lack of benefits is observed where additional helpers appear redundant (Dickinson and Hatchwell, 2004). Paradoxical helpers can be selected for by reducing the recipient's reproductive volatility if:

$$rb_\sigma > \frac{c_\mu}{v} + c_\sigma \quad (3.3)$$

2. Actors may be selected to harm the average reproductive success of their relatives ($b_\mu < 0$, $c_\mu > 0$). The harm is outweighed by a reduction in the recipient's reproductive volatility (*Figure 3.2*) if:

$$rb_\sigma > \frac{c_\mu - rb_\mu}{v} + c_\sigma \quad (3.4)$$

3. Altruists that reduce their recipients' reproductive volatility can be favoured by selection in the absence of environmental stochasticity, but only when population size (N) is low: in very small populations (Starrfelt and Kokko, 2012) or in small demes with negligible dispersal (Lehmann and Balloux, 2007). Effects on variance, σ^2 , not volatility, are used here for notational convenience (Appendix A5):

$$r \left(b_{\mu} + \frac{b_{\sigma^2}}{N\mathbb{E}_{\pi}[\bar{w}]} \right) > c_{\mu} + \frac{c_{\sigma^2}}{N\mathbb{E}_{\pi}[\bar{w}]} \quad (3.5)$$

4. Very strong altruistic effects ($b_{\sigma} \gg 0$) can undermine the success of the altruist genotype (Figure 3.3; Appendix B1–4). Altruists that substantially reduce their recipients' reproductive volatility spread rapidly. As successful altruists reach high frequencies, the coefficient of variation in average reproductive success ($v = \frac{\sigma_{\pi}[\bar{w}]}{\mathbb{E}_{\pi}[\bar{w}]}$) tends towards zero (Figure 3.4). When v is small, any b_{σ} has a small effect (Inequality 3.2), so altruistic bet-hedgers undermine the condition (high v) that favoured them (Figure 3.4a,b). This frequency-dependence can generate polymorphisms of altruists and defectors (Figure 3.4c), provided that allele frequency does not fluctuate intensively, which can otherwise destabilise the equilibrium (Figure 3.5) and lead to fixation (Lande, 2007).

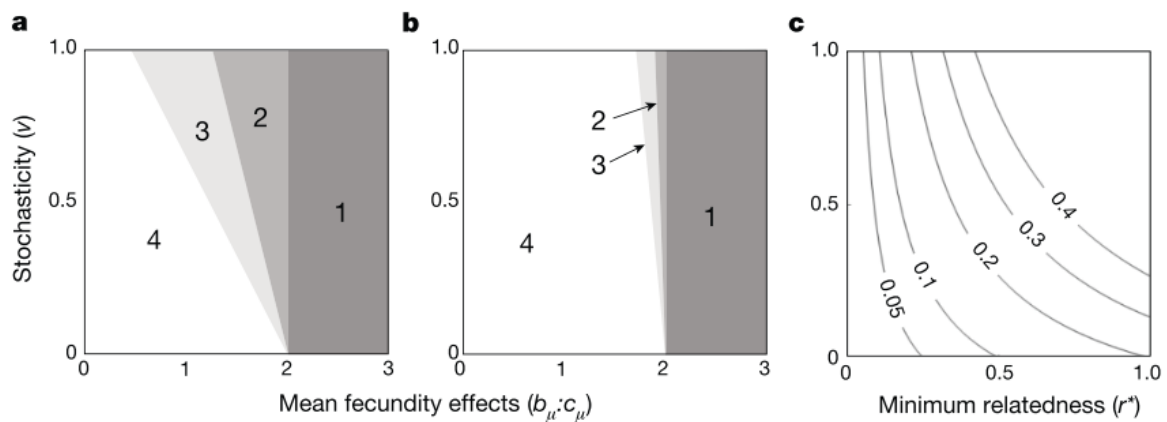


Figure 3.2 | Increased stochasticity can increase the potential for selection of altruistic behaviour. Without stochastic effects, altruism evolves when $rb_{\mu} > c_{\mu}$ (shown in region '1' in **a** and **b** for $c_{\mu} = 1$, and $r = 0.5$). As stochasticity v increases, the power of $b_{\sigma}:c_{\sigma}$ benefits increases, reducing the ratio of $b_{\mu}:c_{\mu}$ needed for the evolution of altruism. **(a)** In this scenario, altruists secure a high $b_{\sigma} = 0.75$, considerably increasing the scope for altruism (extending region '1' to region '2'). Actors may also reduce the volatility of their personal fecundity (here, $c_{\sigma} = -0.4$), reducing the magnitude of the total cost C below c_{μ} and increasing the potential for altruism further (extending to region '3'). Altruism is always deleterious in region '4'. **(b)** In this scenario, altruists secure a low $b_{\sigma} = 0.1$ and personal volatility reduction of $c_{\sigma} = -0.1$ (regions as in **a**). Comparing **a** ($b_{\sigma} = 0.75$) and **b** ($b_{\sigma} = 0.1$), larger reductions of recipient volatility (higher b_{σ}) result in larger increases in the inclusive fitness of the actor. **(c)** The minimum relatedness required for the evolution of altruism under different c_{μ} values (curved lines, from $c_{\mu} = 0.05$ to 0.4 , when $b_{\sigma} = 0.75$, $c_{\sigma} = 0$ and $b_{\mu} = 0.2$); as stochasticity (v) increases, the minimum required relatedness (r^*) decreases.

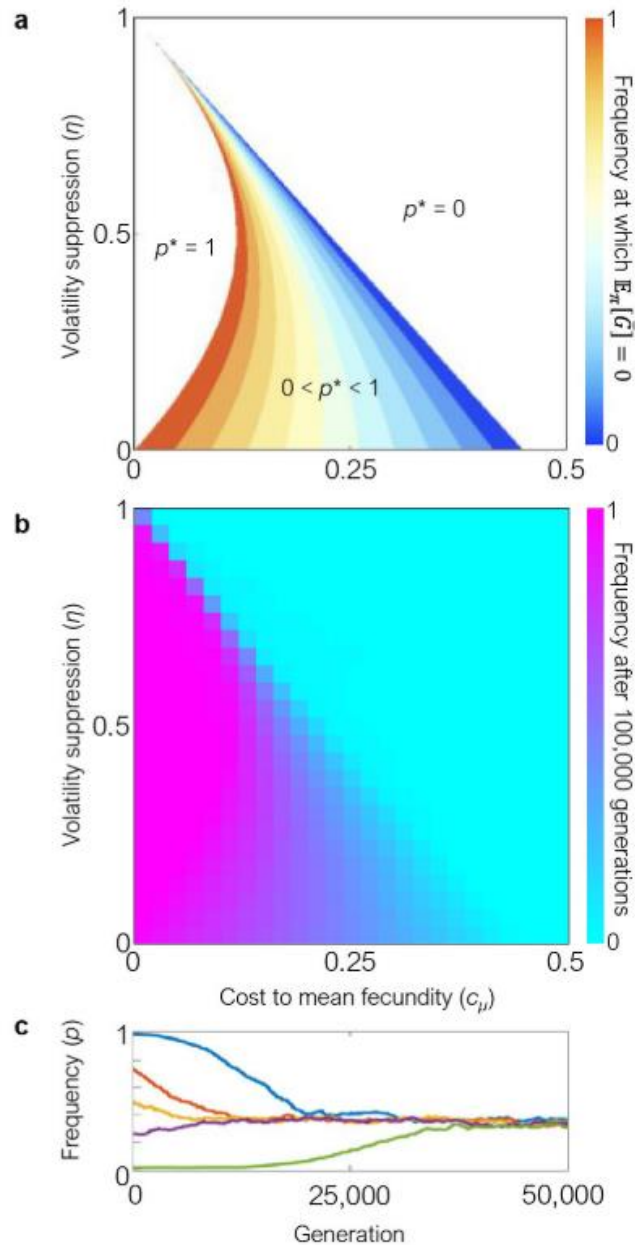


Figure 3.3 | The interaction between the frequency of altruists and the effectiveness of altruism. (a) The stochastic Hamilton's rule predicts that selection on volatility-suppressing altruism with fixed costs and benefits can generate negative frequency dependence and is sensitive to mild mean-fecundity costs (c_μ). We evaluate a population undergoing synchronous fluctuations to identify the frequency p^* at which there is no expected change in allele frequency. We illustrate the result with individual fecundities of 4 and 1 in good and bad years respectively. Relatedness is $r = 0.5$. **(b)** Simulated population outcomes (frequency after 100,000 generations) match predictions of the stochastic Hamilton's rule in **a**. Warmer colours (pink) denote higher polymorphic frequencies of altruists. In this haploid model (Appendix B), 1% of breeding spots are available each year for replacement by offspring that year: with such constraints on the magnitude of the response to selection, radical stochastic shifts in allele frequency over single generations do not occur, allowing the population to settle at equilibria where all alleles have equal expected relative fitness without being continually displaced (Figure 3.5). **(c)** Competing an altruistic allele against a defector allele reveals the action of frequency-dependent selection. Here, populations experiencing costs of $c = 0.2$ and $\eta = 0.466$ converge to $p^* = 0.359$ from any initial frequency (coloured lines show five starting frequencies from 0.001 to 0.999), as predicted by the stochastic Hamilton's rule.

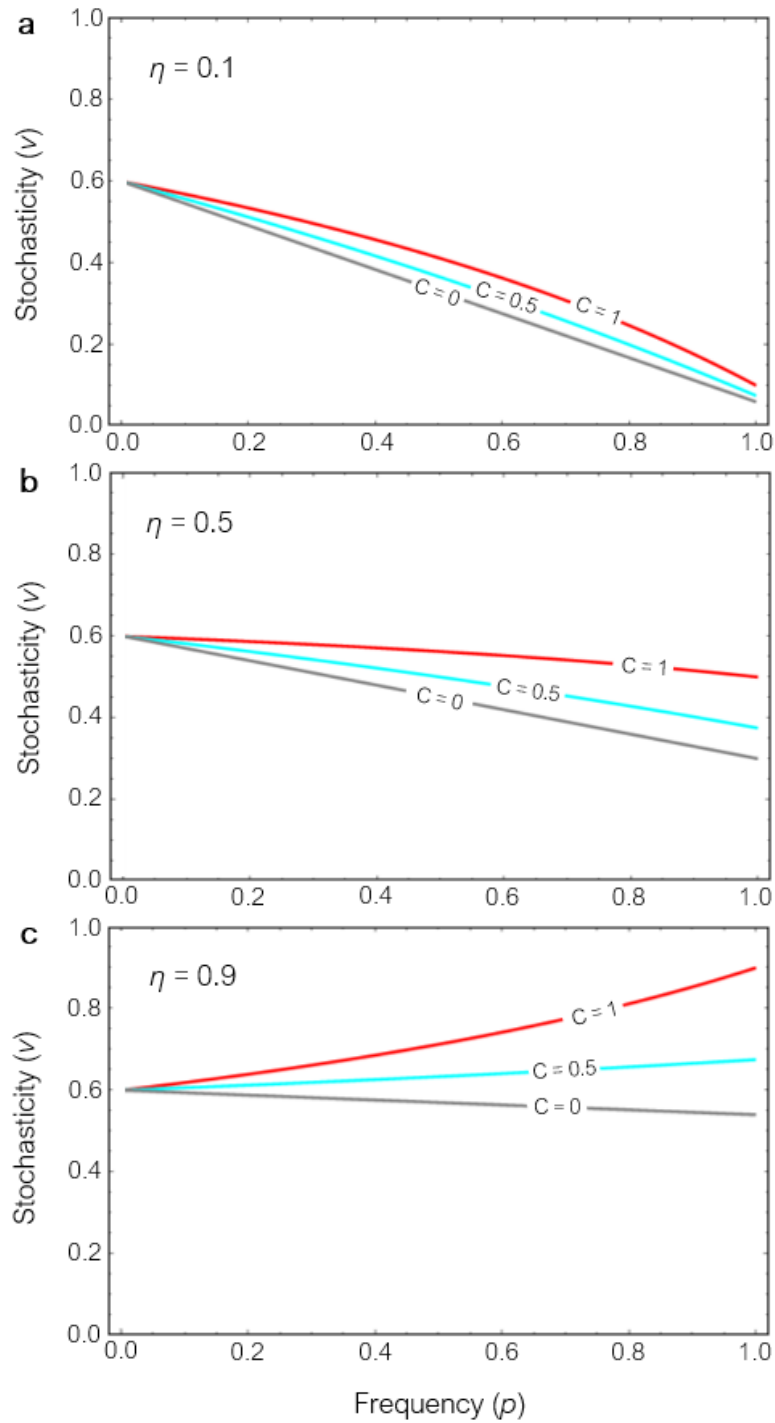


Figure 3.4 | **Stochasticity as a function of bet-hedger frequency.** Stochasticity $v = \frac{(p\eta + (1-p))\sigma_{00}}{\mu_{00} - pc}$ for the model of altruistic bet-hedging in Appendix B plotted against frequency (p) and cost (c) for three different values of η (where lower values of η denote greater buffering of recipients from the environment). **(a-b)** When η is small, representing high levels of volatility reduction, v declines steeply with p across the range of costs. **(c)** When η is large, the sign of the effect of p on v depends on c . Values of other parameters: $z_1 = 4$, $z_2 = 1$, $d = 0.5$.

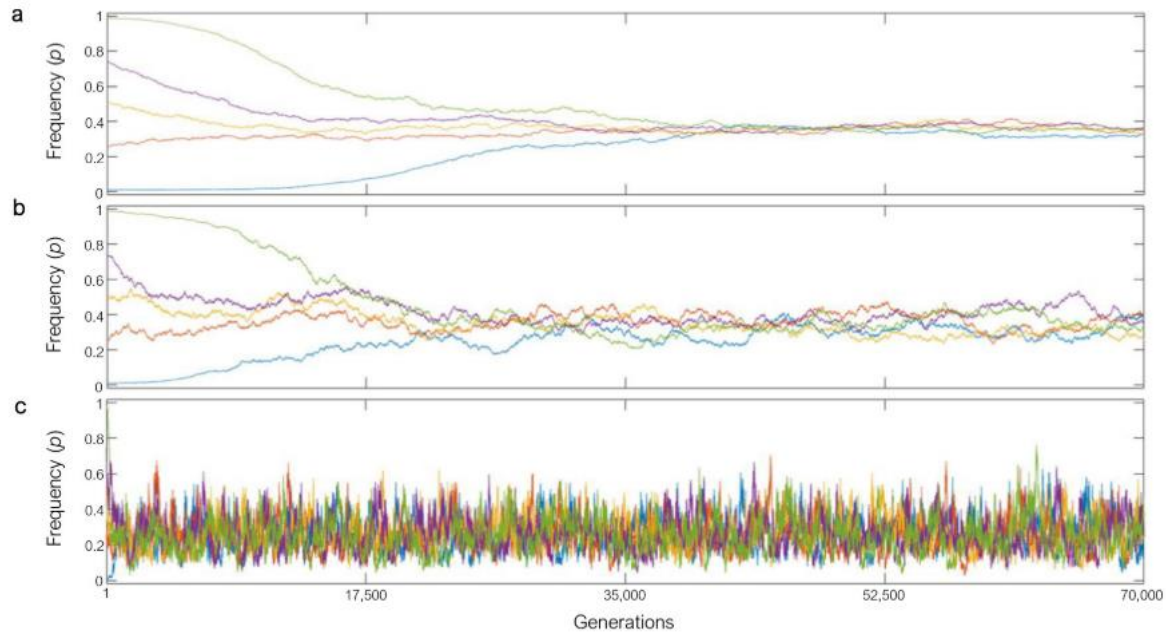


Figure 3.5 | Weak selection negates the capacity of temporal autocorrelation to drive the frequency of altruistic bet-hedgers away from the convergence frequency. Individual-based simulations from five different initial frequencies of an altruistic bet hedging allele (p) competing against a non-cooperator. **(a)** The population has zero temporal autocorrelation (environmental state in each generation is random). **(b)** The population has strong temporal autocorrelation (environmental state in the next generation has a 90% probability of remaining the same as in the current generation). Despite higher amplitude fluctuations, this population converges to the same point (from the five different starting frequencies) as the uncorrelated population **(a)**. **(c)** The same population is simulated with greater gene frequency changes (10% of the resident genotype frequencies are available to change each generation). The population is repeatedly carried to frequencies far from the convergence point. In this case, the utility of the stochastic Hamilton's rule is both identifying whether a given trait is immune from invasion by competitors, and identifying the expected generational change at each frequency p . Parameters are $z_1 = 4$, $z_2 = 1$, $\alpha = 0.5$.

Apparent reduction of recipient reproductive volatility (implying $b_{\sigma} > 0$) has been shown in starlings (Rubenstein, 2011), sociable weavers (Covas *et al.*, 2008), woodpeckers (Koenig and Walters, 2015), wasps (Wenzel and Pickering, 1991), and allodapine bees (Stevens *et al.*, 2007). We illustrate a volatility-reduction route to sociality with two examples. First, we consider sister–sister cooperation in facultatively-social insects (as in certain carpenter bees, where a means-based Hamilton’s rule is violated; Rehan *et al.*, 2014). In strongly stochastic environments, altruism could evolve between haplodiploid sisters when values of mean fecundity alone would predict it to be deleterious, as predicted by Inequality 3.2 (Figure 3.6a) and simulations of haplodiploid populations (Figure 3.6b; Appendix C1). Second, using published estimates of mean fecundity and high stochasticity in Galapagos mockingbirds (*Mimus parvulus*), we indicate how volatility effects could favour cooperative breeding even if helping increases the recipient’s average fecundity only as much as it reduces the actor’s ($c_{\mu} = b_{\mu}$; Figure 3.6c; Appendix C2).

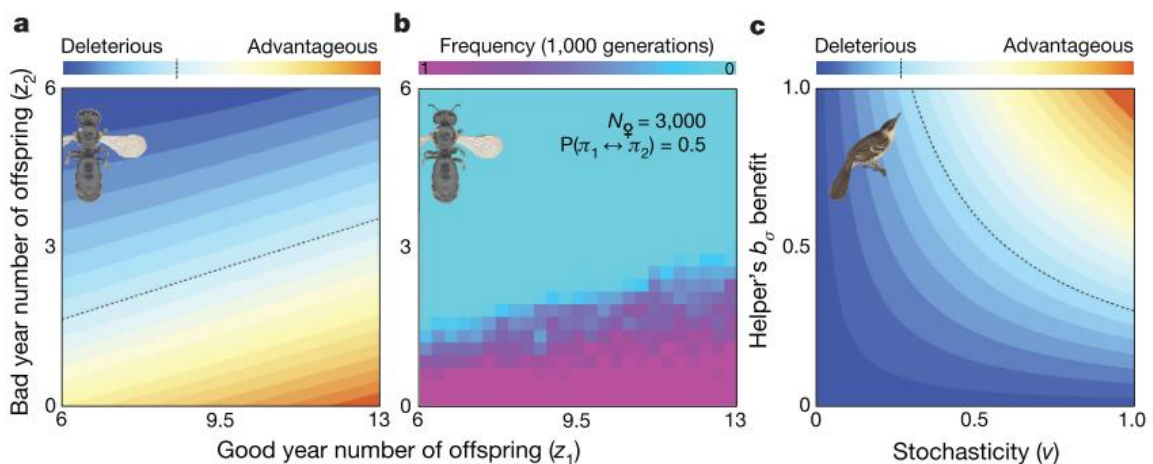


Figure 3.6 | Empirical studies of Hamilton’s rule may benefit from incorporating stochasticity. (a) Model of sister–sister cooperation between facultatively social insects: volatility effects can drive the invasion of altruists in regions of parameter space (below the dashed line) in which the means-based Hamilton’s rule ($rb_{\mu} > c_{\mu}$) is violated. **(b)** These predictions are matched in an individual-based haplodiploid simulation. In both **a** and **b**, good and bad years occur equally ($d_{\square} = 0.5$) at random. In Appendix B, we discuss temporal correlation. Coordinates plot average frequency across five replicate simulations after 1,000 generations, from an initial frequency $P = 0.05$. **(c)** In high-stochasticity conditions, helpers may buffer breeders from profound environmental fluctuations (Cockburn and Russell, 2011; Rubenstein, 2011). We estimate rb_{μ} values in the Galapagos mockingbird, and show that volatility effects can, in principle, drive cooperation (above the dashed line) even when mean fecundity costs c_{μ} cancel out b_{μ} (here, $b_{\mu} = c_{\mu} = 0.3$). See Appendix C. *Image of bee*, K. Walker (CC-BY 3.0 AU); *image of mockingbird*, Biodiversity Heritage Library (CC-BY 2.0).

Inequality 3.2 reveals three core conditions for altruistic bet-hedging. First, members of the non-altruistic genotype suffer synchronous fluctuations in lifetime reproductive success driven by environmental state (high v) that can be stabilised by sociality ($b_{\sigma} > 0$). Second, relatedness (r) is above

the threshold $r^* = \frac{c_\mu + v c_\sigma}{b_\mu + v b_\sigma}$. Third, actors either cannot predict environmental fluctuations or cannot generate phenotypes for different conditions (*Figure 3.7; Appendix B5*). If actors can obtain and utilise information at sufficiently low costs (rendering the environment predictable), plastic cooperation outcompetes constitutive cooperation (increasing b_μ and reducing c_μ).

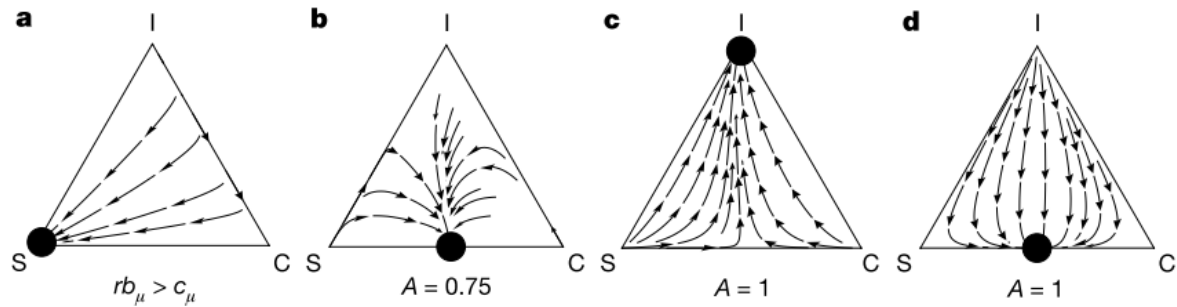


Figure 3.7 | The trade-off between constitutive and inducible altruism in a stochastic world depends on plasticity costs and information reliability. We show a population fluctuating randomly between a good and a bad environmental state, comprising three alleles: ‘selfish’ (S), for which the carriers never cooperate; ‘constitutive cooperators’ (C), for which the carriers always cooperate; and ‘inducible cooperators’ (I) for which the carriers cooperate only when they believe they are in the bad (low-fecundity) state. Information reliability is set by A (actors diagnose true state with probability A). Apexes represent monomorphic populations. Without social behaviour, individuals obtain four and one offspring in good and bad states respectively. Cooperation confers on recipients 1.5 additional offspring in bad states but reduces recipient fecundity by 0.2 offspring in good states, and costs actors 0.5 offspring in all states. **(a)** When considering only mean fecundity, the means-based Hamilton’s rule $rb_\mu > c_\mu$, commonly used empirically, mistakenly predicts that selfishness (S) will dominate. Under stochastic conditions, cooperation evolves. **(b)** Constitutive cooperators invade (until reaching a mixture of altruists and defectors) when information is imperfect ($A = 0.75$) and there is a plasticity cost (0.1 offspring). **(c)** When the reliability of information is increased ($A = 1$), plastic cooperators outcompete constitutive cooperators. **(d)** Increasing plasticity costs, however (here, from 0.1 to 0.3 offspring), eliminates plasticity benefits, enabling constitutive cooperators to invade. Vectors show directions of expected changes in frequencies: these represent continuous expected trajectories when frequencies are constrained to change by small amounts per generation. Relatedness $r = 0.5$ in all plots. Details are provided in Appendix B.

Synchronous fluctuations (high v) are generated when different patches within the population experience correlated environmental changes (*Figure 3.1b*). If offspring disperse across environmentally uncorrelated patches (Starrfelt and Kokko, 2012) but compete at a whole-population level, v falls. Likewise, iteroparity and long generations across different environmental conditions reduce v , whilst correlated exposure to environmental fluctuations within lifetimes increases v . For these reasons, Inequality 3.2 suggests that the most promising avenues to detect b_σ -driven sociality may occur among social microbes, which can experience: (i) population-wide fluctuations (high v); (ii) short generations (high v); (iii) competing clones (high r); and (iv) opportunities to confer homeostasis

on others ($b_{\sigma} > 0$), including through the construction of biofilms (Lowery *et al.*, 2017) and incipiently-multicellular clusters withstanding profound abiotic and biotic stress.

We have shown that altruistic effects on recipient volatility are visible to selection. Significantly, Hamilton's rule identifies ultimate payoffs by incorporating any effects of population structure (Gardner *et al.*, 2011). To make case-specific predictions, researchers should, accordingly, utilise explicit information on population structure and ecology. The empirical challenge to detect volatility-suppressing sociality will best be met using tailored models guided by field data for specific scenarios, led by the general framework of inclusive fitness theory (Gardner *et al.*, 2011; Bourke, 2014a; Birch, 2017). In summary, Hamilton's rule reveals the action of selection under stochasticity: shielding relatives from a volatile world can drive the evolution of sociality.

Table 3.1 | Parameters of the model

Notation	Definition	Expression
N	Population size	–
w_x	Number of surviving offspring (reproductive success) of the x th individual	–
\bar{w}	Mean reproductive success in the population	–
π	Environmental state within the set of states Π	–
G_x	Genetic value of individual x	–
r	Relatedness	β_{G_y, G_x}
z_x	Trait value of individual x	–
$\ll^k \bar{w} \gg$	k th central moment of \bar{w} across Π	$\mathbb{E}_\pi[(\bar{w} - \mathbb{E}_\pi[\bar{w}])^k]$
$\ll w_x, {}^k \bar{w} \gg$	k th mixed moment of reproductive success of individual x and \bar{w} across Π	$\mathbb{E}_\pi[(w_x - \mathbb{E}_\pi[w_x])(\bar{w} - \mathbb{E}_\pi[\bar{w}])^k]$
ν	Stochasticity of the environment	$\frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}$
ρ_x	Correlation between w_x and \bar{w} across Π	$\frac{\mathbb{E}_\pi[w_x \bar{w}] - \mathbb{E}_\pi[w_x] \cdot \mathbb{E}_\pi[\bar{w}]}{\sigma_\pi[w_x] \sigma_\pi[\bar{w}]}$
B	Total benefit in Hamilton's rule under stochasticity	$\beta_{\mathbb{E}_\pi[\frac{w_y}{\bar{w}}], G_x}$ Partial regression of a focal individual's genetic value on a social partner's expected relative fitness
C	Total cost in Hamilton's rule under stochasticity	$-\beta_{\mathbb{E}_\pi[\frac{w_x}{\bar{w}}], G_x}$ Partial regression of a focal individual's genetic value on its own expected relative fitness
b_μ	Mean fecundity benefit in stochastic Hamilton's rule	$\beta_{\mathbb{E}_\pi[w_y], G_x}$ Partial regression of a focal individual's genetic value on a social partner's expected number of offspring. We make use of the identity $\beta_{\mathbb{E}_\pi[w_y], G_x} = \beta_{\mathbb{E}_\pi[w_x], G_y}$ in non-class-structured populations.
c_μ	Mean fecundity cost in stochastic Hamilton's rule	$-\beta_{\mathbb{E}_\pi[w_x], G_x}$ Partial regression of a focal individual's genetic value on its own expected number of offspring

b_σ	Volatility-suppressing benefit in stochastic Hamilton's rule	$-\beta_{\rho\sigma\pi[w_y],G_x}$ Partial regression of a focal individual's genetic value on a partner's standard deviation in reproductive success, where the standard deviation is weighted by its correlation with \bar{w} . We make use of the identity $\beta_{\rho\sigma\pi[w_y],G_x} = \beta_{\rho\sigma\pi[w_x],G_y}$ in non-class-structured populations
c_σ	Volatility-suppressing cost in stochastic Hamilton's rule	$\beta_{\rho\sigma\pi[w_x],G_x}$ Partial regression of a focal individual's genetic value on a partner's standard deviation in reproductive success, where the standard deviation is weighted by its correlation with \bar{w}
b_k	k th moment benefit in stochastic Hamilton's rule	$\beta_{\langle\langle w_y, k\bar{w} \rangle\rangle, G_x}$ Partial regression of a focal individual's genetic value on the k th mixed moments of a partner's joint distribution for reproductive success w_y and population average reproductive success \bar{w} . We make use of the identity $\beta_{\langle\langle w_x, k\bar{w} \rangle\rangle, G_y} = \beta_{\langle\langle w_y, k\bar{w} \rangle\rangle, G_x}$ in non-class-structured populations
c_k	k th moment cost in stochastic Hamilton's rule	$-\beta_{\langle\langle w_x, k\bar{w} \rangle\rangle, G_x}$ Partial regression of a focal individual's genetic value on the k th mixed moments of its own joint distribution for reproductive success w_y and population average reproductive success \bar{w} .



This page: Defence postures
by young (black-eyed) *Polistes*
canadensis at Fort Sherman,
Panama.
Photograph: PK.

Chapter 4

4 | Demographic influences on altruistic bet-hedging

4.1 Chapter Summary

When faced by traits that appear deleterious to their bearer's expected reproductive success, biologists often turn to 'bet-hedging' explanations. Bet-hedging theory argues that traits that reduce an individual's expected reproductive success can still be favoured by selection if they sufficiently reduce the uncertainty of reproductive success. In Chapter 3, I showed how bet-hedging theory can be extended to social behaviour. Actors can increase their inclusive fitness by buffering relatives from unpredictable fluctuations in reproductive success, without providing any increase to the expected number of offspring produced by relatives. However, despite widespread speculation that these altruistic bet-hedging effects may be fundamental drivers of sociality amongst insects, birds, and mammals, the ecological conditions that favour sociality in volatile environments remain unclear. In this chapter, I argue that whether altruistic bet-hedging is favoured by selection depends crucially on demography (the structure of the population). Specifically, I use the 'stochastic Hamilton's rule' of the previous chapter to illustrate how two fundamental factors – the spatial scale of environmental fluctuation and the spatial scale of competition – can exert a profound influence over selection for social behaviour in a volatile world.

"Populations are usually viscous and subdivided." (Hamilton, 1972)

4.2 Introduction

Volatile environments can drive the evolution of ‘bet-hedging’ traits (Gillespie, 1974a, 1977), which stabilise their carrier’s fluctuating reproductive success at the cost of reducing their expected reproductive success. Recent speculation has focussed on a possible link between bet-hedging and altruism (Rubenstein, 2011; Cockburn and Russell, 2011): altruists may be able to stabilise the fluctuating reproductive success of relatives, driving the evolution of sociality without necessarily increasing the relatives’ expected reproductive successes. However, selection for bet-hedging traits is crucially determined by demography (Starrfelt and Kokko, 2012). A rich knowledge of demographic influences on non-social bet-hedging has developed in the theoretical literature (Rice and Papadopoulos, 2009; Starrfelt and Kokko, 2012; Schreiber and Moore, 2017; Xue and Leibler, 2017). In this chapter, I focus on extending these principles to social evolution. Specifically, I use the ‘stochastic Hamilton’s rule’ of Chapter 3 to illustrate how two demographic factors – (1) the spatial scale of environmental fluctuation and (2) the spatial scale of competition – can exert considerable influences over the success of social forms of bet-hedging.

A stronger appreciation of demographic influences on bet-hedging may carry wide empirical implications in biology. Bet-hedging is now frequently invoked as an explanation for a remarkable range of social and non-social traits (*Table 4.1*), ranging from avian cooperative breeding (Shen *et al.*, 2017; Guindre-Parker and Rubenstein, 2018) to cancer vascularisation (Gravenmier *et al.*, 2018). In each case, subtle effects of demography may exert considerable influence over the viability of the bet-hedging hypothesis. In particular, two core demographic principles have been established for selection in volatile environments:

1. **Metapopulations are better than panmictic populations at sustaining polymorphisms:** metapopulations of demes connected by some degree of dispersal reduce the probability of one allele going extinct (or fixating) due to a stochastic event (Gillespie, 1974b, 1978; Frank and Slatkin, 1990; Starrfelt and Kokko, 2012).
2. **Bet-hedging can evolve due to demographic stochasticity in large populations, but only if the population is structured into small demes with strong local competition** (Lehmann and Balloux, 2007). When between-deme dispersal occurs after density-dependent regulation within demes (local competition), dispersal has no effect on the outcome of selection: density-dependent regulation completely controls the outcome (Shpak and Proulx, 2007).

Table 4.1 | A sample of recently proposed bet-hedging traits in fields across evolutionary biology (2017–2018)

Trait	Taxa	References
Cooperative breeding	Birds	Shen <i>et al.</i> (2017); Guindre-Parker and Rubenstein (2018)
Reproductive mode	Jellyfish	Schnedler-Meyer <i>et al.</i> (2018)
Clutch size	Frogs	Chen <i>et al.</i> (2018)
Seed germination	Plants	Cuello <i>et al.</i> (2018)
Hormone signalling	Plants	Johnston and Bassel (2018)
Extra-pair paternity	Birds	Yasui and Yoshimura (2018)
Irrationality	Humans	Brennan <i>et al.</i> (2018)
Sex differences	General	Wilkins and Bhattacharya (2018)
Embryology	Polychaetes	Thonig <i>et al.</i> (2017)
Migration routes	Birds	Blackburn <i>et al.</i> (2017)
Social slug formation	Slime moulds	Martínez-García and Tarnita (2017)
Blood supply to cancer	Humans	Gravenmier <i>et al.</i> (2017)
Hatching time	Shrimp	Pinceel <i>et al.</i> (2017)
Egg size	Fish	Shama (2017)
Antibiotic production	Bacteria	Bayramoglu <i>et al.</i> (2017)

Some authors have considered potential links between demography, stochasticity, and social evolution. Levin and Kilmer (1974) and Lehmann *et al.* (2006), for instance, modelled social behaviour in the context of environmental stochasticity in a deme-structured population, although in these models environmental stochasticity entails the complete stochastic destruction of the home deme: actors can invest to reduce the probability that their home deme goes extinct (influencing the fitness of all deme-mates). This is not the sense in which I use environmental stochasticity here, where environmental state is free to fluctuate on a continuous scale within demes: altruists can intervene to reduce the exposure of individual social partners to the fluctuating environment. However, altruism to prevent deme extinction can be seen as an extreme form of volatility-suppressing cooperation: (1) the actor influences the fitness of all deme-mates rather than a specific social partner and (2) environmental stochasticity is extreme and binary (*i.e.*, complete deme extinction versus complete deme survival).

Subsequently, Lehmann and Balloux (2007) modelled *demographic* stochasticity in a deme-structured population, and investigated a potential link between kin selection and stochasticity by exploring how local stochasticity can influence relatedness. Deme-level stochasticity can cause the stochastic extinction of lineages within the deme, inflating relatedness and potentially providing a more

favourable context for kin-selected altruism (Lehmann and Balloux, 2007). Various effects of stochasticity on relatedness have been proposed: for instance, Uyenoyama (1979) highlighted that stochasticity in migration could generate between-deme differences in relatedness. Here, however, I focus on the benefit term in Hamilton's rule, and leave stochastic effects on within-deme relatedness implicit.

In this chapter, I begin to extend to altruistic bet-hedging the key principles developed for non-social bet-hedging against both environmental and demographic stochasticity in a deme-structured population (Frank and Slatkin, 1990; Shpak and Proulx, 2007).

4.3 Grain size of environmental fluctuation

In Chapter 3, I showed that whether altruistic bet-hedging is favoured by selection is determined by a 'stochastic Hamilton's rule':

$$r(b_\mu + vb_\sigma) > c_\mu + vc_\sigma \quad (4.7)$$

where r is relatedness, b_μ is any increased expected absolute fitness of a recipient, b_σ is any decreased recipient uncertainty in absolute fitness, c_μ is any reduced expected absolute fitness of the actor, and c_σ is any increased uncertainty in the actor's absolute fitness. v is the coefficient of variation in population average reproductive success \bar{w} . v is larger when different areas inhabited by the population fluctuate in sync between environmental states. In this section, I show that selection on b_σ and c_σ is greatest when there is a strong correlation in environmental conditions between different spatial areas (high v).

The magnitude of the stochasticity coefficient v depends on the correlation amongst individuals in their exposure to all conditions of the environment. Accordingly, when individuals are distributed across different microenvironments, the degree of correlation in environmental state across microenvironments influences the magnitude of v . Here, I illustrate this principle in a population divided into multiple microenvironments.

Let the population undergoing global competition be distributed across a total of M microenvironment patches, each of which samples its local environmental 'microstate' from an identical distribution. Population-wide environmental state π is, in effect, a specific combination of microstates across a network of spatial patches inhabited by a population. Assuming there are equal numbers of individuals in each patch, the whole-population average reproductive success \bar{w} is equal to the mean of the mean reproductive success \bar{w}_m in each patch m :

$$\bar{w} = \frac{1}{M} \sum_{m=1}^M \bar{w}_m \quad (4.8)$$

Since the scale of competition is the whole population, the stochasticity coefficient v is obtained as the coefficient of variation in whole-population average reproductive success \bar{w} :

$$v = \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]} = \frac{\sigma_\pi \left[\frac{1}{M} \sum_{m=1}^M \bar{w}_m \right]}{\mathbb{E}_\pi \left[\frac{1}{M} \sum_{m=1}^M \bar{w}_m \right]} \quad (4.9)$$

We assume that every patch samples its microstate from an identical distribution with a mean of $\mathbb{E}_\pi[\bar{w}_m] = \mathbb{E}_\pi[\bar{w}]$ and a variance of $\mathbb{V}_\pi[\bar{w}_m]$, but patches can be correlated or uncorrelated in their samples from this distribution. The variance of \bar{w} (*i.e.*, $\sigma_\pi[\bar{w}]^2$) can then be obtained using the general formula for the variance of a mean (since \bar{w} is the mean of a total of M patches, each with its own \bar{w}_m in a particular state π of the population):

$$\mathbb{V}_\pi[\bar{w}] = \mathbb{V}_\pi \left[\frac{1}{M} \sum_{m=1}^M \bar{w}_m \right] = \left(\frac{1}{M} + \frac{M-1}{M} \bar{\rho} \right) \mathbb{V}_\pi[\bar{w}_m] \quad (4.10)$$

$\bar{\rho}$ denotes the average between-patch correlation in average reproductive success \bar{w}_m . As patch number M approaches infinity, this whole-population variance $\mathbb{V}_\pi[\bar{w}]$ converges to a simple function of $\bar{\rho}$ and the within-patch variance $\mathbb{V}_\pi[\bar{w}_m]$ in average reproductive success:

$$\lim_{M \rightarrow \infty} \mathbb{V}_\pi[\bar{w}] = \bar{\rho} \cdot \mathbb{V}_\pi[\bar{w}_m] \quad (4.11)$$

$\mathbb{V}_\pi[\bar{w}]$ is the square of the numerator of v . Therefore, in a population distributed over many patches, v can be defined as follows, where v_m is the coefficient of variation in average reproductive success within a single patch (*i.e.*, patch-level stochasticity, $v_m = \frac{\sigma_\pi[\bar{w}_m]}{\mathbb{E}_\pi[\bar{w}_m]}$):

$$\lim_{M \rightarrow \infty} v = \frac{\sqrt{\bar{\rho} \cdot \mathbb{V}_\pi[\bar{w}_m]}}{\mathbb{E}_\pi[\bar{w}_m]} = \frac{\sigma_\pi[\bar{w}_m]}{\mathbb{E}_\pi[\bar{w}_m]} \cdot \sqrt{\bar{\rho}} = v_m \sqrt{\bar{\rho}} \quad (4.12)$$

Equation 4.12 shows that whole-population stochasticity v approaches within-patch stochasticity v_m as between-patch correlation approaches 1 (full correlation). This illustrates the fundamental point, emphasised by Starrfelt and Kokko (2012) for non-social bet-hedging, that selection on variation effects (b_σ and c_σ in Inequality 4.7) is driven by whole-population environmental fluctuation when the scale of competition is at the level of the whole population (global competition), and that the ‘grain size’ (Starrfelt and Kokko, 2012) of environmental fluctuation (the size of completely correlated areas of the population) is key in determining the strength of selection.

4.4 The spatial scales of competition and fluctuation

In Chapter 3 and the previous section, I followed the familiar assumption (both in the literature on Hamilton’s rule and the literature on bet-hedging) that the boundaries of the population are the same as the boundaries of the scale of competition (Gardner *et al.*, 2011; Starrfelt and Kokko, 2012; Schreiber, 2015). In this scenario, the actor’s offspring compete for places in the next generation with the whole population. It is then irrelevant whether the actor happens to live in an area in which others produce disproportionately more offspring than elsewhere. Neighbours are not more directly in competition with the actor than individuals living in foreign areas.

Here, I relax this assumption. The previous work implicitly assumed no extra competition within spatial areas. Let a ‘deme’ be defined broadly as a subpopulation living in a specific area. In this section, I allow density regulation to occur at the scale of individual demes before dispersal. I show that local fluctuations can select for altruistic bet-hedging (both individual and altruistic) *if and only if* density-regulation occurs at least partially at the deme scale. This extends the insights of Shpak and Proulx (2007) from non-social bet-hedging to altruistic bet-hedging *sensu* Chapter 3. For clarity, I will begin by presenting the main results concerning the interaction of the spatial scales of competition and fluctuation, and then explain how each result is derived.

4.4.1 Environmental stochasticity

The first main result is the form taken by the stochastic Hamilton’s rule when the spatial scales of competition and fluctuation are made explicit (by giving them their own coefficients). For a population consisting of demes that are free to fluctuate independently in local environmental state, I find that a trait is expected to spread in the population due to selection if the following inequality is satisfied:

$$r \left(\overbrace{b_\mu + \underbrace{av^\bullet b_\sigma^\bullet}_{\text{Local risk benefit}} + \underbrace{(1-a)v^\circ b_\sigma^\circ}_{\text{Global risk benefit}}}_{\text{Total Hamiltonian benefit (B)}} \right) > \overbrace{c_\mu + \underbrace{av^\bullet c_\sigma^\bullet}_{\text{Local risk cost}} + \underbrace{(1-a)v^\circ c_\sigma^\circ}_{\text{Global risk cost}}}_{\text{Total Hamiltonian cost (C)}} \quad (4.13)$$

This further unpacking of Hamilton’s rule makes explicit the two demographic parameters we are interested in (*Figure 4.1*): the spatial scale of competition (determined by a) and the spatial scale of environmental fluctuation (determined by v^\bullet and v°). First, the parameter a denotes the spatial scale of competition, here split across two levels: competition for limited spaces in the next generation occurring (1) against local deme-members and (2) against any individual from the global population.

Higher α means that competition is more local; lower α means that competition is more global. Second, Inequality 4.13 captures the spatial scale of environmental fluctuation, using the coefficients v^\bullet and v° . Whereas in the previous chapter I used a single measure of stochasticity (v) for the whole population, in Inequality 4.13 I split the influences on stochasticity (as experienced by a focal individual) into local (v^\bullet) and global (v°). Informally (formal definitions are provided in ‘*Derivation*’ below), local influences on stochasticity are fluctuations in average reproductive success on the local deme: as local fluctuations become more profound, v^\bullet rises in value. Likewise, global influences on stochasticity are fluctuations in average reproductive success across the whole population: as global fluctuations become stronger, v° rises in value.

r denotes relatedness (relative to the actor’s competitors). As in Chapter 3, b_μ denotes the actor’s effect on the expected reproductive success of a recipient and c_μ the actor’s effect on its own expected reproductive success. However, the terms dealing with the actor’s effects on reproductive volatility (b_σ^\bullet , b_σ° , c_σ^\bullet , and c_σ°) are now slightly subtler than previously. Throughout this chapter, ‘ \bullet ’ is used to denote ‘local’ and ‘ \circ ’ is used to denote ‘global’. As in Chapter 3, the volatility terms denote the actor’s effects on its own reproductive volatility and the reproductive volatility of the recipient, where volatility is the standard deviation in the focal individual’s reproductive success multiplied by how much its reproductive success correlates with any fluctuations in the average reproductive success amongst its competitors.

The biological implication of Inequality 4.13 is that an organism inhabiting a population structured into independently-fluctuating demes can profitably buffer its relatives from environmentally-driven fluctuations in average reproductive success on the local deme ($v^\bullet > 0$) even at a personal cost to its expected reproductive success ($c_\mu > 0$). If an ecologist surveys a population through the generations and shows no fluctuations in average reproductive success (where the average is taken across all individuals in the population), they would be correct in concluding that there are no global influences on stochasticity. In Inequality 4.13, this means that v° (the term capturing global stochasticity) is equal to zero. At a local level, however, independent demes may be fluctuating considerably in their average reproductive success, each driven by local environmental effects. Some demes might be experiencing a local explosion in disease, others an unexpected fall in predator abundance, others an unexpected rise in predator abundance, still others a rare increase in a favourable food item, and so on through myriad combinations of environmental conditions. To simplify the interpretation, Inequality 4.13 assumes that all demes sample their environmental state from a common distribution. In other words, when each deme is considered independently, the probability that it is currently in each of the environmental states is the same for all demes. Very few demes may be experiencing a food bonanza,

but all demes had the same probability that it would occur. This assumption is not strictly necessary, and I provide a more general expression that allows for demes to differ in their probabilities of being in each state in the ‘*Derivation*’ section (page 77). However, committing to this assumption helps to simplify the expression, and therefore to illustrate the central point: when there is selection on altruistic bet-hedging, the spatial scales of competition and fluctuation exert strong influences on the outcome.

The biological intuition underlying this point is that bet-hedging alleles only gain their advantage during periods when their competitors are suffering poor average reproductive success; at these moments, the increase to the bet-hedger’s relative fitness is enough to offset any decreases to relative fitness caused by a lower expected reproductive success. It is crucial, then, that bet-hedgers experience a fluctuating background (average reproductive success amongst their competitors) in order to secure these benefits during episodes of harsh environmental states. If demes are fluctuating independently ($v^* > 0$) in a globally non-fluctuating population ($v^\ominus = 0$), and competition is global ($a = 0$), there is no scope for bet-hedging. On the other hand, as competition becomes increasingly local (*i.e.*, as a gets closer to 1), the bet-hedgers find themselves against a fluctuating background of competitors, and begin to gain the critical advantage.

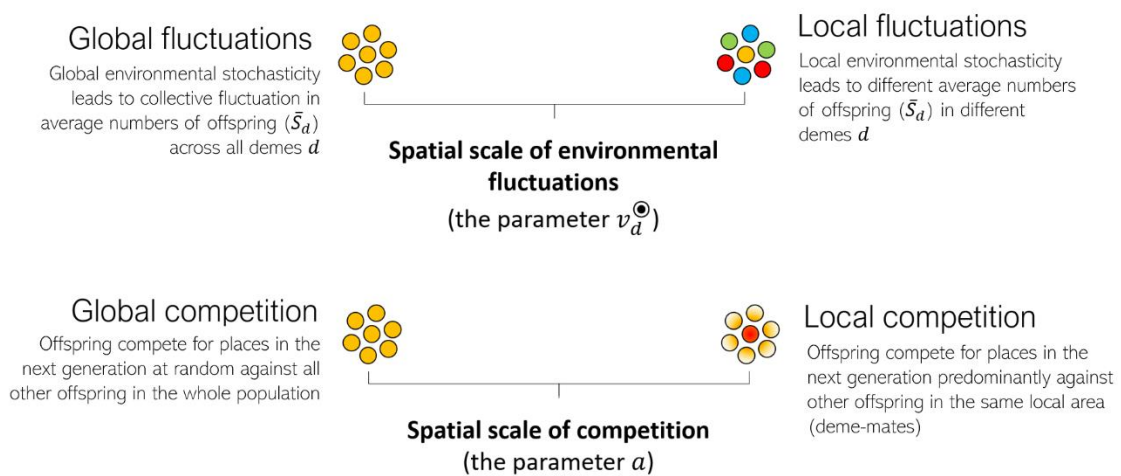


Figure 4.1 | Two key aspects of demography determine the power of selection on bet-hedging, both non-social and altruistic: (upper panel) the spatial scale of environmental fluctuations; (lower panel) the spatial scale of competition.

4.4.2 Demographic stochasticity

The second main result in this section is the form taken by Hamilton's rule when individual demes experience no *environmental* fluctuations but individuals within the demes independently experience unpredictability in their reproductive successes around some central value. By chance, some individuals do well; also, by chance, others do poorly. This situation is one of pure *demographic* (as opposed to *environmental*) stochasticity. Because individuals are exposed to stochastic variation, the average reproductive success within demes can fluctuate stochastically – provided that the number of individuals in the deme (N_d) is small enough that individual-level fluctuations can exert a meaningful influence over the deme's average reproductive success (Melbinger and Vergassola, 2015). For this reason, N_d now appears in the condition for selection when we derive the stochastic Hamilton's rule for demographic stochasticity in a deme-structured population:

$$r \left(b_\mu + \frac{a}{N_d} \frac{b_{\sigma^2}^\bullet}{\mathbb{E}_\pi[\bar{S}_g]} \right) > c_\mu + \frac{a}{N_d} \frac{c_{\sigma^2}^\bullet}{\mathbb{E}_\pi[\bar{S}_g]} \quad (4.14)$$

Local risk benefit
Local risk cost

$\mathbb{E}_\pi[\bar{S}_g]$ is the expected average reproductive success across the whole population. I provide formal definitions of $c_{\sigma^2}^\bullet$ and $b_{\sigma^2}^\bullet$ in detail in the derivation below, but, informally, they describe the actor's effects on its own and its recipient's variances in reproductive success respectively. In these coefficients, there is no correlation term, by definition: demographic stochasticity is defined by individuals experiencing stochastic variation in reproductive success independently of one another. $c_{\sigma^2}^\bullet$ and $b_{\sigma^2}^\bullet$ are the direct and simple effects on the variance in reproductive success. In a situation of pure demographic stochasticity, one individual may unexpectedly produce more offspring than normal; by chance, another individual might also produce unexpectedly more offspring than normal, but these two individuals are enjoying entirely unconnected episodes of good luck. Here, there is no underlying environmental cause that leads to correlated fluctuation across individuals. Inequality 4.14 is very similar to the result we derived in Chapter 3 (Inequality 3.5) for demographic stochasticity in a single population with global competition (*i.e.*, where $N_d = N$).

The biological implication of Inequality 4.14 is that a social organism can profitably buffer its close relatives (high r) from stochastic variation in reproductive success ($b_{\sigma^2}^\bullet > 0$) even when individuals sample their reproductive success independently of other individuals. However, unlike the environmental stochasticity described by Inequality 4.13, this situation occurs only under restrictive biological conditions, which we might expect to be rare. Specifically, competition must occur locally

($a > 0$) within demes of very small size (small N_d). Accordingly, Inequality 4.14 highlights in a social setting the key point established for non-social bet-hedging traits by Shpak and Proulx (2007) and Lehmann and Balloux (2007): demographic stochasticity can drive bet-hedging when deme size (N_d) is small. As the number of individuals on the deme rises (high N_d), the fraction $\frac{a}{N_d}$ (which determines the viability of volatility-suppressing altruism under conditions of pure *demographic* stochasticity) goes towards zero, eliminating the importance of volatility effects and restoring Hamilton's rule to the means-only form commonly used empirically ($rb_\mu > c_\mu$).

Inequalities 4.13 and 4.14 emphasise one of the key points I argued in Chapter 3, this time in the context of a deme-structured population: *environmental* stochasticity is likely to be a much more powerful driver of altruistic bet-hedging than *demographic* stochasticity. In the next section, I provide derivations of these two inequalities.

4.4.3 Derivation

In this section, I provide derivations of Inequality 4.13 and of Inequality 4.14 in turn. Here, I apply the multilevel Price equation⁶ (Price, 1972) to the context of individuals i within demes d (subpopulations). In this context, the multilevel Price equation states that the change in the average breeding value for a trait of interest is the sum of between-deme selection (given by the covariance between deme-level fitness and average breeding value for the deme) and within-deme selection (given by the expected covariance between individual fitness and individual breeding value, across demes):

$$\Delta \bar{G} = \underbrace{\mathbb{C}_d \left(\frac{\bar{W}_d}{\bar{w}}, \bar{G}_d \right)}_{\text{Between-deme selection}} + \underbrace{\mathbb{E}_d \left[\mathbb{C}_i \left(\frac{W_{id}}{\bar{w}}, G_{id} \right) \right]}_{\text{Within-deme selection}} \quad (4.15)$$

G denotes breeding value for the trait of interest. As in Chapter 3, this might, for instance, be $G = 1$ for carriers of an allele and $G = 0$ for non-carriers. d denotes the identity of the deme ($d \in D$). Every individual in the population has its own breeding value. G_{id} denotes the breeding value of the i th individual within deme d . The average of breeding values for the deme d is denoted \bar{G}_d . w_{id} is the absolute fitness of the i th individual in the deme d . The average of all w_{id} within the deme d is \bar{w}_d . \bar{w} is the average absolute fitness across demes ($\bar{w} = \frac{1}{D} \sum_{d=1}^D \bar{w}_d$), which is also the average absolute

⁶ The well-known derivation of the multilevel Price equation (Okasha, 2004; Frank, 2012; Gardner, 2015c) is provided in Appendix D (page 253).

fitness across all N individuals ($\bar{w} = \frac{1}{N} \sum_{d=1}^D \sum_{i=1}^{N_d} w_{id}$) in the special case in which demes are equal in size (*i.e.*, when N_d is the same for all demes d).

Accordingly, we can account for stochasticity by taking the expectation of Equation 4.15 to obtain the condition for an expected increase in average breeding value ($\mathbb{E}_\pi[\Delta\bar{G}] > 0$), meaning that selection favours the trait of interest on average across states of the environment:

$$\underbrace{\mathbb{C}_d \left(\mathbb{E}_\pi \left[\frac{\bar{w}_d}{\bar{w}} \right], \bar{G}_d \right)}_{\text{Expected between-deme selection}} + \underbrace{\mathbb{E}_d \left[\mathbb{C}_i \left(\mathbb{E}_\pi \left[\frac{w_{id}}{\bar{w}} \right], G_{id} \right) \right]}_{\text{Expected within-deme selection}} > 0 \quad (4.16)$$

To capture the tension between local and global competition, we introduce an element of density-dependence: it is harder to raise an offspring successfully to maturity when doing so requires struggling against a large number of other competitors locally. There are various ways of incorporating density-dependence into models of social evolution (van Dyken, 2010). Here, I consider the scenario in which density-dependence arises in the transition from juveniles to adulthood (henceforth, density-dependent juvenile survival) because the local environment has a limited carrying capacity.

I follow Frank (1998), Gardner and West (2004), and van Dyken (2010) in making a simplifying assumption: across the whole population, all individuals experience the same magnitude of local density-dependence. This allows us to treat the spatial scale of competition parameter a (introduced in section 4.4.1) as a constant. Following Frank (1998), express the fitness of the focal individual i in deme d w_{id} as:

$$w_{id} = \frac{S_{id}}{a\bar{S}_d + (1-a)\bar{S}_g} \quad (4.17)$$

Every individual in each deme id produces a number of juveniles S_{id} before density-dependent regulation of juvenile survival. An individual i on deme d produces S_{id} juveniles (*Figure 4.2a*); density-dependence during juvenile survival converts this absolute number to a fitness value w_{id} (*Figure 4.2b*); traits associated with higher fitness values spread in the population, and others are selected against (*Figure 4.2c*). Note that w_{id} can be smaller or larger than S_{id} : it is a measure of relative success, relative specifically to the focal organism's competitors: juveniles produced (S_{id}) survive to adulthood with a probability determined by the number of competitor offspring in the competitive neighbourhood.

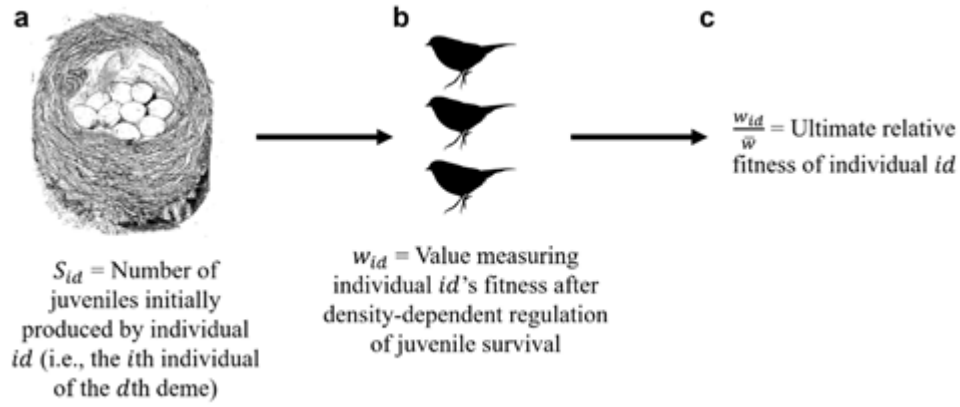


Figure 4.2 | **Density-dependent juvenile survival.** (a) Individual id produces S_{id} juveniles. (b) This juvenile production is converted into a fitness value w_{id} , the value of which depends on the extent of local versus global competition (the parameter a) during density-dependent regulation of juvenile survival to adulthood. (c) The trait of interest will become more common in the population if carriers of the trait tend to have a higher fitness value w_{id} than the average member of the population (\bar{w}). Nest image: BHL (CC).

To clarify the meaning of the scale of competition parameter a , it is helpful to consider the two extreme cases ($a = 0$ and $a = 1$). If there is no local competition ($a = 0$), the individual's fitness (Equation 4.17) is simplified to the number of juveniles it can produce relative to the average number of juveniles produced across the whole population:

$$w_{id} = \frac{S_{id}}{\bar{S}_g} \quad (4.18)$$

The average fitness \bar{w} in the population (Equation 4.16) is then equal to 1. In other words, the average number of juveniles produced in the population (\bar{S}_g) is the average across all individuals ($\bar{S}_g = \frac{1}{N} \sum_{i=1}^N S_{id}$), and so cancels out of the equation for \bar{w} :

$$\bar{w} = \frac{1}{N} \sum_{i=1}^N \frac{S_{id}}{\bar{S}_g} = \frac{1}{\bar{S}_g} \left(\frac{1}{N} \sum_{i=1}^N S_{id} \right) = 1 \quad (4.19)$$

Similarly, if there is complete *local* competition ($a = 1$), the individual's fitness (Equation 4.17) is also simplified:

$$w_{id} = \frac{S_{id}}{\bar{S}_d} \quad (4.20)$$

This case of complete local competition ($a = 1$) means that the change in the relative frequency of the focal allele in the population is just the total of all the within-deme struggles for juvenile survival to adulthood occurring independently across separate demes. For instance, we can imagine a deme in which the average individual has produced two juveniles ($\bar{S}_d = 2$). Assume that all other demes have

been much more successful: in each of these demes, the average individual has produced one hundred juveniles ($\bar{S}_d = 100$). If there is complete local competition ($a = 1$), juveniles on the focal deme will never face density-dependent competition for survival against the high numbers of juveniles produced in the rest of the population. Accordingly, an individual i who produces four juveniles on the focal deme will have a fitness value (w_{id}) of two (*i.e.*, $w_{id} = \frac{S_{id}}{\bar{S}_d} = \frac{4}{2} = 2$). A less fortunate individual i who produces four juveniles on one of the other demes will have a fitness value (w_{id}) of 0.04 (*i.e.*, $w_{id} = \frac{S_{id}}{\bar{S}_d} = \frac{4}{100} = 0.04$). To ask whether, across the whole population, there is an increase or a decrease in the frequency of the focal allele, we then ask whether carrying the allele leads to a higher relative fitness on average across all demes.

When there is pure local competition ($a = 1$), we do not need to consider the fact that individuals on different demes may be producing different absolute numbers of juveniles before density-dependence occurs: with $a = 1$, the outcome of selection depends entirely on within-deme selection rather than between-deme selection. If $a = 1$, the average fitness w_{id} on the deme (\bar{w}_d) must be equal to 1 (*i.e.*, $\bar{w}_d = \frac{\bar{S}_d}{\bar{S}_d}$). As is the case when $a = 0$ (above), the average w_{id} in the whole population (\bar{w}) must also be equal to 1 if $a = 1$. Substituting $\bar{w}_d = \bar{w} = 1$ into Inequality 4.16, the condition for selection to favour the trait of interest ($\mathbb{E}_\pi[\Delta\bar{G}] > 0$) can then be simplified, because between-deme selection vanishes (a covariance with a constant is equal to zero):

$$\underbrace{\mathbb{E}_d \left[\mathbb{C}_i \left(\mathbb{E}_\pi \left[\frac{S_{id}}{\bar{S}_d} \right], G_{id} \right) \right]}_{\substack{\text{Expected} \\ \text{within-deme} \\ \text{selection}}} > 0 \quad (4.21)$$

However, in the more general case where an individual's competitors come from more than one spatial level in the population (*i.e.*, *partly* from the local deme and *partly* from the global population of all demes, $0 \leq a \leq 1$), \bar{w} is not equal to 1. The between-deme selection covariance of Inequality 4.16 remains in the condition for selection to favour the trait of interest. In this case, substituting the expression for w_{id} (Equation 4.17) into Inequality 4.16 results in:

$$\underbrace{\mathbb{C}_d \left(\mathbb{E}_\pi \left[\frac{\bar{w}_d}{\bar{w}} \right], \bar{G}_d \right)}_{\substack{\text{Expected} \\ \text{between-deme} \\ \text{selection}}} + \underbrace{\mathbb{E}_d \left[\mathbb{C}_i \left(\mathbb{E}_\pi \left[\frac{S_{id}}{\bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)} \right], G_{id} \right) \right]}_{\substack{\text{Expected} \\ \text{within-deme} \\ \text{selection}}} > 0 \quad (4.22)$$

For future uses of this inequality (Inequality 4.22), it will be convenient to express the expected between-deme selection in the form of the product of a regression slope and the variance. In the terms of Price (1972), these are the ‘*intensity of selection*’ between demes and the ‘*variation on which selection acts*’ between demes, respectively:

$$\underbrace{\mathbb{C}_d \left(\mathbb{E}_\pi \left[\frac{\bar{w}_d}{\bar{w}} \right], \bar{G}_d \right)}_{\text{Expected between-deme selection}} = \underbrace{\beta_{\mathbb{E}_\pi \left[\frac{\bar{w}_d}{\bar{w}} \right], \bar{G}_d}}_{\text{"Intensity of selection"}} \underbrace{\mathbb{V}_d[\bar{G}_d]}_{\text{"Variation on which selection acts"}} \quad (4.23)$$

The aim now is to rearrange Inequality 4.22 so that we separate the effects of local stochasticity and global stochasticity: obtaining separate terms for local and global stochasticity will make clear how they each influence the outcome of selection. The crucial term to rearrange appears in the within-deme selection covariance above. We focus on the i th individual’s within-deme fitness (the average, across environmental states, of the number of juveniles produced by i relativized by the number of juveniles produced by i ’s competitors):

$$\text{Within deme fitness} = \mathbb{E}_\pi \left[\frac{S_{id}}{\bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)} \right] \quad (4.24)$$

Equation 4.24 is the expectation of a ratio of two random variables (the numerator and the denominator are both random variables). To expand expectations of ratios into the underlying statistical moments characterising each random variable, we can use the Delta method (an application of a Taylor series approximation), as in Chapter 3 (Rice, 2008; Starrfelt and Kokko, 2012). Specifically, the expectation of a ratio of random variables (X and Y) can be approximated in the following way:

$$\mathbb{E} \left[\frac{X}{Y} \right] \approx \frac{1}{\mathbb{E}[Y]} \left(\mathbb{E}[X] - \frac{\mathbb{C}[X, Y]}{\mathbb{E}[Y]} \right) \quad (4.25)$$

In the same way, we can substitute the numerator and denominator of Equation 4.24 into X and Y respectively, in Equation 4.25, and then carry the constants a and $(1-a)$ out of the covariance terms to approximate within-deme fitness:

$$\begin{aligned} \text{Within deme fitness} &\approx \frac{1}{\mathbb{E}_\pi[\bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)]} \left(\mathbb{E}_\pi[S_{id}] - a \frac{\mathbb{C}_\pi[S_{id}, \bar{w}\bar{S}_d]}{\mathbb{E}_\pi[\bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)]} \right. \\ &\quad \left. - (1-a) \frac{\mathbb{C}_\pi[S_{id}, \bar{w}\bar{S}_g]}{\mathbb{E}_\pi[\bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)]} \right) \end{aligned} \quad (4.26)$$

In Equation 4.26, the term $\mathbb{E}_\pi[\bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)]$ appears in several places. Biologically, this term represents the expected fitness (over environmental states π) of the average competitor of a member of deme d . If competition for juvenile survival to adulthood is entirely local ($a = 1$), the expected fitness of an average competitor is $\mathbb{E}_\pi[\bar{w}\bar{S}_d]$. If competition for juvenile survival to adulthood is entirely global ($a = 0$), the expected fitness of an average competitor is $\mathbb{E}_\pi[\bar{w}\bar{S}_g]$. Note that \bar{w} appears in each expectation as a scaling factor, relativising fitness. To simplify the notation, henceforth denote the fitness of the average competitor of a member of deme d by z_d (i.e., $z_d = \bar{w}(a\bar{S}_d + (1-a)\bar{S}_g)$). z_d is free to differ for members of different demes, because \bar{S}_d can take on different values in different demes. Below (in the section titled ‘Special cases’), I will return to the special case in which all demes sample their environmental state independently from a shared probability distribution, which leads to a useful simplification of the argument.

It is clearer to express correlations rather than covariances. Since $\mathbb{C}_\pi[X, Y] = \rho_{X,Y}\sigma[X]\sigma[Y]$, we can express Equation 4.26 as:

$$\text{Within deme fitness} \approx \frac{1}{\mathbb{E}_\pi[z_d]} \left(\mathbb{E}_\pi[S_{id}] - a \frac{\sigma_\pi[\bar{w}\bar{S}_d]}{\mathbb{E}_\pi[z_d]} \rho_{S_{id}, \bar{w}\bar{S}_d} \sigma_\pi[S_{id}] - (1-a) \frac{\sigma_\pi[\bar{w}\bar{S}_g]}{\mathbb{E}_\pi[z_d]} \rho_{S_{id}, \bar{w}\bar{S}_g} \sigma_\pi[S_{id}] \right) \quad (4.27)$$

Local and global sources of stochasticity

In Equation 4.27, there are two sources of stochasticity that influence the within-deme fitness of individual id : local and global. First, there are fluctuations in the fitness of average competitors on the local deme d (represented in Equation 4.27 by the standard deviation over environmental states $\sigma_\pi[\bar{w}\bar{S}_d]$). Second, there are fluctuations in the fitness of the average competitor in the global population (represented in Equation 4.27 by the standard deviation over environmental states $\sigma_\pi[\bar{w}\bar{S}_g]$). In Chapter 3, I defined a stochasticity coefficient v as the coefficient of variation in population average reproductive success (standard deviation divided by the expectation of average reproductive success in the population). Here, I take a similar approach. However, rather than a single term v for all stochasticity, I split stochasticity into the two sources of fluctuation (local and global). First, define local stochasticity as the fluctuation in the local deme’s average fitness (relative to the expected fitness of the average competitor of a member of deme d):

$$v_d \equiv \frac{\sigma_\pi[\bar{w}\bar{S}_d]}{\mathbb{E}_\pi[z_d]} \quad (4.28)$$

The subscript d denotes the deme on which this stochasticity coefficient applies. In the general case, different demes are free to show different levels of stochasticity. I will return below to the special case

in which demes draw their environmental state from a common distribution. The superscript ‘•’ denotes ‘local’; I separate it from the subscript d to highlight that different demes d can experience different stochasticities v^\bullet , in principle.

Second, define global stochasticity as the fluctuation in the whole population’s average fitness (relative to the expected fitness of the average competitor of a member of deme d):

$$v_d^\circledast \equiv \frac{\sigma_\pi[\bar{w}\bar{S}_g]}{\mathbb{E}_\pi[z_d]} \quad (4.29)$$

The superscript ‘ \circledast ’ denotes ‘global’. Again, I separate it from the subscript d to highlight that members of different demes can experience different ‘global’ stochasticities v^\circledast . Biologically, this means that, although the raw fluctuation in population-wide average reproductive success ($\sigma_\pi[\bar{w}\bar{S}_g]$) is by definition the same for every member of every deme, its importance depends on the fitness of an average competitor, which can differ between demes. Informally, this can be understood in terms of the severity of fluctuations relative to the focal individual’s expectation of average fitness: for the same magnitude of fluctuation, an individual on a deme where individuals have, on average, 50 offspring will experience population-wide fluctuations as less profound than an individual on a deme where individuals have, on average, only 20 offspring. The relative size of fluctuation is magnified as $\mathbb{E}_\pi[z_d]$ becomes smaller, which is why the stochasticity terms capture the relative importance of stochasticity to the organism when optimising its fitness.

To clarify these two sources of stochasticity (local and global), it is worth noting how they depend on the spatial scale of competition (a). When $a = 0$, competition is completely global. In this case, all individuals on all demes face the same average competitor. The denominator of the stochasticity coefficients (the expected fitness of an average competitor, $\mathbb{E}_\pi[z_d]$) is now the same from the perspective of any deme d . In summary, the denominator ($\mathbb{E}_\pi[z_d]$) scales the magnitude of each stochasticity coefficient according to the average fitness that the focal individual is competing against. The numerators ($\sigma_\pi[\bar{w}\bar{S}_d]$ and $\sigma_\pi[\bar{w}\bar{S}_g]$) measure the degree to which local and global average fitness fluctuate.

To include explicit terms for the spatial scales of competition and fluctuation in the condition for selection to favour the trait of interest, we substitute the within-deme fitness for individual id (Equation 4.27) into the condition for selection to favour the trait of interest (Inequality 4.22):

$$\begin{aligned}
& \overbrace{\beta_{\mathbb{E}_\pi[\frac{\bar{w}_d}{\bar{w}}], \bar{G}_d} \mathbb{V}_d[\bar{G}_d]}^{\text{Expected between-deme selection}} \\
+ \mathbb{E}_d \left[\underbrace{\mathbb{C}_i \left(\frac{1}{\mathbb{E}_\pi[Z_d]} \left(\mathbb{E}_\pi[S_{id}] - \alpha v_d^\bullet \rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}] - (1 - \alpha) v_d^\circ \rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}] \right), G_{id} \right)}_{\text{Expected within-deme selection}} \right] & > 0
\end{aligned} \tag{4.30}$$

It is worth recapping the biological meaning of Inequality 4.30. Each individual in the population samples its number of juveniles (S_{id}) from its own private probability distribution. Each individual's distribution is characterised by its own expected value ($\mathbb{E}_\pi[S_{id}]$) and its own standard deviation ($\sigma_\pi[S_{id}]$). The key message of bet-hedging theory is that variation in fitness at the level of the individual can only exert an influence over the outcome of selection if it is correlated with fluctuations in other individuals (Starrfelt and Kokko, 2012); this is because bet-hedgers gain their advantage during periods when the general population is underperforming (amplifying the reproductive value of any successful reproduction). If there are no correlated fluctuations, there can be no fluctuating reproductive value.

Because we are interested in effects occurring at different spatial levels in the population (local competition and global competition), there are two forms of correlation to consider: the correlation of the focal individual's juvenile production (S_{id}) with local fluctuations ($\rho_{S_{id}, \bar{w} \bar{s}_d}$ in Inequality 4.30) and the correlation with global fluctuations ($\rho_{S_{id}, \bar{w} \bar{s}_g}$ in Inequality 4.30). In many biologically relevant cases, these correlation terms can be completely ignored. For instance, if all individuals in a focal deme will do better than they normally do when the deme is in a favourable environmental state (and do worse than they normally do when the deme is in an unfavourable environmental state), the underlying correlation here is simply 1. Correlation therefore vanishes from Inequality 4.30. Biologically, this describes a reasonable scenario – or at least a close approximation of reality: in a drought, all individuals do worse than they would normally do; in a bonanza, all individuals do better than they would normally do. Inequality 4.30 is not committed to this simplifying condition, however biologically reasonable it may be. Nonetheless, it is worth noting that these underlying correlations exert little effect on the outcome under a broad range of biologically reasonable scenarios, which helps to simplify the interpretation. Last, note that each volatility term in Inequality 4.30 ($\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}]$ and $\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}]$) is preceded by a negative sign. The biological meaning here is that stochasticity in the focal individual's ability to produce juveniles ($\sigma_\pi[S_{id}]$) penalises their total fitness only if these stochastic effects are correlated with fluctuations amongst the focal individual's average competitors.

Now that we have a general condition for selection in which the spatial scale of competition (a) and the spatial scale of fluctuation (v_d^* and v_d^*) are explicit, we can turn to social behaviour. Specifically, we aim to capture social effects on the reproductive uncertainty of social partners, and ask how these social effects are selected under different spatial scales of competition and fluctuation.

Regression slopes for different aspects of fitness

I follow the form of Hamilton's rule developed by Queller (1992a), in which the fitness of a focal individual is described by a multiple linear regression on its own and its social partner's genotypes (see Chapters 1 and 3). The genotype of the focal individual id appears in Inequality 4.30 as G_{id} . Denote the genotype of the social partner jd as G_{jd} . Whereas Queller (1992a) used a single response variable (the organism's fitness), here we are interested in different components of fitness, specifically the mean and volatility in reproductive success. We therefore use more than one response variable. In Inequality 4.30, there are three key components of the focal individual's fitness. These are:

1. its expected number of juveniles produced ($\mathbb{E}_\pi[S_{id}]$);
2. its standard deviation in juvenile production correlated with local competitors ($\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}]$);
and
3. its standard deviation in juvenile production correlated with global competitors ($\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}]$).

Accordingly, describe each one using multiple regressions on G_{id} and G_{jd} :

$$\mathbb{E}_\pi[S_{id}] = \alpha_{\mathbb{E}_\pi[S_{id}]} + \beta_{\mathbb{E}_\pi[S_{id}], G_{id}} G_{id} + \beta_{\mathbb{E}_\pi[S_{id}], G_{jd}} G_{jd} + \epsilon_{\mathbb{E}_\pi[S_{id}]} \quad (4.31)$$

$$\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}] = \alpha_{\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}]} + \beta_{\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}], G_{id}} G_{id} + \beta_{\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}], G_{jd}} G_{jd} + \epsilon_{\rho_{S_{id}, \bar{w} \bar{s}_d} \sigma_\pi[S_{id}]} \quad (4.32)$$

$$\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}] = \alpha_{\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}]} + \beta_{\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}], G_{id}} G_{id} + \beta_{\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}], G_{jd}} G_{jd} + \epsilon_{\rho_{S_{id}, \bar{w} \bar{s}_g} \sigma_\pi[S_{id}]} \quad (4.33)$$

In each expression, the intercept terms (α) capture the 'baseline' values for each component of fitness, before the effects of the focal individual's genotype (G_{id}) and the genotype of its social partner (G_{jd}) are considered. The error terms (ϵ) capture variation across the fitted regression lines. Both the intercepts (α) and error terms (ϵ) will vanish subsequently from the analysis (discussed below), so we need only focus on the partial regression terms (β).

To make the biological meanings of each partial regression slope β more explicit, we now denote them as follows. First, let c_μ denote the effect of the focal individual on its own expected fecundity:

$$c_\mu = -\beta_{\mathbb{E}_\pi[S_{id}], G_{id}} G_{id} \quad (4.34)$$

c_μ is the ‘cost’ term to the expected number of juveniles produced. Note that I follow the convention of defining the cost term with a negative sign (Gardner *et al.*, 2011), which ultimately leads to the condition $rB - C > 0$. When substituted into the regression equation, we add a negative in front of the cost term.

Second, the effect of a social partner on the focal individual’s expected number of juveniles (before density-dependent regulation of juvenile survival):

$$b_\mu = \beta_{\mathbb{E}_\pi[S_{id}], G_{jd}} \quad (4.35)$$

b_μ denotes the benefit provided by a social partner jd (whose genotype is G_{jd}) to the expected number of juveniles that the focal individual can produce ($\mathbb{E}_\pi[S_{id}]$). A social partner may, for instance, be able to provision the focal individual with additional resources, guard the nest, or provide a ‘life insurance’ benefit (Field *et al.*, 2000). Note that we are focusing on social effects experienced by a focal individual (the so-called ‘neighbour-modulated’ approach; Gardner *et al.*, 2011). Assuming an absence of class structure, benefit terms of this type are exactly equal to the benefit term *provided* by the focal individual on the deme d (i.e., $b_\mu = \beta_{\mathbb{E}_\pi[S_{id}], G_{jd}} = \beta_{\mathbb{E}_\pi[S_{jd}], G_{id}}$), because they are in fact parts of regressions taken across the whole deme: the components of Hamilton’s rule are taken across the whole competitive population (Queller, 1992a, 1992b). We can therefore switch our perspective easily and describe b_μ as the effect of a focal individual on a social partner. This takes us from a ‘neighbour-modulated’ Hamilton’s rule to an ‘inclusive fitness’ Hamilton’s rule.

Next, let $c_{\sigma, d}^\bullet$ denote the effect of the focal on its own (locally-correlated) uncertainty in juvenile production:

$$c_{\sigma, d}^\bullet = \beta_{\rho_{S_{id}, \bar{w}_d} \sigma_\pi[S_{id}], G_{id}} \quad (4.36)$$

$c_{\sigma, d}^\bullet$ measures the extent to which focal individual id (whose genotype is G_{id}) fails or succeeds in buffering itself from local fluctuations in reproductive success. As previously, the superscript ‘ \bullet ’ highlights that this is the component of fitness dealing with the individual’s ability to buffer *local* fluctuations on deme d . If possessing a higher genetic value G_{id} is associated with a higher level of locally-correlated stochasticity in the focal individual’s reproduction ($\rho_{S_{id}, \bar{w}_d} \sigma_\pi[S_{id}]$), the regression slope $c_{\sigma, d}^\bullet$ is positive. When we come to substitute this term back into the condition for selection, we

will find that it is preceded by a negative sign. This makes biological sense: higher levels of reproductive stochasticity reduce the focal individual's total fitness.

Next, let $b_{\sigma,d}^{\bullet}$ denote the effect of a social partner on the focal individual's (locally-correlated) uncertainty in juvenile production:

$$b_{\sigma,d}^{\bullet} = -\beta_{\rho_{S_{id},\bar{w}\bar{s}_d}} \sigma_{\pi[S_{id}],G_{jd}} \quad (4.37)$$

If social partners successfully buffer the focal individual from local stochasticity, the regression slope here is negative, which increases fitness. In order that the benefit term $b_{\sigma,d}^{\bullet}$ captures a positive increment to fitness, we therefore add the negative sign: a negative slope $\beta_{\rho_{S_{id},\bar{w}\bar{s}_d}} \sigma_{\pi[S_{id}],G_{jd}}$ leads to a positive benefit $b_{\sigma,d}^{\bullet}$.

Next, let $c_{\sigma,d}^{\odot}$ denote the effect of the focal on its own (globally-correlated) uncertainty in juvenile production:

$$c_{\sigma,d}^{\odot} = \beta_{\rho_{S_{id},\bar{w}\bar{s}_g}} \sigma_{\pi[S_{id}],G_{id}} \quad (4.38)$$

$c_{\sigma,d}^{\odot}$ is identical to $c_{\sigma,d}^{\bullet}$ with the exception that here we are dealing with the correlations with global fluctuations ($\rho_{S_{id},\bar{w}\bar{s}_g}$) rather than correlations with local deme fluctuations ($\rho_{S_{id},\bar{w}\bar{s}_d}$). It is important to note that $c_{\sigma,d}^{\odot}$ is specific to the deme d : it is the extent to which actors in deme d buffer themselves from global fluctuations. To maintain maximum generality, we allow actors in other demes to achieve this to greater or lesser degrees, meaning that $c_{\sigma,d}^{\odot}$ is a deme-specific fitness effect. In the special case where actors have the same buffering effect on their own reproduction regardless of which deme they are present in, $c_{\sigma,d}^{\odot}$ is the same for all demes across the whole population.

Finally, let $b_{\sigma,d}^{\odot}$ denote the effect of a social partner on the focal individual's (globally-correlated) uncertainty in juvenile production:

$$b_{\sigma,d}^{\odot} = -\beta_{\rho_{S_{id},\bar{w}\bar{s}_g}} \sigma_{\pi[S_{id}],G_{jd}} \quad (4.39)$$

As with $c_{\sigma,d}^{\odot}$ above, $b_{\sigma,d}^{\odot}$ is identical to $b_{\sigma,d}^{\bullet}$ with the exception that here we are dealing with the correlations with global fluctuations ($\rho_{S_{id},\bar{w}\bar{s}_g}$) rather than correlations with local deme fluctuations ($\rho_{S_{id},\bar{w}\bar{s}_d}$). Similarly, $b_{\sigma,d}^{\odot}$ is specific to the deme d : it is the extent to which social partners in deme d buffer their recipients from global fluctuations. This social effect is free to differ between demes. As with $c_{\sigma,d}^{\odot}$, the simplest special case is where social partners have the same buffering effect in all demes, such that $b_{\sigma,d}^{\odot}$ is the same in all demes across the whole population.

For a behaviour or trait of interest, we now have three forms of ‘cost’ paid by the actor (c_μ , $c_{\sigma,d}^\bullet$, and $c_{\sigma,d}^\circ$). We also have three forms of ‘benefit’ enjoyed by the recipient (b_μ , $b_{\sigma,d}^\bullet$, and $b_{\sigma,d}^\circ$). These six terms appear in the regression equations for three components of the focal individual’s fitness ($\mathbb{E}_\pi[S_{id}]$, $\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}]$, and $\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}]$). To recap:

$$\mathbb{E}_\pi[S_{id}] = \alpha_{\mathbb{E}_\pi[S_{id}]} - c_\mu G_{id} + b_\mu G_{jd} + \epsilon_{\mathbb{E}_\pi[S_{id}]} \quad (4.40)$$

$$\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}] = \alpha_{\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}]} + c_{\sigma,d}^\bullet G_{id} - b_{\sigma,d}^\bullet G_{jd} + \epsilon_{\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}]} \quad (4.41)$$

$$\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}] = \alpha_{\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}]} + c_{\sigma,d}^\circ G_{id} - b_{\sigma,d}^\circ G_{jd} + \epsilon_{\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}]} \quad (4.42)$$

To obtain the condition for selection in a form that is recognisable as Hamilton’s rule, we now substitute these terms into Inequality 4.30:

$$\begin{aligned} & \text{Expected between-deme selection} \\ & \overbrace{\beta_{\mathbb{E}_\pi[\frac{\bar{w}_d}{\bar{w}}], \bar{G}_d} \mathbb{V}_d[\bar{G}_d]} \\ & + \mathbb{E}_d \left[\frac{1}{\mathbb{E}_\pi[Z_d]} \mathbb{C}_i \left(\alpha_{\mathbb{E}_\pi[S_{id}]} - c_\mu G_{id} + b_\mu G_{jd} + \epsilon_{\mathbb{E}_\pi[S_{id}]} - av_d^\bullet (\alpha_{\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}]} \right. \right. \\ & \left. \left. + c_{\sigma,d}^\bullet G_{id} - b_{\sigma,d}^\bullet G_{jd} + \epsilon_{\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}]} \right) \right. \\ & \left. - (1-a)v_d^\circ \left(\alpha_{\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}]} + c_{\sigma,d}^\circ G_{id} - b_{\sigma,d}^\circ G_{jd} + \epsilon_{\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}]} \right), G_{id} \right] > 0 \end{aligned} \quad (4.43)$$

By the linearity of covariances ($\mathbb{C}[X+Y, Z] = \mathbb{C}[X, Z] + \mathbb{C}[Y, Z]$):

$$\begin{aligned} & \text{Expected between-deme selection} \\ & \overbrace{\beta_{\mathbb{E}_\pi[\frac{\bar{w}_d}{\bar{w}}], \bar{G}_d} \mathbb{V}_d[\bar{G}_d]} \\ & + \mathbb{E}_d \left[\frac{1}{\mathbb{E}_\pi[Z_d]} \left(\mathbb{C}_i(\alpha_{\mathbb{E}_\pi[S_{id}], G_{id}) - c_\mu \mathbb{C}_i(G_{id}, G_{id}) + b_\mu \mathbb{C}_i(G_{jd}, G_{id}) \right. \right. \\ & \left. \left. + \mathbb{C}_i(\epsilon_{\mathbb{E}_\pi[S_{id}], G_{id}) \right. \right. \\ & \left. \left. - av_d^\bullet \left(\mathbb{C}_i(\alpha_{\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}], G_{id}) + c_{\sigma,d}^\bullet \mathbb{C}_i(G_{id}, G_{id}) - b_{\sigma,d}^\bullet \mathbb{C}_i(G_{jd}, G_{id}) \right) \right. \right. \\ & \left. \left. + \mathbb{C}_i(\epsilon_{\rho_{S_{id},\bar{w}\bar{s}_d}\sigma_\pi[S_{id}], G_{id}) \right) \right. \\ & \left. - (1-a)v_d^\circ \left(\mathbb{C}_i(\alpha_{\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}], G_{id}) + c_{\sigma,d}^\circ \mathbb{C}_i(G_{id}, G_{id}) - b_{\sigma,d}^\circ \mathbb{C}_i(G_{jd}, G_{id}) \right. \right. \\ & \left. \left. + \mathbb{C}_i(\epsilon_{\rho_{S_{id},\bar{w}\bar{s}_g}\sigma_\pi[S_{id}], G_{id}) \right) \right] > 0 \end{aligned}$$

(4.44)

As in Chapter 3, we can now remove from this inequality any covariances with a constant (which are, by definition, equal to zero). We assume that any covariances with the error terms (ϵ) in Equations 4.40–4.42 are equal to zero (Birch and Marshall, 2014). The covariances involving intercepts (α) and error terms (ϵ) can therefore be dropped from Inequality 4.44.

We now make within-deme relatedness (henceforth, r_d) explicit for the deme d . Let r_d be the regression of partner genetic value (G_{jd}) on the focal individual's genetic value (G_{id}) across all individuals within deme d :

$$r_d = \frac{\mathbb{C}_i(G_{id}, G_{jd})}{\mathbb{V}_i[G_{id}]} \quad (4.45)$$

Substituting Equation 4.45 into Inequality 4.44 (the condition for selection, $\mathbb{E}_\pi[\Delta\bar{G}] > 0$):

$$\begin{aligned} & \overbrace{\beta_{\mathbb{E}_\pi[\frac{\bar{w}_d}{\bar{w}}], \bar{G}_d} \mathbb{V}_d[\bar{G}_d]}^{\text{Expected between-deme selection}} \\ + \underbrace{\mathbb{E}_d \left[\frac{1}{\mathbb{E}_\pi[z_d]} \left(r_d b_\mu - c_\mu - a v_d^\bullet (c_{\sigma,d}^\bullet - r_d b_{\sigma,d}^\bullet) - (1-a) v_d^\circ (c_{\sigma,d}^\circ - r_d b_{\sigma,d}^\circ) \right) \mathbb{V}_i[G_{id}] \right]}_{\text{Expected within-deme selection}} > 0 \end{aligned} \quad (4.46)$$

Thus, we have partitioned variance in allele frequency into two components: within-deme variance ($\mathbb{V}_i[G_{id}]$ for each deme d) and between-deme variance ($\mathbb{V}_d[\bar{G}_d]$).

Special case

Inequality 4.46 captures the general condition for selection of the trait of interest. Here, relatedness, social fitness effects, non-social fitness effects, deme size, and the magnitude and type of environmental fluctuation are free to differ between demes, and demes are free to accumulate different allele frequencies through time such that, at the start of the time interval considered by Inequality 4.46, there may already exist considerable differences between demes in the frequency of different traits. In this section, I show how a simpler expression (Inequality 4.13) can be derived, in which it is easier to see the effects of the scale of competition (a) and the spatial scale of fluctuation (v_d^\bullet and v_d°). This requires simplifying assumptions that eliminate the sources of between-deme heterogeneity listed at the start of this paragraph.

Consider the following special case:

1. Let each patch exist as an independent arena of environmental fluctuation within a well-mixed global population undergoing density-dependent regulation of juvenile survival to adulthood.
2. On reaching adulthood, let juveniles disperse at random across the population (*i.e.*, assume global dispersal).
3. Previous adults die when the new generation disperses (*i.e.*, assume discrete adult generations without overlap).
4. Let demes be identical but independent fluctuating arenas of environmental change. In other words, all demes are equally likely to suffer drought, or food abundance, or local increases in parasite pressure. Some demes will fall into one environmental state, others into another, but the probability of each state is now identical across demes.

Because this special case assumes fully random dispersal of adults at the end of each discrete generation, the alleles of interest will be in essentially equal frequencies in any two areas of the population. We can define a well-mixed population of adults as possessing a constant variance in breeding value $\mathbb{V}_{id}[G_{id}]$ within all demes on patches: for all demes $d \in D$ on separate patches, $\mathbb{V}_{id}[G_{id}]$ is equal to the global variance in allele frequency $\mathbb{V}_i[G_i]$ across the whole population. Likewise, because all demes have the same allele frequency, they have the same average breeding value \bar{G}_d . Accordingly, there is no variance in \bar{G}_d between demes ($\mathbb{V}_d[\bar{G}_d] = 0$), so between-deme selection is zero in Inequality 4.46. It is important to note that this is a significant simplifying assumption: it has long been appreciated that $\mathbb{V}_d[\bar{G}_d]$ can be nonzero simply due to ‘*sampling errors in colonization*’ (Uyenoyama, 1979) during between-deme dispersal.

Because we have now introduced the assumption that demes are identical but independent fluctuating arenas, $\mathbb{E}_\pi[z_d]$ (the expectation over stochasticity of the average fitness of a competitor of an individual in deme d) is the same for all demes. It can therefore be carried outside of the expected within-deme selection term in Inequality 4.46 and divided out of the inequality. Local and global sources of stochasticity (v_d^\bullet and v_d° respectively) are now no longer deme-specific, so we can drop the subscripts ‘ d ’. Inequality 4.46 can now be simplified to:

$$\underbrace{\mathbb{E}_d[r_d b_\mu - c_\mu - av^\bullet(c_{\sigma,d}^\bullet - r_d b_{\sigma,d}^\bullet) - (1-a)v^\circ(c_{\sigma,d}^\circ - r_d b_{\sigma,d}^\circ)]}_{\text{Expected within-deme selection}} > 0 \quad (4.47)$$

In the additional special case where demes do not differ in any way except environmental state (and therefore their baseline fecundity \bar{S}_d), Inequality 4.47 can be further simplified. Relatedness (r_d), direct fitness effects (c_μ , $c_{\sigma,d}^\bullet$, and $c_{\sigma,d}^\circ$), and indirect fitness effects (b_μ , $b_{\sigma,d}^\bullet$, and $b_{\sigma,d}^\circ$) are no longer deme-specific. Rather, relatedness and the fitness effects of behaviour are the same wherever the focal individual is in the population. We can remove all the subscripts ‘ d ’, and we reach Inequality 4.13:

$$r \left(\overbrace{b_\mu + \underbrace{av^\bullet b_\sigma^\bullet}_{\text{Local risk benefit}} + \underbrace{(1-a)v^\circ b_\sigma^\circ}_{\text{Global risk benefit}}}^{\text{Total Hamiltonian benefit (B)}} \right) > \overbrace{c_\mu + \underbrace{av^\bullet c_\sigma^\bullet}_{\text{Local risk cost}} + \underbrace{(1-a)v^\circ c_\sigma^\circ}_{\text{Global risk cost}}}^{\text{Total Hamiltonian cost (C)}}$$

Selection can favour altruistically buffering relatives ($r > 0$) from local environmental fluctuations ($b_\sigma^\bullet > 0$) if competition is local ($a > 0$) and the local deme experiences stochastic fluctuations in average reproductive success ($v^\bullet > 0$), even if there are no fluctuations globally ($v^\circ \approx 0$).

Demographic stochasticity

We have now derived Inequality 4.13 (the condition for altruistic bet-hedging to evolve by *environmental* stochasticity in a deme-structured population). We now turn to Inequality 4.14 (the condition for altruistic bet-hedging to evolve by *demographic* stochasticity in a deme-structured population).

Consider a population of a very large number of demes in a well-mixed population subject to local demographic stochasticity and local density-dependent regulation. At a whole population scale, despite the potential for fluctuation in individual \bar{S}_d values between different demes, there is no fluctuation in \bar{S}_g . By the law of large numbers across many demes, there is negligible fluctuation in whole-population average juvenile production \bar{S}_g and negligible fluctuation in whole-population average fitness (after density-dependent juvenile survival) \bar{w} . At the limit of an infinite number of independent demes with intra-demic demographic stochasticity, \bar{w} can therefore be treated as a constant across environmental states (*i.e.*, it converges in probability) – which I do in the following steps. Thus, under demographic stochasticity at the limit of infinite deme number, we can write:

$$\mathbb{C}_\pi(S_{id}, \bar{w}\bar{S}_d) = \bar{w}\mathbb{C}_\pi(S_{id}, \bar{S}_d) \quad (4.48)$$

$$\mathbb{C}_\pi(S_{id}, \bar{w}\bar{S}_g) = 0 \quad (4.49)$$

Using the Delta method (Equation 4.25), within-deme fitness (Equation 4.24) can now be approximated as:

$$\mathbb{E}_\pi \left[\frac{S_{id}}{Z_d} \right] \approx \frac{1}{\bar{w}\mathbb{E}_\pi[a\bar{S}_d + (1-a)\bar{S}_g]} \left(\mathbb{E}_\pi[S_{id}] - a \frac{\bar{w}\mathbb{C}_\pi(S_{id}, \bar{S}_d)}{\bar{w}\mathbb{E}_\pi[a\bar{S}_d + (1-a)\bar{S}_g]} \right) \quad (4.50)$$

\bar{w} cancels out of the fraction. Under the definition of demographic stochasticity, $\mathbb{C}_\pi(S_{id}, S_{jd}) = 0$ for all $j \neq i$. Note that:

$$\mathbb{C}_\pi(S_{id}, \bar{S}_d) = \mathbb{C}_\pi\left(S_{id}, \frac{1}{N_d} \sum_{j=1}^{N_d} S_{jd}\right) = \frac{\mathbb{V}_\pi[S_{id}]}{N_d} \quad (4.51)$$

Substituting Equation 4.51 into Equation 4.50, individual id 's within-deme fitness can be written as:

$$\mathbb{E}_\pi\left[\frac{S_{id}}{Z_d}\right] \approx \frac{1}{\bar{w}\mathbb{E}_\pi[a\bar{S}_d + (1-a)\bar{S}_g]} \left(\mathbb{E}_\pi[S_{id}] - \frac{a}{N_d} \frac{\mathbb{V}_\pi[S_{id}]}{\mathbb{E}_\pi[a\bar{S}_d + (1-a)\bar{S}_g]} \right) \quad (4.52)$$

We will commit to the assumptions in the 'special case' above: we assume a single well-mixed population where allele frequencies are the same throughout the population, rather than showing a patchy distribution between demes. Under this simplifying assumption:

$$\mathbb{E}_\pi[\bar{S}_d] = \mathbb{E}_\pi[\bar{S}_g] \quad (4.53)$$

Therefore:

$$\mathbb{E}_\pi[a\bar{S}_d + (1-a)\bar{S}_g] = \mathbb{E}_\pi[\bar{S}_g] \quad (4.54)$$

As in the 'special case' above, the uniform nature of the population also removes the scope for between-deme selection, since $\mathbb{V}_d[\bar{G}_d] = 0$. The condition for selection is then:

$$\mathbb{E}_d \left[\mathbb{C}_i \left(\mathbb{E}_\pi[S_{id}] - \frac{a}{N_d} \frac{\mathbb{V}_\pi[S_{id}]}{\mathbb{E}_\pi[\bar{S}_g]}, G_{id} \right) \right] > 0 \quad (4.55)$$

Using Queller's regression method (following the same series of steps as we have just done for environmental stochasticity), we obtain Inequality 4.14:

$$r \left(b_\mu + \underbrace{\frac{a}{N_d} \frac{b_{\sigma^2}}{\mathbb{E}_\pi[\bar{S}_g]}}_{\text{Local risk benefit}} \right) > c_\mu + \underbrace{\frac{a}{N_d} \frac{c_{\sigma^2}}{\mathbb{E}_\pi[\bar{S}_g]}}_{\text{Local risk cost}}$$

where volatility-increasing cost $c_{\sigma^2} = \beta_{\mathbb{V}(S_{id}), G_{id}}$ and volatility-reducing benefit $b_{\sigma^2} = -\beta_{\mathbb{V}(S_{id}), G_{jd}}$.

In other words, when Inequality 4.14 is satisfied, altruistic bet-hedging can evolve in a large population that appears to show no aggregate fluctuation, because fluctuations are occurring at a local level alongside local competition. Local demographic stochasticity ($\sigma_\pi[\bar{S}_d] > 0$) within the population generates a fluctuating background reproductive success over local demes, despite the essential absence of wholesale fluctuation at a global scale ($\sigma_\pi[\bar{S}_g] \approx 0$). When individuals face local competition for reproductive success (higher values of the local density-dependent competition parameter a), local chance fluctuations in baseline reproductive success (\bar{S}_d) provide the volatile background necessary for

bet-hedgers to invade. Bet-hedgers then dampen exposure to individual-level reproductive uncertainty – either for their own reproductive success ($c_\sigma^\bullet < 0$) and/or for the success of relatives ($b_\sigma^\bullet > 0, r > 0$).

When alleles do not differ in expected reproductive success ($rb_\mu - c_\mu = 0$), any slight reduction in the uncertainty of a relative's reproduction ($b_{\sigma z}^\bullet > 0, r > 0$) is expected to be favoured by selection for any combination of deme size N_d and value of nonzero local competition a , although the marginal change in expected outcome will be extremely slight at high N_d . The ratio $\frac{a}{N_d}$ exerts a strong control over the scope for bet-hedging to invade by demographic stochasticity. When $a = 1$ (*i.e.*, the whole population is a single deme), Inequality 4.14 recovers the expansion of the stochastic Hamilton's rule for demographic stochasticity of Chapter 3.

4.5 Evolutionarily stable strategy in a simple game

To explore the effects of demography on altruistic bet-hedging, I illustrate altruistic bet-hedging with local competition in a simple game in which cooperators and defectors inhabit a population composed of identical demes on patches showing independent environmental fluctuations. To find the evolutionarily stable strategy (ESS), we consider whether a monomorphic population is resistant to invasion by a mutant at different scales of competition a .

In the case where phenotype is entirely determined by genotype ($G_{id} = z_{id}$), we can translate between HRG and a partial derivative version of Hamilton's rule expressed in terms of phenotypes (Gardner *et al.*, 2010). This requires committing to an assumption of weak selection (Birch, 2016b). Let z denote focal phenotype and z' denote partner phenotype.

Because the environmental state on each deme's patch is fluctuating independently, there is no inter-deme correlation in reproductive success: by the law of large numbers (given a large or infinite number of demes D), there is no fluctuation in average fecundity at a whole population scale (v_d^\circledast is zero). Accordingly, global sources of stochasticity can be set to zero in Hamilton's rule. For Inequality 4.13, the corresponding partial derivative expression is:

$$\frac{dw}{dz} = \frac{\partial \mathbb{E}_\pi[S_{id}]}{\partial z'} r + \frac{\partial \mathbb{E}_\pi[S_{id}]}{\partial z} - av_d^\bullet \left(\frac{\partial \rho_{S_{id}, \bar{s}_d} \sigma_\pi[S_{id}]}{\partial z} + \frac{\partial \rho_{S_{id}, \bar{s}_d} \sigma_\pi[S_{id}]}{\partial z'} r \right) \quad (4.56)$$

The ESS phenotype must satisfy:

$$\left. \frac{dw}{dz} \right|_{z=z'=z^*} = 0 \quad (4.57)$$

$$\left. \frac{d^2 w}{dz^2} \right|_{z=z'=z^*} < 0 \quad (4.58)$$

To illustrate the role of patchy stochasticity, consider a haploid asexual population of two alleles (selfish and cooperative). Environmental state of each deme fluctuates equally and unpredictably between two environmental states π , a high fecundity state 1 and a low fecundity state 2. The selfish allele never cooperates. The cooperative allele eliminates local environmental effects on fecundity, such that recipients obtain their expected (pre-density-regulation) fecundity $\mathbb{E}_\pi[S]$ in all states. Individuals without cooperative partners have fecundity S_{π^*} , which depends on the local environmental state π^* . Cooperators pay a cost C . Payoffs are therefore defined according to the simple matrix in *Table 4.2*:

Table 4.2 | State-dependent payoffs to row player given their own behaviour and behaviour of a partner (columns)

	Cooperative	Selfish
Cooperative	$\mathbb{E}_\pi[S] - C$	$S_{\pi^*} - C$
Selfish	$\mathbb{E}_\pi[S]$	S_{π^*}

The phenotype z in this case is the probability of acting cooperatively. Consider the interaction between two players with phenotypes z (focal individual) and z' (partner individual). Given there are two states (1 and 2), the expected fecundity (before density-regulation) of the focal individual is:

$$\mathbb{E}_\pi[S_{id}] = \frac{S_1 + S_2}{2} - zC \quad (4.59)$$

In other words, the expected fecundity payoff (where the expectation is taken across environmental states) does not depend on the social partner's phenotype z' : it only depends on the focal individual's phenotype z . We therefore only need one partial derivative for expected fecundity:

$$\frac{\partial \mathbb{E}_\pi[S_{id}]}{\partial z} = -C \quad (4.60)$$

We also need the partial derivatives for $\rho_{S_{id}, \bar{S}_d} \sigma_\pi[S_{id}]$. Because there are two states, and one of these states carries a higher fecundity for everyone ($S_1 > S_2$), the correlation term $\rho_{S_{id}, \bar{S}_d} = 1$ for all individuals on the deme. Fecundity volatility is then:

$$\sigma_\pi[S_{id}] = (1 - z') \sqrt{0.25(S_1 - S_2)^2} \quad (4.61)$$

In other words, fecundity volatility (standard deviation across environmental states) does not depend on the focal individual's phenotype z : it only depends on the partner individual's phenotype z' . If the partner increases the rate of defection (*i.e.*, reduces z'), the focal is exposed to increased fecundity volatility. We therefore need one partial derivative on fecundity volatility, because the first term in the brackets in Equation 4.56 is zero:

$$\frac{\partial \sigma_{\pi}[S_{id}]}{\partial z'} = -0.5\sqrt{(S_1 - S_2)^2} \quad (4.62)$$

The final variable we need is intra-demic stochasticity. In the limit of an infinite number of demes D , whole-population-state-specific population average reproductive success (\bar{w}_{π}) converges in probability to a constant (x). Taking the limit of an infinite number of demes therefore simplifies the local stochasticity coefficient v_d^* . The constant x can be carried outside of both the numerator and the denominator, and cancelled out:

$$v_d^* \equiv \frac{\sigma_{\pi}[F_d]}{\mathbb{E}_{\pi}[Z_d]} = \frac{x\sigma_{\pi}[\bar{S}_d]}{x\mathbb{E}_{\pi}[a\bar{S}_d + (1-a)\bar{S}_g]} = \frac{\sigma_{\pi}[\bar{S}_d]}{a\mathbb{E}_{\pi}[\bar{S}_d] + (1-a)\mathbb{E}_{\pi}[\bar{S}_g]} \quad (4.63)$$

Let demes represent discrete arenas in a well-mixed population on patches be equal in size N_d , equal in genetic variance, and sampling their environmental state as identical and independent random variables. According, $\mathbb{E}_{\pi}[\bar{S}_d] = \mathbb{E}_{\pi}[\bar{S}_g]$, and:

$$v_d^* = \frac{\sigma_{\pi}[\bar{S}_d]}{\mathbb{E}_{\pi}[\bar{S}_d]} = \frac{\sqrt{(S_1 - S_2)^2(\bar{z} - 1)^2}}{S_1 + S_2 - 2c\bar{z}} \quad (4.64)$$

Intra-demic volatility in baseline fecundity ($\sigma_{\pi}[\bar{S}_d]$) depends on the intra-demic frequency of defection ($1 - \bar{z}$): in this scenario (*Table 4.2*), higher rates of local defection generate higher levels of local stochasticity. Because we are solving for the ESS strategy, we consider a mutant allele invading a population that is otherwise monomorphic (evaluate at $z' = z = \bar{z}$; Gardner, Griffin and West, 2010).

The frequency of each type of interaction follows the α coefficient of Gardner *et al.* (2011), as in Chapter 3, applied here within demes rather than at a whole population scale (*Table 4.3*). Intra-demic relatedness r_d is then equal to α .

Evaluating $\left. \frac{dw}{dz} \right|_{z=z'=z^*} = 0$ gives the candidate ESS:

$$\left. \frac{dw}{dz} \right|_{z=z'=z^*} = -C - a \left(\frac{\sqrt{(S_1 - S_2)^2(\bar{z} - 1)^2}}{S_1 + S_2 - 2c\bar{z}} \right) (-0.5\sqrt{(S_1 - S_2)^2}r) = 0 \quad (4.65)$$

The predicted ESS level of cooperation is then given by:

$$z^* = \frac{ar(S_1 - S_2)^2 - 2c(S_1 + S_2)}{-4c^2 + ar(S_1 - S_2)^2} \quad (4.66)$$

z^* increases with a . Intuitively, in a globally stable metapopulation with stochastic demes, the ESS level of volatility-suppressing cooperation increases as the scale of competition (Figure 4.3a). becomes increasingly intra-demic (Figure 4.3b).

Table 4.3 | Interaction frequencies within the deme d

Focal individual's phenotype (z)	Partner individual's phenotype (z')	Frequency within the local deme d
0	0	$\alpha(1-p) + (1-\alpha)(1-p)^2$
0	1	$(1-\alpha)p(1-p)$
1	0	$(1-\alpha)p(1-p)$
1	1	$\alpha p + (1-\alpha)p^2$

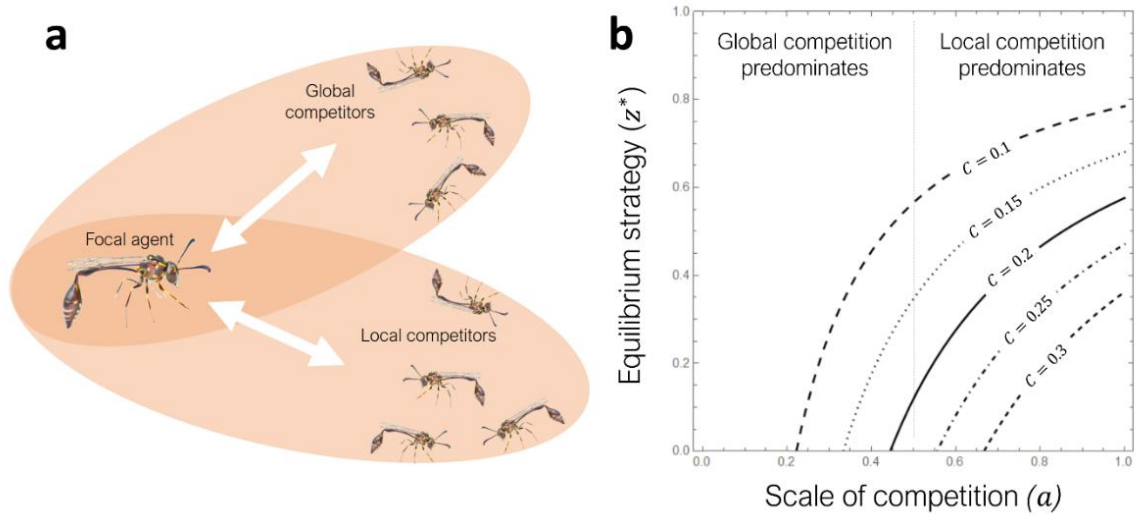


Figure 4.3 | Intuitively, buffering relatives from local sources of stochasticity can evolve when the scale of competition is local. (a) Focal individuals experience two sources of competition (global and local), and therefore two sources of stochasticity. (b) Here, I plot five different cost values for the payoffs in the simple bet-hedging game in Table 4.2 and show the strategy z^* . $r = 0.5$; $S_1 = 4$; $S_2 = 1$.

4.6 Individual-based simulation

In the previous section, we solved directly for equilibrium strategies under the simplifying assumption that demes are identical in all parameters except local patch environmental state. This reveals the contribution of the fluctuating environment without the confounding effect of alternative sources of

inter-patch variation (e.g. variation in social effects between demes driven by local frequency-dependence). Practically, this means that individuals are effectively allocated randomly to demes each generation after selection (surviving adult offspring disperse across the landscape). As a result, demes do not develop locally-distinct allele frequencies, so starting allele frequencies on each patch for each bout of selection do not vary in space as we move over the landscape. This means that both (1) local frequency-dependence through the generations and (2) group selection between demes can be eliminated when solving for the ESS.

In this section, I show (using individual-based simulations) that relaxing this assumption – and instead permitting local build-up of independent intra-demic allele frequencies – has a relatively slight effect on the outcome in this simple cooperative game. Despite permitting local allele clustering, the simulation outcomes echo the analytical predictions in *Figure 4.3b*. Environmental fluctuation alone accounts for the major part of variation in outcomes.

I use simulations in *MATLAB* in discrete generations (code is provided in Appendix 2). For each deme, I allow asexual individuals to interact according to *Table 4.2* and *Table 4.3*, and vary the scale of competition by sampling a proportion a of future deme members from the home deme (in proportion to payoffs) and a proportion $1 - a$ from the offspring pool of the whole metapopulation (also in proportion to payoffs). Intermediate levels of cooperation predicted by a mixed ESS (Equation 4.27) can be achieved by either a (1) monomorphic population playing a mixed strategy or (2) a polymorphic population playing distinct pure strategies (Maynard Smith, 1973): in either case, the same predicted average level of cooperation ($\bar{z} = z^*$) will be achieved. Here, I compete two fixed strategies: constitutive cooperators ($z = 1$) versus constitutive defectors ($z = 0$).

Outcomes at two different cost values are shown in *Figure 4.4*, and follow the predictions of the unpacked Hamilton's rule (*Figure 4.3*). Constitutive cooperators ($z = 1$) invade a population of constitutive defectors ($z = 0$) to a metapopulation-level polymorphic equilibrium. This can occur when the scale of competition is sufficiently high to expose individuals to strong local fluctuations in baseline fecundity (*Figure 4.5*)

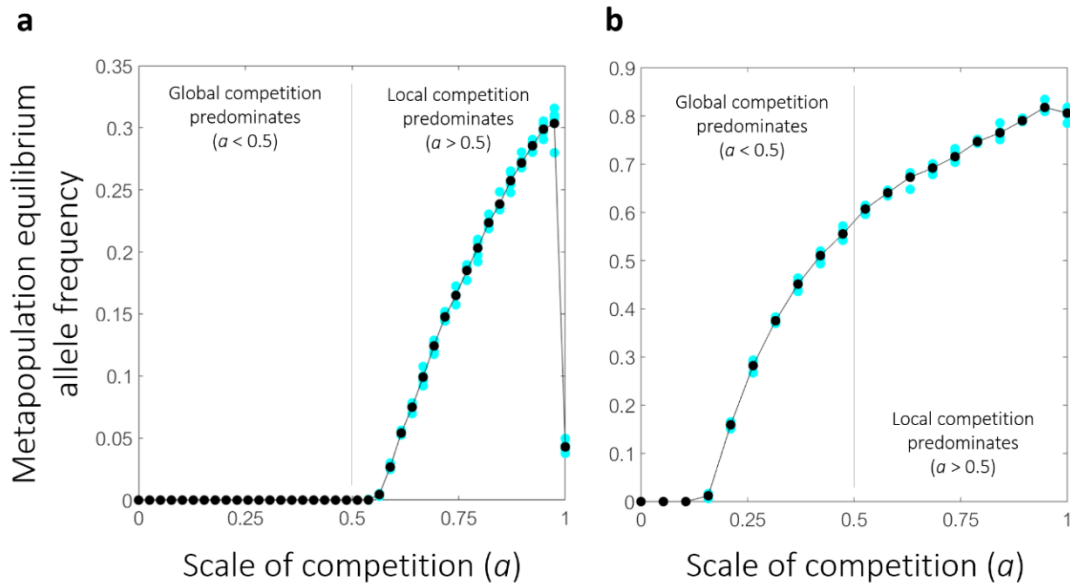


Figure 4.4 | Altruistic bet-hedgers invade fine-grained metapopulations with stochastic demes and local (intra-demic) competition. Simulation outcomes follow the analytical predictions in *Figure 4.3*. **(a)** Costs of cooperation $c = 0.3$; **(b)** Costs of cooperation $c = 0.1$. In each figure, each scale of competition value a is simulated five times (up to either fixation or 10,000 generations): mean end frequency across replicates is shown in black; individual replicates are shown in blue. Note that when competition is entirely local ($a = 1$) in the higher cost simulation (panel **a**), high levels of stochastic extinctions on demes occur, and cannot be reversed by migration (the ‘rescue effect’). This leads to a drop to a low frequency: there is a high risk of permanent stochastic extinction on each deme. $N_d = 1,000$, $D = 1,000$, $r = 0.5$, $S_1 = 4$, $S_2 = 1$, $P(\pi_1^* \leftrightarrow \pi_2^*) = 0.5$. Simulations start at $p = 0.01$.

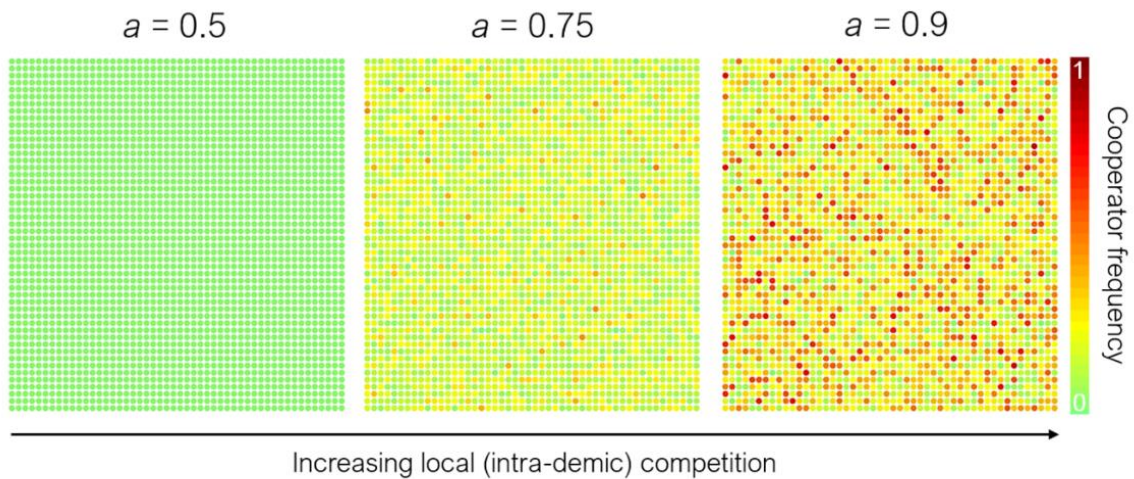


Figure 4.5 | Simulation results confirm that higher levels of local competition (a) lead to more successful penetration of the metapopulation by altruistic bet-hedgers. Each circle depicts a deme; the matrix is the entire metapopulation. Warmer colours denote higher intra-demic frequencies of the cooperator (altruistic bet-hedging). After 1,000 generations, the cooperator allele is extinct when competition is half-local and half-global ($a = 0.5$). The cooperator is polymorphically stable with non-cooperators at a whole-metapopulation level when competition is increasingly intra-demic ($a = 0.75$). When competition is highly intra-demic ($a = 0.9$), the effect of local environmental fluctuations is significantly amplified, leading to increased penetration of altruistic bet-hedging across the metapopulation. Cooperators start at $p = 0.05$ in all simulations. $N_d = 1,000$, $D = 400$, $r = 0.5$, $S_1 = 4$, $S_2 = 1$, $c = 0.3$, $P(\pi_1^* \leftrightarrow \pi_2^*) = 0.5$.

4.7 Stable coexistence of altruistic bet-hedgers and defectors in metapopulations

In Chapter 3, I showed that altruistic bet-hedging can generate intermediate allele frequencies at which there is zero expected change due to selection ($\mathbb{E}_\pi[\Delta\bar{G}] = 0$). However, I also emphasised that these expected polymorphisms can be vulnerable to collapse: a chance run of the same environmental state across a sequence of generations can drive one allele to fixation. This point has been made repeatedly in the non-social bet-hedging literature: a recent synthesis (Dean *et al.*, 2017) expresses it concisely as ‘*rare extended periods of environmental stasis purge variation, especially when selection is strong.*’

Intuitively, polymorphisms should be less vulnerable in metapopulations (Frank and Slatkin, 1990; Starrfelt and Kokko, 2012). At a metapopulation scale, the amplitude of allele frequency change is reduced. The duration required of any ‘*extended periods of environmental stasis*’ (Dean *et al.*, 2017) to drive fixation is increased. By making specific assumptions about the population, Frank and Slatkin (1990) note that the variance of the change in allele frequency across D demes is intra-demic variance divided by D . In this section, I show how this result can be arrived at from the Price equation formalism adopted in this chapter. The variance of allele frequency change is the variance of the multilevel Price equation (Equation 4.15):

$$\mathbb{V}_\pi[\Delta\bar{G}] = \mathbb{V}_\pi \left[\frac{\mathbb{C}_d(\bar{w}_d, \bar{G}_d) + \mathbb{E}_d[\mathbb{C}_i(w_{id}, G_{id})]}{\bar{w}} \right] \quad (4.67)$$

As above, we assume that group selection between demes is either absent or negligible ($\mathbb{C}_d(\bar{w}_d, \bar{G}_d) = 0$). Expressed in terms of the within-deme selection gradient, where W_{id} is the relative fitness of individual id ($W_{id} = \frac{w_{id}}{\bar{w}}$):

$$\mathbb{V}_\pi[\Delta\bar{G}] = \mathbb{V}_\pi \left[\mathbb{E}_d \left[\beta_{W_{id}, G_{id}} \mathbb{V}_\pi[G_{id}] \right] \right] \quad (4.68)$$

In the special case in which each deme has the same within-deme allele frequencies, $\mathbb{V}_\pi[G_{id}]$ is identical across all demes (denote this value γ), and can be removed from the expectation over demes:

$$\mathbb{V}_\pi[\Delta\bar{G}] = \mathbb{V}_\pi \left[\mathbb{E}_d[\beta_{W_{id}, G_{id}}] \right] \gamma \quad (4.69)$$

Under this unique condition, differences in the response to selection between demes are due solely to different values of the regression slope $\beta_{W_{id}, G_{id}}$ in different demes. If the set of state-dependent fitness effects is the same for all demes, then each deme samples $\beta_{W_{id}, G_{id}}$ from a common distribution. When these two simplifying conditions occur, the variance in allele frequency change is:

$$\mathbb{V}_\pi[\Delta\bar{G}] = \left(\frac{1}{D} + \frac{D-1}{D}\bar{\rho}_\beta\right)\mathbb{V}_\pi[\beta_{W_{id},G_{id}}]\gamma \quad (4.70)$$

where $\bar{\rho}_\beta$ is the average correlation in $\beta_{W_{id},G_{id}}$ across demes.

When the average correlation in the action of selection $\beta_{W_{id},G_{id}}$ between demes is zero ($\bar{\rho}_\beta = 0$), the variance in allele frequency change is the within-deme variance divided by the number of demes (D):

$$\mathbb{V}_\pi[\Delta\bar{G}] = \frac{\mathbb{V}_\pi[\beta_{W_{id},G_{id}}]}{D}\gamma \quad (4.71)$$

Accordingly, increasing deme structure (increasing D) and reducing inter-demic state correlations (reducing $\bar{\rho}_\beta$) reduces the variance of the probability distribution of possible changes in whole-metapopulation allele frequency. Without high-amplitude fluctuations, populations are infrequently displaced from the polymorphism frequency at which there is no expected change due to selection. I confirm this effect by adjusting the individual-based simulation: when deme number is small, additional demes prevent stochastic extinction (*Figure 4.6*), and high deme number D stabilises global fluctuation when local competition a is high (*Figure 4.7*) but not when local competition a is low (*Figure 4.8*).

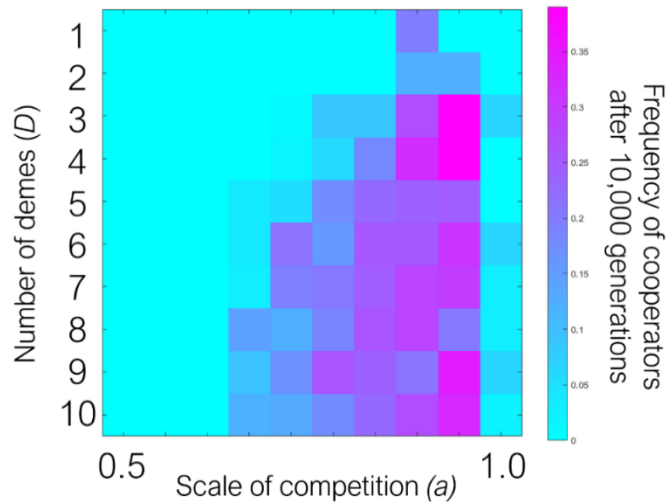


Figure 4.6 | **When populations are subdivided into few demes, additional demes increase the viability of altruistic bet-hedging.** We consider a population of 1,000 individuals, and connect it to 1–9 additional demes of 1,000 individuals. At all deme numbers, local (intra-demic) competition across the resulting metapopulation increases its capacity to sustain cooperation. Colours represent average relative frequencies sampled at 10,000 generations across five replicate simulations at each parameter combination. $N_d = 1,000$, $r = 0.5$, $S_1 = 4$, $S_2 = 1$, $C = 0.3$, $P(\pi_1^* \leftrightarrow \pi_2^*) = 0.5$.

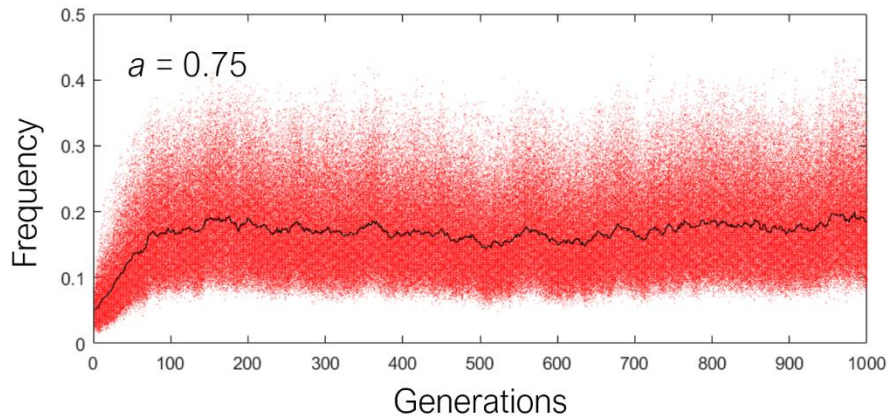


Figure 4.7 | **Metapopulations invaded by altruistic bet-hedgers maintain low-amplitude fluctuations in bet-hedger frequency, despite high-amplitude fluctuations at the level of individual demes.** Whole-metapopulation allele frequency is shown by the solid black line; red dots mark all intra-demic allele frequencies. The aggregate effect of uncorrelated environmental fluctuations across demes stabilises the global frequency despite high intra-demic stochasticity. Here, intra-demic competition predominates ($a = 0.75$). $N_d = 1,000$, $D = 400$, $r = 0.5$, $S_1 = 4$, $S_2 = 1$, $C = 0.3$, $P(\pi_1^* \leftrightarrow \pi_2^*) = 0.5$.

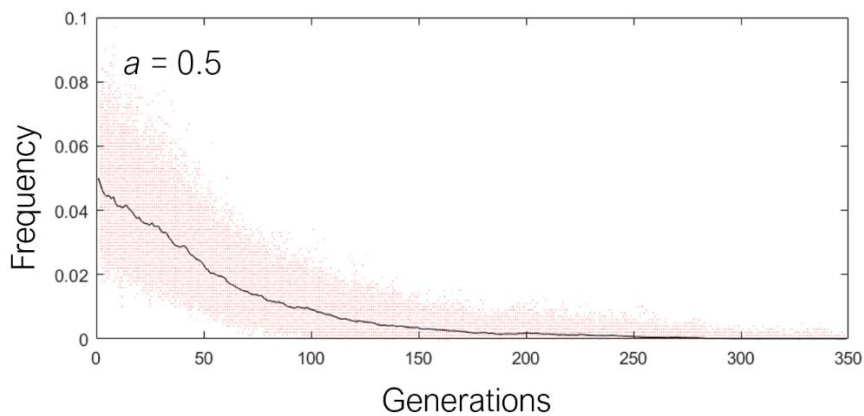


Figure 4.8 | **With rising global competition, local stochasticity is unable to sustain altruistic bet-hedging: bet-hedgers are not exposed to sufficiently high levels of stochasticity in their cooperative neighbourhood.** Whole-metapopulation allele frequency is shown by the solid black line; red dots mark all intra-demic allele frequencies. $N_d = 1,000$, $D = 400$, $r = 0.5$, $S_1 = 4$, $S_2 = 1$, $C = 0.3$, $P(\pi_1^* \leftrightarrow \pi_2^*) = 0.5$.

4.8 Conclusion

In this chapter, I have used the stochastic Hamilton's rule to capture the principle that populations that are globally stable (*i.e.*, showing no temporal fluctuation in population average reproductive success) can sustain bet-hedging, as long as local stochasticity is strong and competition is local. By

including social effects, this chapter extends this principle to altruistic as well as non-social bet-hedging. In particular, I have emphasised that empirical bet-hedging explanations based on demographic – as opposed to environmental – stochasticity face a high burden of proof. In line with Shpak and Proulx (2007) and Lehmann and Balloux (2007), biologists arguing from demographic stochasticity should demonstrate that size of the competitive neighbourhood is sufficiently small to allow average reproductive success to undergo meaningful local temporal fluctuations.

In summary, the viability of altruistic bet-hedging is influenced by several key parameters, which have been discussed in various non-social bet-hedging contexts (Frank and Slatkin, 1990; Shpak and Proulx, 2007; Lehmann and Balloux, 2007; Starrfelt and Kokko, 2012; Schreiber, 2015). Here, I (1) extend these results to social evolution by showing how they influence different components of a stochastic Hamilton's rule and (2) analyse bet-hedging with the scale of competition made explicit in a single coefficient. The key parameters are: (a) the scale of competition, (b) local and global sources of stochasticity, (c) deme population size (in the case of intra-demic demographic stochasticity), and (d) deme number (in the case of local competition). The crucial importance of demography highlights an important empirical direction for resolving the emerging links between sociality and stochasticity. To uncover the tantalising potential role of bet-hedging in social evolution, especially in the evolution of cooperative breeding and eusociality (Stevens *et al.*, 2007; Cockburn and Russell, 2011; Rubenstein, 2011), we must first identify the spatial scale at which the recipients of altruism face competition for reproduction and survival.



Road to Sinnamary, French Guiana

Chapter 5

5 | Drifting in *Polistes canadensis*: do drifters pursue a specific behavioural strategy?

5.1 Chapter Summary

Workers in the Neotropical paper wasp *Polistes canadensis* show high levels of between-colony movement (a behaviour known as ‘drifting’). As a result, ‘drifter’ workers appear to squander helping effort on foreign colonies, paying a high cost to indirect fitness with no apparent justification. Although observed by W. D. Hamilton and flagged as a paradoxical ‘anomaly’ to inclusive fitness theory in 1964, drifters in *P. canadensis* continue to pose an unsolved problem for the logic of kin selection. Here, using radio-frequency identification (RFID) tagging and behavioural observation, I ask whether drifters differ from non-drifters in cooperative behaviour, aggression, size, and dominance rank. Experimental removal of queens in an RFID-tagged population of 1,450 wasps showed that, contrary to expectation, drifters are not universally low-ranking subordinates, and are found at all levels of dominance hierarchies. Drifters do not differ from non-drifters in ovary activation or participation in the struggle for nest-inheritance. I find no evidence that drifting is part of a specific set of correlated behaviours: drifter wasps are indistinguishable from non-drifters in behavioural and morphological phenotype.

5.2 Introduction

Eusocial societies play host to a diversity of actors with different – and sometimes incompatible – agendas (Starks, 1996; Tibbetts, 2007; Jandt *et al.*, 2013). In the simple eusocial wasps, a ‘queen’ monopolises reproduction whilst her subordinate ‘workers’ raise the brood. This sharp division of labour arises socially rather than physiologically (Boomsma and Gawne, 2018; Sumner *et al.*, 2018); workers are capable of mating and egg-laying, but refrain from doing so whilst the queen maintains her social dominance (Tibbetts *et al.*, 2011). To understand how organisms maximise fitness within these dynamic and heterogeneous societies (Theraulaz *et al.*, 1990), biologists have long sought to identify sets of correlated behavioural traits. However, the ultimate drivers of behavioural diversity are not fully understood (Zanette and Field, 2009; Torres *et al.*, 2013; Wright *et al.*, 2018), and pinpointing drivers of behavioural variation within the colony is a central focus for the field (Wright *et al.*, 2018).

It is now clear that wasps in the simple eusocial genus *Polistes* traffic between colonies at high rates (a behaviour known as ‘drifting’). A number of authors have reported between 10% and 56% of wasps visiting neighbouring colonies (*P. canadensis*: Pickering 1980; Sumner *et al.*, 2007; Lengronne 2013; *P. chinensis*: Kasuya 1981; *P. jadwigae*: Tsuchida and Itô 1987). The discovery of high rates of drifting in *Polistes* suggests a potentially neglected driver of behavioural variation in simple eusocial societies: in principle, drifters and non-drifters may pursue different inclusive fitness agendas (Sumner *et al.*, 2007). However, we lack detailed behavioural profiles for drifting wasps. Here, I ask whether drifters differ from non-drifters in the key traits that characterise *Polistes* wasps.

Why drifting exists at all has long been a paradox (Hamilton, 1964b; Pickering, 1980; Sumner *et al.*, 2007; Lengronne, 2013; Nonacs, 2017). By drifting to a neighbour colony, a *Polistes canadensis* worker experiences more than a two-fold reduction in relatedness to the brood (changing her indirect fitness interests; Sumner *et al.*, 2007), is exposed to an alternative dominance hierarchy (changing her direct fitness interests), and may risk aggressive rejection (potentially leading to injury or death). Drifting in social insects has often been linked to direct fitness maximisation (Blacher *et al.*, 2013; Härtel *et al.*, 2006). In bumblebees (*Bombus terrestris*), Blacher *et al.* (2013) conclude that fertile drifters are pursuing a pre-determined strategy of parasitic egg-laying in unrelated colonies. In the common yellowjacket (*Vespula vulgaris*), Oliviera *et al.* (2016) find that incoming drifters possess active ovaries at a frequency five times greater than residents. In the Cape honeybee (*Apis mellifera capensis*), a mutant lineage of females reproduces clonally, parasitically lays eggs, and drifts through the colony population as a superorganismal version of transmissible cancer (Beekman and Oldroyd, 2008). In each case, drifting is part of a parasitic behavioural strategy: drifting correlates with egg-laying and behavioural traits that permit successful infiltration of hostile colonies.

In contrast to these results from other taxa, *P. canadensis* drifters have previously been shown to lack active ovaries. A general lack of ovary activation suggests a reason for drifting other than parasitic egg-dumping (Sumner *et al.*, 2007). The prevailing hypothesis is that *P. canadensis* drifters are non-reproductive workers attempting to maximise indirect fitness by strategically directing help to related neighbour queens (Hamilton, 1964b; Sumner *et al.*, 2007; Lengronne *et al.*, 2012): this hypothesis would predict that drifting correlates with ‘cooperative’ behaviours (*e.g.*, high rates of foraging and low rates of aggression, and a lack of participation in the struggle for nest inheritance). An alternative direct fitness possibility is that, given the potential for frequent queen supersedure in *P. canadensis* (Toth *et al.*, 2016), drifters may visit multiple colonies to maximise their chance of participating in a competitive inheritance struggle following the death or loss of foreign queens (Sumner *et al.*, 2007), at which point ovaries can be activated. If drifting is associated with a specialist strategy (*e.g.*, minimising foraging and

maximising dominance), it is possible that individuals with different body sizes show different tendencies to drift, which I test here.

In this chapter, I use a combination of radio-frequency identification (RFID) tagging and field censuses to identify drifters in *P. canadensis*. I then use experimental queen removal to trigger the aggressive fight for nest inheritance on focal colonies, which reveals the otherwise-cryptic dominance status of wasps on the colony. I then test the following hypotheses: (1) drifters and non-drifters differ in total behavioural profiles; (2) drifters and non-drifters differ in dominance during the nest inheritance struggle; (3) drifters target nest inheritance opportunities; and (4) drifters and non-drifters differ physically (body size and ovary activation).

5.3 Methods

5.3.1 Study site and species

P. canadensis L. is an independent-founding simple eusocial wasp, distributed widely across South and Central America (Figure 5.1a; West-Eberhard, 1986; Carpenter, 1996). The genus *Polistes* comprises around two-hundred species distributed in both temperate and tropical habitats, and has developed into a model genus for social evolution, largely because nests lack covering envelopes and so allow non-invasive observation. As a tropical polistine, *P. canadensis* nests are founded year-round by both single foundresses and closely-related co-foundresses (West-Eberhard, 1986; Sumner, Kelstrup and Fanelli, 2010; Lengronne, 2013; Southon et al., unpublished); this differs from the seasonal nest-founding that characterises the well-studied temperate *Polistes* species *P. dominula*, where nests are founded synchronously after foundresses emerge from a winter hibernation (Leadbeater et al., 2011). Typically one individual (the ‘queen’) becomes the egg-layer (monogyny) whilst co-foundresses and her daughters act as non-reproductive workers (Sumner et al., 2010). Unlike an ‘advanced’ eusocial species, reproductive division of labour is not driven by strict and irreversible morphologically-imposed differentiation into distinct ‘queen’ and ‘worker’ roles in *Polistes* (West-Eberhard, 1986; Sumner et al., 2010; though see De Souza et al., 2016, for evidence of incipient physical differentiation between workers and queens in *P. ferreri* and *P. versicolor*). Instead, reproductive division of labour arises behaviourally: helpers ‘choose’ to help, but remain capable of activating ovaries, mating, and egg-laying. Nonetheless, experimental data reveals a decline in fertility and loss in behavioural plasticity with age (Sumner et al., 2010; Bell, 2016): younger individuals are likely to be more competitive and successful queen replacements.

Colonies proceed through a stereotyped nesting cycle, divided into three broad phases: (1) pre-emergence (before the emergence by pupation of the first offspring), (2) post-emergence (beginning with the first emergence), and (3) declining phase (the end of a colony's life, characterised by brood death, workers absconding, a decline in queen fecundity, and the eventual collapse of the colony). If the resident queen dies before the nest has entered terminal decline, queen succession can occur; the new queen is established through extended aggressive dominance confrontations (this chapter), rather than following a peaceful age-based convention. Colonies typically occur in aggregations (Sumner et al., 2007; Lengronne, 2013), frequently on derelict or undisturbed buildings (Jeanne, 1979; Pickering, 1980; Giray et al., 2005; Sumner et al., 2007, 2010, Torres et al., 2009, 2013).

P. canadensis shows some behavioural differences across the range, but the extent to which these reflect local adaptation versus plasticity remains unstudied. Although evidence remains incomplete, the nesting cycle of *P. canadensis* is likely to differ latitudinally as a consequence of latitudinal differences in nest architecture. In the Guianas and Amazon, colonies are split into closely packed but discrete combs oriented horizontally, potentially to limit brood loss to parasites (Jeanne, 1979; Downing and Jeanne, 1986), whereas Central American and Colombian colonies possess only a single comb suspended vertically (West-Eberhard, 1986). The modular nature of *P. canadensis* nests in French Guiana (unlike Panama) may enable nesting sites to be used in perpetuity through a sequence of queens ('serial polygyny') as new combs are annexed and old combs are removed. In Panama, by contrast, nests are typically composed of a single comb, and the destruction of one comb consequently results in the complete destruction of the entire brood (see Chapter 5). Colonies face whole-comb predation by army ants and birds, and brood loss to predatory dipteran larvae (see Chapter 5) alongside lepidopteran and hymenopteran parasitoids (Jeanne, 1979). Individual workers also face high death rates: Sumner et al. (2007) estimate a 7% chance of death per day.

I studied a free-living aggregation of 33 *P. canadensis* colonies (32 post-emergence and one pre-emergence) in Sinnamary, French Guiana (Rue Damerette: 5°22'27.12", -52°57'26.64"). The site was within 350 m of the Flueve Sinnamary river in a small town surrounded by lowland tropical forest (*Figure 5.1b*), and within an abandoned house (*Figure 5.1c*).

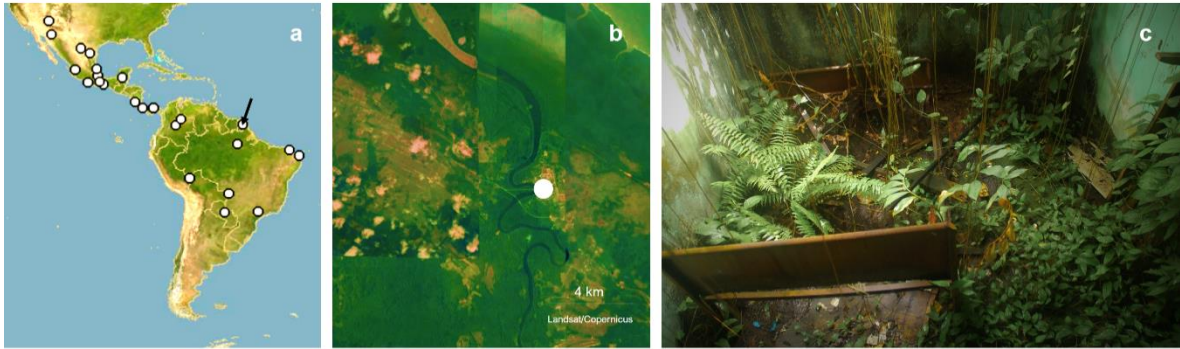


Figure 5.1 | **Study site.** (a) French Guiana (black arrow) is in the mid-Neotropical range of *P. canadensis*. White circles denote distribution records of *P. canadensis* from the Global Mapper project (Polistes Foundation, 2018). (b) The study population was in the small town of Sinnamary. (c) The focal aggregation inhabited a derelict house (part of the interior shown). Photograph: PK.

5.3.2 RFID tagging and paint marking

For each colony, I identified egg-layers (single queens) by observing egg replacement after experimentally removing an egg, which typically occurs within 30 min. Egg-layers were marked with a unique paint code on the thorax, and (as queens remain on the nest at all times) did not receive RFID tags. I radio tagged and colour marked 1,450 adult wasps across the 33 colonies (Figure 5.2), representing effectively the entire adult population. I removed wasps gently from colonies using forceps, and tagged and marked each individual swiftly to minimise disturbance. I attached low-frequency passive RFID tags (GiS TS-Q5 BeeTags, 18 mg, less than 1% of female mass; Sumner et al., 2007) with unique hexadecimal number codes to the thorax with a small quantity of cyanoacrylate Loctite glue, and held the wasp for 30 s to ensure fixture.

I added wasp-specific colour codes to the upper half of the wings using Posca pens (standardly used for paint-marking on the thorax; Yagound *et al.*, 2017). I measured the wing length of each wasp (to the nearest hundredth of a millimetre) using digital callipers; wing length is a commonly used proxy for total body size in *Polistes* (Nonacs and Reeve, 1995). I also recorded eye colour (older wasps possess red eyes, whilst wasps <3 days old possess black and brown eyes; Pickering 1980). Since Strepsiptera parasites are known to influence *Polistes* nest-leaving and aggregation behaviour by brain manipulation (Geffre *et al.*, 2017), I inspected all wasps for Strepsiptera, and recorded if the puparia or the cephalothorax of strepsipterans were extruding from the abdominal stergites. I released wasps immediately after inspection to ensure stable fixture of the tag and that glue was restricted to a small area of the upper thorax (and so not affecting wing movement). Young adults (black or brown eyes) were placed back on the colony with forceps to ensure safe return, as they may not yet have oriented from the nest. Older adults were released near the colony and monitored to ensure capable flying with

the tag (Sumner *et al.*, 2007). Wasps were retagged following the same method if the tag was lost during the experiment.



Figure 5.2 | **RFID-tagging and colour coding.** Each wasp ($n = 1,450$) received a unique RFID tag and a six-colour individual paint code on the wings. GiS TS-Q5 BeeTags are the smallest commercially available passive transponder RFID tags, weighing 18 mg, which minimises weight carried by wasps. Tags do not have a detectable influence on wasp drifting (Sumner *et al.*, 2007). Photograph: PK.

I fitted each colony with 2–6 GiS TS-A27 RFID antennae (representing equal coverage by nest size) with 3 cm detection radii (Sumner *et al.*, 2007), comprising a total of 64 RFID antennae across the aggregation. Each antenna was paired with a separate data-reader (GiS TS-R64) to record the detection times of the individually identified tags. Data were collected from readers at the end of each detection day (after 7 pm). Readers and antennae were powered using an array of nine car batteries wired with electrical cords. Colonies were screened with acetate sheets, which restricted wasp flight paths to within approximately 10 cm of the antennae, following methods in Sumner *et al.* (2007) and Lengronne (2013), where colony screening did not deter continued entry and exit. When the same wasp was detected more than once within a two-minute time window, all observations after the first were discounted (*i.e.*, repeat detections within 120 s were treated as a single detection); 120 s allows sufficient time for the wasp to pass the antennae (a single detection bout). Wasps were not detected on the nest, but rather on entry and exit flightpaths. Note that the data are silent on whether wasps were entering or exiting during any one detection bout, and not all passages past the antennae are detectable; we therefore do not calculate time on nest for individuals.

I surrounded each colony with RFID antennae in 360 degrees (Figure 5.3). Because colonies in *P. canadensis* are comprised of multiple combs in the southern part of the range (see *Study site and species*, above), the antennal array differs here to that used by Sumner *et al.* (2007), who studied a Panamanian population and so placed RFID antennae over the front of single vertically hanging comb.

I matched RFID data with behavioural observations, associated daily censuses, and *ad libitum* records (when an observer noted a wasp in a foreign colony opportunistically, outside of an observation window) in both the pre- and post- manipulation phases. In all analyses, a ‘drifter’ was defined as any wasp detected via any method (tagging, RFID, and visual observations) on two or more colonies across the monitoring period (pre-manipulation and post-manipulation phases). To identify drifters, I used a combination of automated and visual methods to maximise detection probability and minimise false negatives (drifters not detected drifting). Note that by classifying individuals according to whether or not they actually drifted during the monitoring period, we make no prior assumptions about whether individuals are in two distinct adaptive classes, follow a continuum of drifting probabilities, or all become drifters with the same random events. This question is distinct from whether or not drifting is associated with specific behavioural strategies. For instance, in bumble bees (*Bombus terrestris*) drifting may occur accidentally (a random distribution per individual), but – once individuals find themselves in foreign colonies – they may up-regulate a specific set of opportunistic behaviours (Birmingham *et al.*, 2004; but see Blacher *et al.*, 2013).

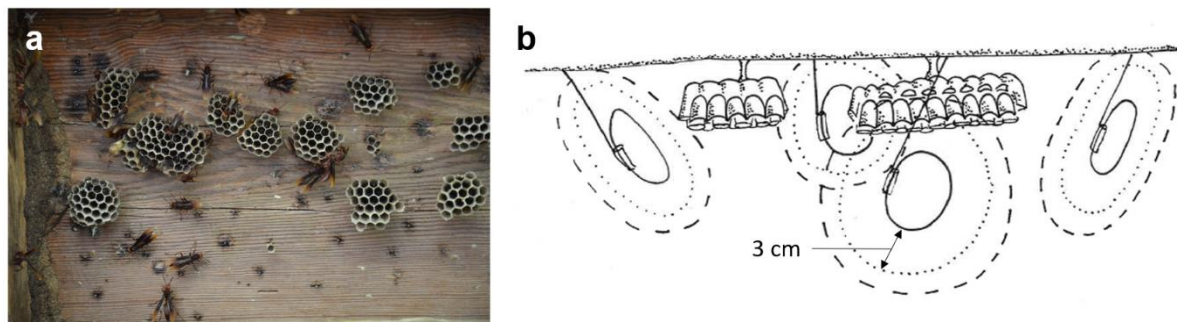


Figure 5.3 | *P. canadensis* colonies in the Guianas and Amazon are comprised of multiple horizontally-positioned combs (Jeanne, 1979). (a) View of a colony in Sinnamary. Photograph courtesy of Dr B. Corbara. (b) RFID antennae positioned around the combs. Antennae reading ranges are shown by dotted lines.

5.3.3 Monitoring responses of drifters to experimental removal of the queen

To ask whether drifting wasps participate in the competition for nest inheritance, I experimentally removed queens within the colony aggregation. A similar experiment has been performed for the advanced eusocial common wasp *Vespula vulgaris* (Oliveira *et al.*, 2016), in which queen removal was triggered on two focal colonies within an artificial aggregation of four colonies. Removing the resident queen alters the expression of dominance behaviour considerably (Tibbetts and Huang, 2010). In tropical *Polistes*, the resulting nest-inheritance struggle – in which high-ranking subordinates compete to become the single egg-layer – is characterised by stereotyped aggressive interactions and ritualised

submission postures between interacting pairs of wasps, allowing a robust dominance network to be constructed. To minimise disturbance to the wider population (and so maximise ecological validity), I restricted the queen-removal manipulation to a subset of seven of the 33 colonies within the aggregation; henceforth, these experimentally manipulated colonies are referred to as the ‘focal colonies’. Previous research on *P. canadensis* drifting has shown that drifting networks are typically structured into local clusters: close nests form partially discrete drifting subnetworks, such that disturbance in one part of the subnetwork is likely to affect other colonies in the subnetwork (Sumner *et al.*, 2007; Lengronne 2013). Accordingly, to minimise confounding interactions between queen removals at different colonies, I used stratified random sampling by dividing the aggregation into seven visually identifiable colony clusters and randomising selection of the focal colony within each cluster.

To test whether drifters change their behaviour by targeting nest inheritance opportunities when they arise, I monitored the nest visitation networks of all 1,450 RFID-tagged wasps either side of the queen removals. I sampled the pre-manipulation aggregation using RFID for seven days before and seven days following manipulation (9 pm–7 pm each day). Following Lengronne (2013), I used worker-to-brood ratio as a measure of the needs of the colony. I counted brood and recorded adult group sizes at the beginning of each manipulation phase and 12 days after queen removal. Brood counts were made during the daytime by shining a torch into each cell, recording the number of eggs, larvae (small, medium, and large, following Bell, 2016), and pupae present. To record adult group size accurately, colony size was censused at night (after 9 pm) using a red-light torch.

5.3.3.a *Behavioural observations*

To quantify aggressive and cooperative behaviours (Itô, 1985; Bell, 2016), I recorded all on-nest behaviours and social interactions (*Table 5.1*). Behaviours were recorded in a series of 2 h daily observation windows (using manual recording of behaviours in field observation supplemented with video recording, to allow for more observation windows than are possible from manual observations alone). I observed colonies for seven days pre-manipulation and a minimum of seven days post-manipulation. If the struggle for nest inheritance continued beyond seven days, observations were continued until (1) a new queen was confirmed by observation of egg-laying (both observed behaviourally and following experimental removal of an egg to precipitate egg replacement), and (2) subsidence of on-nest aggression. Focal colonies were therefore tracked for 7, 11, 12, 12, 23, and 26 days post-manipulation.

Here, I have followed the established method, as used in previous analyses of drifting in *Polistes* (Sumner *et al.*, 2007; Lengronne 2013), of assigning wasps to a starting colony based on where they are

initially tagged. For most individuals, this will be the natal colony (Sumner *et al.*, 2007); however, in some cases, wasps may be drifting when tagged. For a minority of drifters, the starting colony will not be the natal colony. In this thesis, I explicitly use the term ‘tagging colony’ as the colony where wasps began the experiment. With this caveat, I define a drifting wasp as an ‘in-drifter’ on the focal colony if it was tagged on a different colony, and an ‘out-drifter’ if the focal colony is also the tagging colony and the wasp was recorded on a separate nest.

Table 5.1 | Ethogram of key monitored behaviours. Behaviours identified as ‘aggressive’ were used in the percolation-conductance algorithm to predict dominance percentile.

Social behaviour (and abbreviation in PCA plot)	Aggressive	Cooperative	Description
Antennation	×	✓	Antennal inspection of wasp <i>B</i> by wasp <i>A</i>
Receive trophallaxis (<i>Rec T</i>)	×	✓	Transfer of liquid food by regurgitation from wasp <i>B</i> to wasp <i>A</i>
Receive food (<i>Rec F</i>)	×	✓	Transfer of solid food from large food ball from wasp <i>B</i> to wasp <i>A</i>
Bite	✓	×	Bite to wings, legs, head, or thorax of wasp <i>B</i> by wasp <i>A</i>
Lunge	✓	×	Sudden fast approach of wasp <i>A</i> towards wasp <i>B</i> without walking or moving tarsi placement
Chase	✓	×	Fast pursuit of wasp <i>B</i> by wasp <i>A</i> across the comb surface
Sting	✓	×	Attempted sting by wasp <i>A</i> , accompanied by abdomen twisted underneath thorax towards wasp <i>B</i>
Dominate	✓	×	Submission posture (flattened body, pressed to nest surface) adopted by wasp <i>B</i> post-antennation or close approach by wasp <i>A</i>
Deny	✓	×	Wasp <i>A</i> refuses to transfer food to wasp <i>B</i> following solicitation by <i>B</i>
Falling fight	✓	×	<i>A</i> and <i>B</i> both fall from the nest during a struggle, with one or both individuals grasping the other
Non-social behaviour	Description		
Check cells	Inspection of multiple cells (brood-containing or empty)		
Feed brood	Transfer of water or foodstuff to larva. Head fully within a brood-containing cell for a minimum of 5 s.		
Build cells	Layering of pulp to build a new cell or add to an existing cell		
Process food	Manipulation of a solid food ball by mandibles		
Abdominal wagging (<i>Ab wag</i>)	Rapid horizontal vibration of abdomen		
Arrive/leave	Arrival or departure from the nest (foraging)		
Larval cannibalism	Consumption of live brood		
Lay egg	Production of a new egg in an empty cell		

5.3.3.b *Reproductive status*

At the completion of all nest inheritance competitions (26 days following queen removal), I collected identified drifters still present ($n = 35$) together with a random sample of non-drifters ($n = 41$). Note that the small number of surviving tagged drifters available for collection is due to the rapid turnover of the population (in Sumner *et al.*, 2007, daily mortality probability for individual wasps was 7%) and the difficulty of recovering specific individuals (a similar proportion of surviving target wasps was recovered by Sumner *et al.*, 2007). I scored ovaries for developmental status following the five categories of Gobbi *et al.* (2006), listed in Figure 5.4.

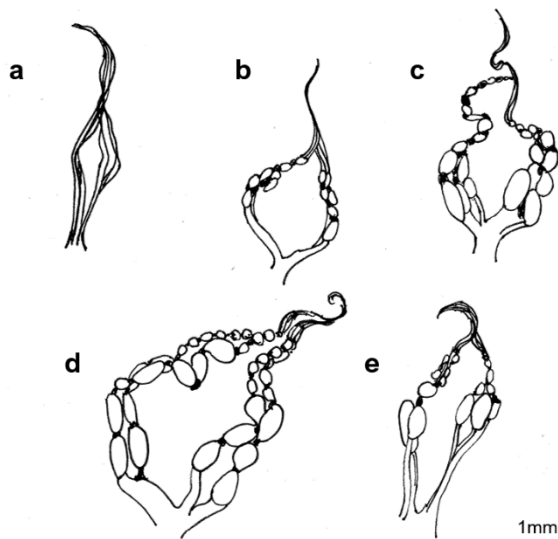


Figure 5.4 | Grades of ovary development. (a) Ovarioles lack oocytes. (b) Ovarioles carry small, early-stage oocytes. (c) Large, maturing oocytes at fork in ovary. (d) Large number of highly-mature oocytes. (e) Resorption of oocytes in a previously mature ovary. Figure redrawn and adapted from Gobbi *et al.* (2006).

5.3.3.c *Statistical methods*

Analyses: I used Bayesian mixed models in *WinBUGS* (Lunn *et al.*, 2000) with diffuse (wide variance) normal priors (Kéry, 2010) for fixed effects and $\mathcal{N}(0, \tau_u)$ for random effects, with diffuse gamma hyperpriors for τ_u . I ran all analyses for 100,000 iterations of Markov Chain Monte Carlo (MCMC) using Gibbs sampling and zero thinning (Link and Eaton, 2012), and assessed cross-chain convergence via the Gelman-Rubin diagnostic (Gelman and Rubin, 1992). In all models, convergence occurred quickly. For each model, I present the means, medians, and 95% credible intervals for the relevant parameters.

Throughout this and subsequent chapters, I treat non-overlap with zero of the 95% credible intervals as grounds for concluding the effect to be plausibly different from zero (Kéry, 2010), *i.e.* 'credible'. All credible effects are highlighted in bold in the results tables below. For model selection, I used Bayesian model averaging via indicator variable selection by assigning each predictor i an indicator variable g_i with a Bernoulli (0.5) prior (Kuo and Mallick, 1998; Ntzoufras, 2002). Higher values of g_i (*i.e.*, closer to 1) indicate a higher rate of contributing to the optimum model during MCMC. For each averaged model, I present the posterior estimates for each parameter, together with the posterior mean for each associated selection indicator g_i in brackets.

For model checking, I calculated Bayesian residuals within *WinBUGS*, and assessed graphically for autocorrelation. I used posterior predictive checks of the fitted model by (1) confirming graphically that the observed scatter falls within the credible region predicted by the fitted model, (2) checking that standardised residuals fall between -2.0 and 2.0 for most data points (Conn *et al.*, 2018), and (3) calculating goodness-of-fit 'posterior predictive p -values' (PPPs) for Normal linear models. The optimal model should have a PPP of 0.5 (Gelman, 2013). There are multiple candidate test statistics for the PPP (Conn *et al.*, 2018); each one is a measure of the discrepancy between model and data. Here, I followed Kéry (2010) in using the residual sum-of-squares as the discrepancy measure.

I tested the following four hypotheses:

Hypothesis 1: Drifters and non-drifters differ in total behavioural profiles. All behavioural analyses were restricted to wasps that featured in behavioural observations on the focal colonies ($n = 230$ non-drifters, $n = 55$ in-drifters, $n = 41$ out-drifters). First, to confirm that queen removal led to an up-regulation of aggression on the focal colonies, I used a simple mixed model of wasp aggression with focal colony as a random effect. I used principal components analysis (PCA) to detect correlations between all behaviours in the ethogram (*Table 5.1*) including all data from pre- and post- manipulation phases in order to ask directly whether manipulation drives a shift in PCA score. I used the *R* package *FactoMineR* (Lê *et al.*, 2008), and visualised results using the package *factoextra* (Kassambara and Mundt, 2017). All variables were mean-centred and standardised by variance before PCA (Abdi and Williams, 2010). I ran mixed models separately for the first and second principal component, with focal colony, tagging colony, and wasp as random effects, experimental phase (*i.e.*, pre- and post- manipulation) as a dummy variable, and wasp type (non-drifter, in-drifter, or out-drifter) as a categorical fixed effect.

Hypothesis 2: Drifters and non-drifters differ in dominance during the nest inheritance struggle. I tested the hypothesis that drifters are low ranking subordinates: participation and success in the nest inheritance struggle reveal whether wasps are low or high in the dominance hierarchy. I inferred dominance hierarchy percentiles using the six post-manipulation aggressive networks revealed by

queen removal. To obtain estimated dominance ranks for the colonies undergoing the nest inheritance struggle ($n = 242$ wasps), I used the percolation-conductance algorithm provided by the package *Perc* in *R* (Fujii *et al.*, 2016) on all behaviours classified as 'aggressive' in *Table 5.1*. This algorithm allows for inferences to be made on dominance networks by taking indirect social links into account. Because dominance status is largely cryptic until aggressive confrontations are triggered by the death of the resident queen, dominance percentile ranks refer to ranks on the focal colonies undergoing the nest inheritance struggle, not the natal or tagging colony of drifters. I used a linear model of within-colony inferred dominance percentile, with wasp type (non-drifter, in-drifter, and out-drifter) as a fixed effect. In practice, there may be little difference in dominance status between wasps outside the upper percentiles; I therefore also used a more focused logistic model, with a dummy response variable for whether the focal wasp was within the upper tenth percentile for predicted dominance status on the colony.

Hypothesis 3: Drifters target nest inheritance opportunities. If drifters show a shared response to queen loss, I expect the drifter class as a whole (out-drifters and in-drifters) to change its investment in the focal colonies following manipulation. I tested this hypothesis using a binary logistic regression, in which individual drifters have two options: (1) visit non-focal colonies (queenright) or (2) visit focal colonies (queenless after manipulation). To focus on a standardised measure of drifter investment, I restricted the analysis to the 98 RFID-detected drifters (individuals who drift in either the pre- or post-manipulation phase), which constituted 2,141 radio-detections. If drifting occurs randomly across all nests, non-manipulated nests ($n = 26$) should receive 3.71 times as many drifting events as manipulated nests ($n = 7$). To take account of additional pre-existing differences in drifting rate that many occur for extrinsic reasons, I compared the log-odds of drifter preference between the two nest categories either side of the manipulation, with experimental phase and main colony (most visited colony) worker-to-brood ratio as fixed effects. I included drifter and main colony (most visited colony) as random effects.

The preceding analysis did not allow for a diversity of strategies amongst drifters: drifting for nest inheritance might plausibly be a strategy pursued only by a high-ranking subset of drifters. If nest inheritance drifters represent a high-ranking subset of the total drifter class that react strategically to the opportunity for nest inheritance, this subset would be expected to increase time investment in the focal colonies. I therefore ran a more focussed model with the inferred dominance status of individual wasps (generated above by percolation-conductance) as an additional predictor, using the dataset of 44 RFID-detected drifters who featured in the on-colony behavioural data for the simulated annealing of dominance rank, and allowed for an interaction between dominance rank and experimental phase.

Hypothesis 4: Drifters and non-drifters differ physically. First, using wasps for which wing measurements were available ($n = 152$ drifters, $n = 1,055$ non-drifters), I tested for a difference in body size (using wing length as a proxy). Second, to ask whether dissected drifters and non-drifters differ in ovary activation, I used a logistic mixed model with colony as a random effect, in which ovary grade categories C, D, and E were considered ‘active’ and categories A and B were considered ‘inactive’ (Figure 5.4). To test for differences in egg size and egg number between drifters and non-drifters, I used linear mixed models (with colony as a random effect).

5.4 Results

RFID tagging: RFID-tagged colonies ranged in size from 2 to 61 workers. A total of 856 wasps were detected by RFID across the experiment, representing 59.0% of the 1,450 originally RFID-tagged wasps. Of these, 680 wasps (48.9% of the tagged population) were detected more than once by the RFID-antennae. This is similar to the 37.2% of the tagged population in Sumner *et al.* (2007), suggesting that RFID tagging was comparably effective despite the difference in colony architecture between French Guiana and Panama. In the pre-manipulation phase, RFID-detected wasps had 12.9 ± 44.0 (mean \pm SD, range = 1–567) radio-detections. In the post-manipulation phase, RFID-detected wasps had 19.3 ± 56.8 (mean \pm SD, range = 1–505) radio-detections.

In total, two hundred and sixteen drifters (14.9% of the population) were identified. Ninety-eight drifters were detected by RFID alone; an additional 118 were detected by *ad libitum* visual observation and behavioural monitoring. Of the RFID-detected population, 7.2% (49/683) were detected by RFID visiting multiple colonies in the pre-manipulation phase (Figure 5.5a), and 10.4% of the RFID-detected population (65/625) were detected by RFID in the post-manipulation phase (Figure 5.5b). 31 wasps were detected by RFID on only a single colony but one that differed from their tagging colony (which plausibly represent a permanent switch since tagging); including these as drifters, the pre-manipulation RFID-detected drifting rate was 13.1% (80 drifters of 610 wasps detected by RFID in the pre-manipulation). Only 16 wasps were detected by RFID visiting multiple colonies within both phases. Of the total recorded drifters, 66.2% (143/216) appeared on the seven intensively-observed focal colonies at least once during the experiment or tagging. There was no evidence that Strepsiptera infection rates differed between drifters and non-drifters: only four of the 1,450 wasps showed extruding Strepsiptera, each on different colonies.

Queen removal: Queen removal led to aggressive competition for nest inheritance on six of the seven focal colonies; one of the seven colonies was immediately abandoned by adult wasps following queen removal and was removed from analysis. Bites represented the largest percentage of aggressive

interactions (86% of post-manipulation aggression, $n = 2,658$ aggressive interactions), and experimental phase credibly increased the hourly bite rate on the focal colonies (*Table 5.2*).

The six eventual new queens were all resident wasps of the colonies they inherited: no in-drifters inherited the nest. RFID data showed that three of these six new queens showed out-drifting behaviour to foreign colonies before becoming queen: (1) one future queen drifted to the closest neighbour nest during the post-manipulation period; (2) another future queen drifted to the closest neighbour nest during both the pre-manipulation and the post-manipulation periods; and (3) a third future queen drifted to two close neighbours, once each, during the pre-manipulation, and once to one of these neighbours during the post-manipulation. (These accounts of future queens previously drifting are necessarily anecdotal: a formal analysis is impossible with such a small sample.)

Table 5.2 | Posterior estimates for change in hourly bite rate on focal colonies following experimental queen removal. 100,000 iterations MCMC.

Variable (+ indicator)	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	0.028	2.997	0.013	-6.047	0.105	5.988
Experimental phase (queen removal) ($g = 0.988$)	0.368	0.358	0.002	0.199	0.377	0.495
Model precision	1.290	0.084	0.000	1.130	1.288	1.460
Focal colony (random effect) precision	4.3E-13	1.0E-10	6.2E-13	0.000	0.000	1.8E-25
Bayesian R^2	0.015	0.065	3.0E-4	-0.121	0.018	0.133
Posterior predictive p -value	0.498	0.500	0.002	0.000	0.000	1.000

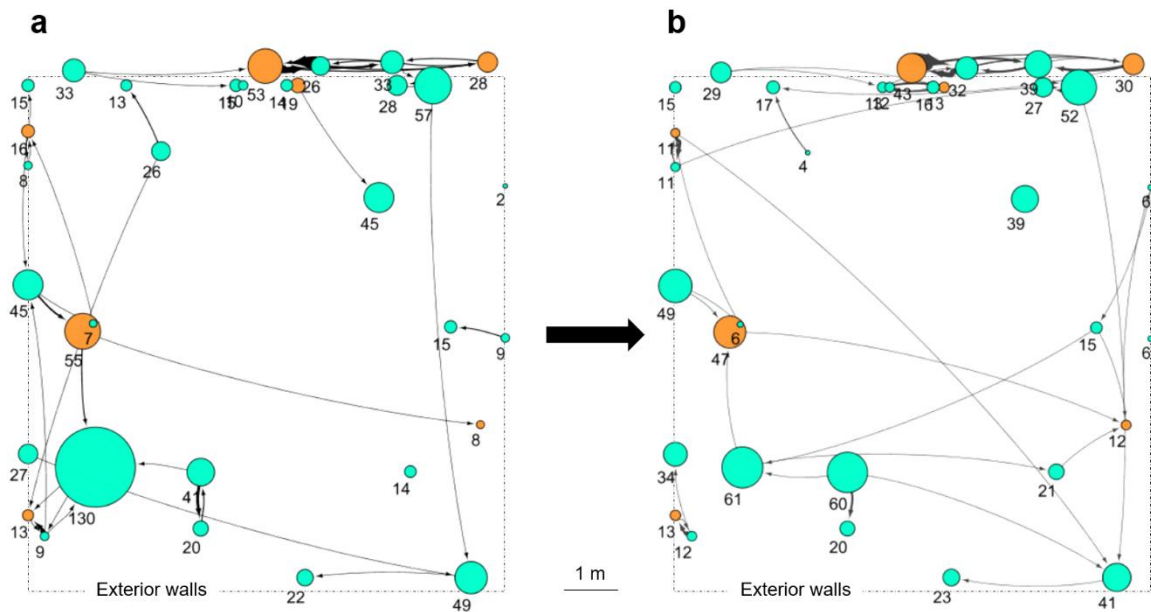


Figure 5.5 | RFID drifting networks (a) before queen removal and (b) after queen removal in an aggregation of 33 colonies. Nodes are separate colonies; weighted edges are wasps drifting from their tagging colony. The seven queen-removal ('focal') colonies are shown in orange. Colonies are annotated and scaled in size by total worker number (value given alongside node) during each phase. Dashed lines denote exterior walls of the building. Networks visualised in *Cytoscape*.

Hypothesis 1: Do drifters and non-drifters differ in total behavioural profiles? There was no evidence that drifters and non-drifters differed in behaviour. In total, 10,137 behavioural acts and social interactions were recorded, 6,887 of which were in the post-manipulation phase (Figure 5.6; Figure 5.7). The first and second principal components of total *P. canadensis* behaviour (Figure 5.8a,b) approximately represent: (1) general activity levels (first principal component) and (2) the spectrum from aggression to cooperation (second principal component). The first and second principal components explained only 32.4% of the total variation, reflecting the high degree of behavioural plasticity displayed by simple eusocial insects (Sumner *et al.*, 2006): individuals perform many colony functions, rather than specialising in narrow behavioural roles. The distribution of low proportions of variance explained by the first three principal components (21.7%, 10.7%, and 7.9%) is close to that reported for *P. canadensis* in Panama with an essentially similar ethogram (Bell 2016; 23.3%, 10.8%, and 8.0% respectively). The null expectation for 21 behaviours (Table 5.1) is that each should explain 4.76% variation per behaviour ($100/21$; horizontal red line in Figure 5.8c). Components above this line are more informative than an analysis of individual behaviours.

Non-drifters, in-drifters, and out-drifters did not differ on either principal component in each mixed model (Table 5.3; Table 5.4), and there was the full overlap of the 95% confidence ellipses for drifters and non-drifters in the PCA (Figure 5.8b). Observation colony and tagging colony had no credible effects (Figure 5.9). However, experimental phase had a credible effect on the second principal component

(Table 5.4, with a high indicator variable $g_i = 0.961$). In the interpretation suggested by Figure 5.8, this implies a shift towards more aggressive behaviours after the removal of the queen.

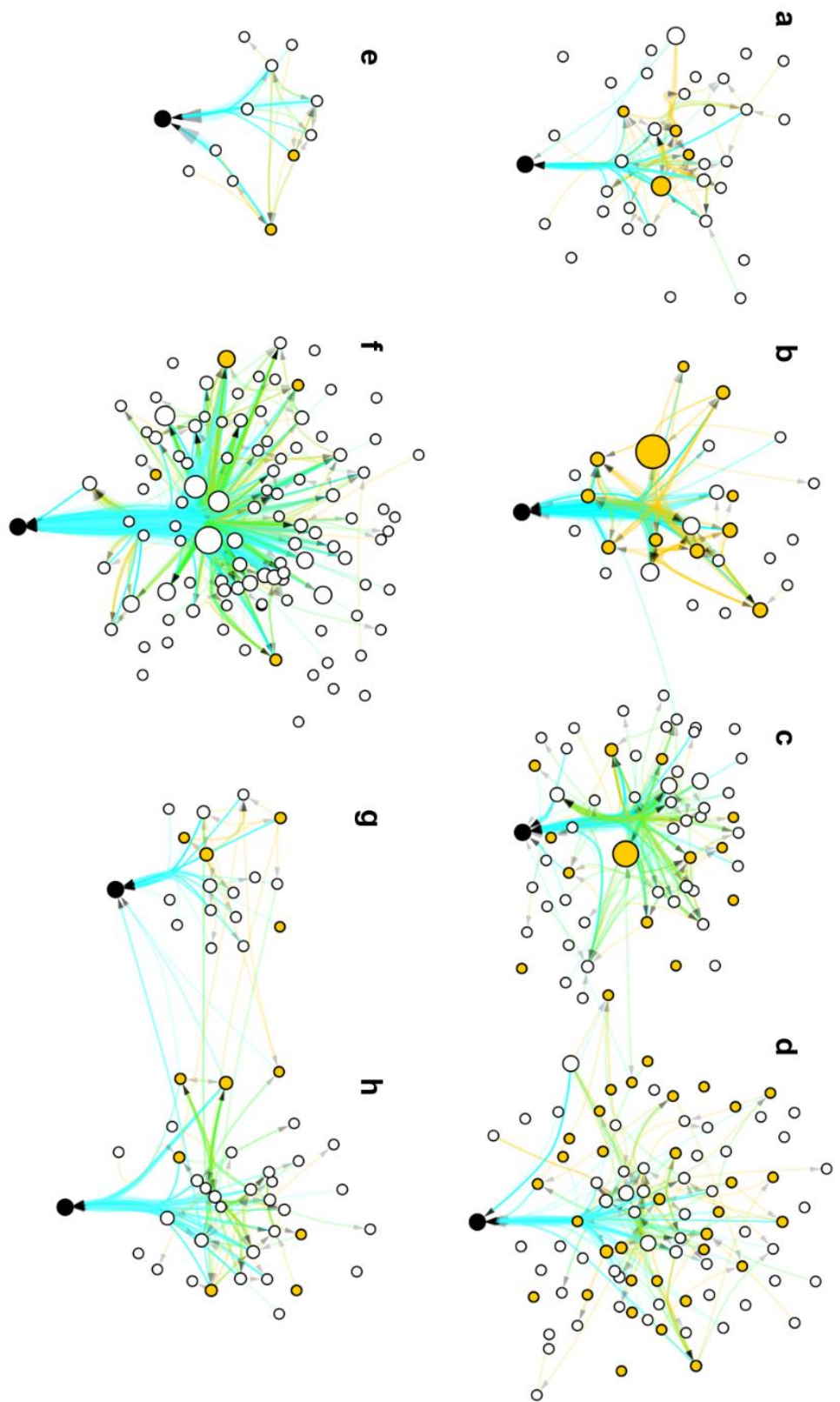


Figure 5.6 | Drifters comprised a large part of the subordinate population (14.9%) and engaged in standard within-colony tasks and behaviours. Shown are 6,887 recorded behaviours across 144 h of observation of the post-manipulation focal colonies (a, b, c, d, f, and h); two close neighbour colonies of f and h (e and g respectively) are also shown. Orange nodes are wasps known to drift within the population; white nodes are wasps not identified drifting; black nodes are separate colonies. Yellow edges denote food and trophallactic transfer between wasps; green edges denote other social interaction (antennation); blue edges denote interactions with the brood (e.g. brood feeding, cell checking) and general colony (e.g. building cells).

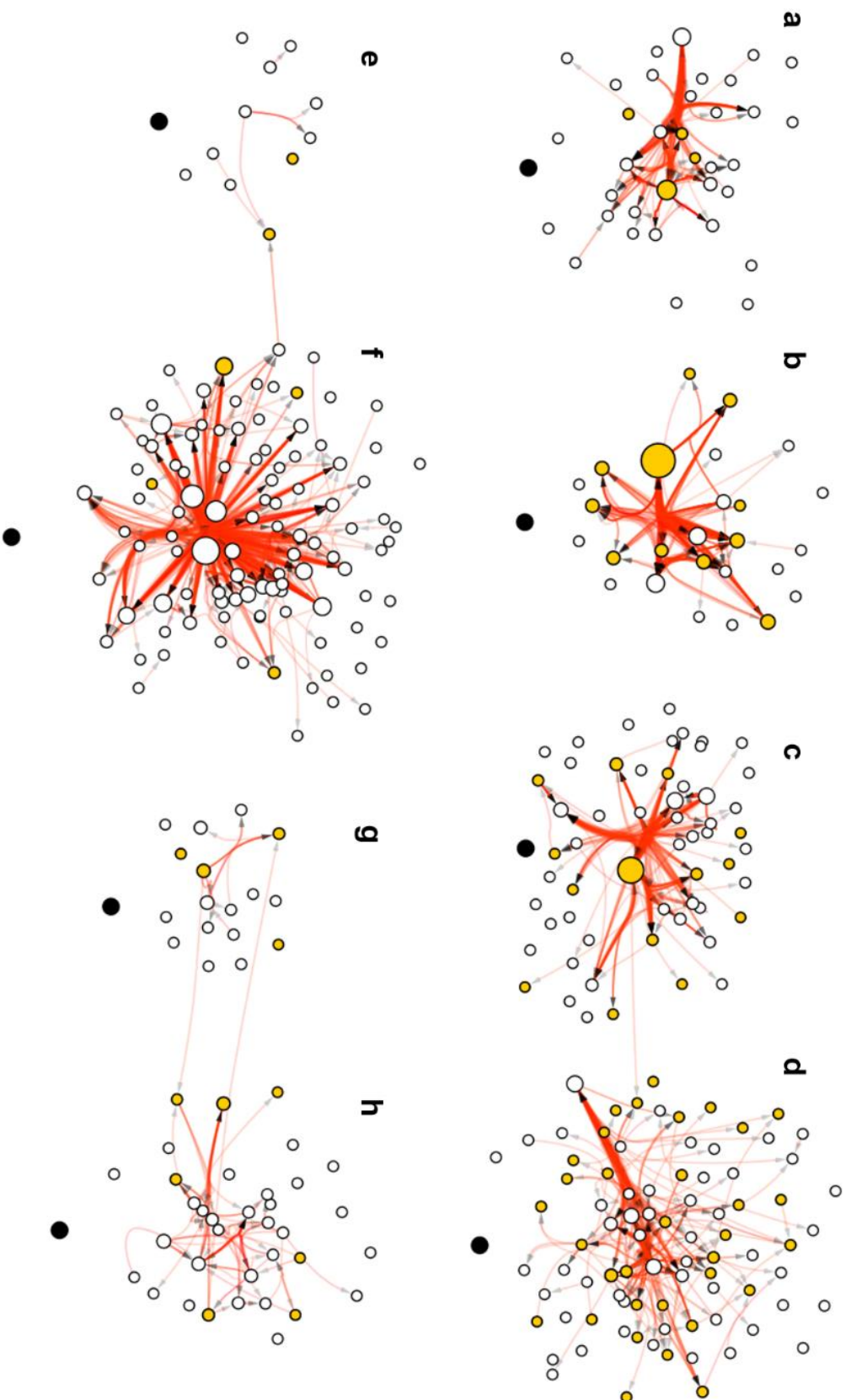


Figure 5.7 | Drifters comprised a large part of the subordinate population (14.9%) and engaged in the post-manipulation competition for nest inheritance similarly to non-drifters. Shown are 6,887 recorded behaviours across 144 h of observation of the post-manipulation focal colonies (a, b, c, d, f, and h); two close neighbour colonies of f and h (e and g respectively) are also shown. Orange nodes are wasps known to drift within the population; white nodes are wasps not identified drifting; black nodes are separate colonies. Aggressive interactions (red edges) include bites, stings, lunges, falling fights, domination postures, and chases.

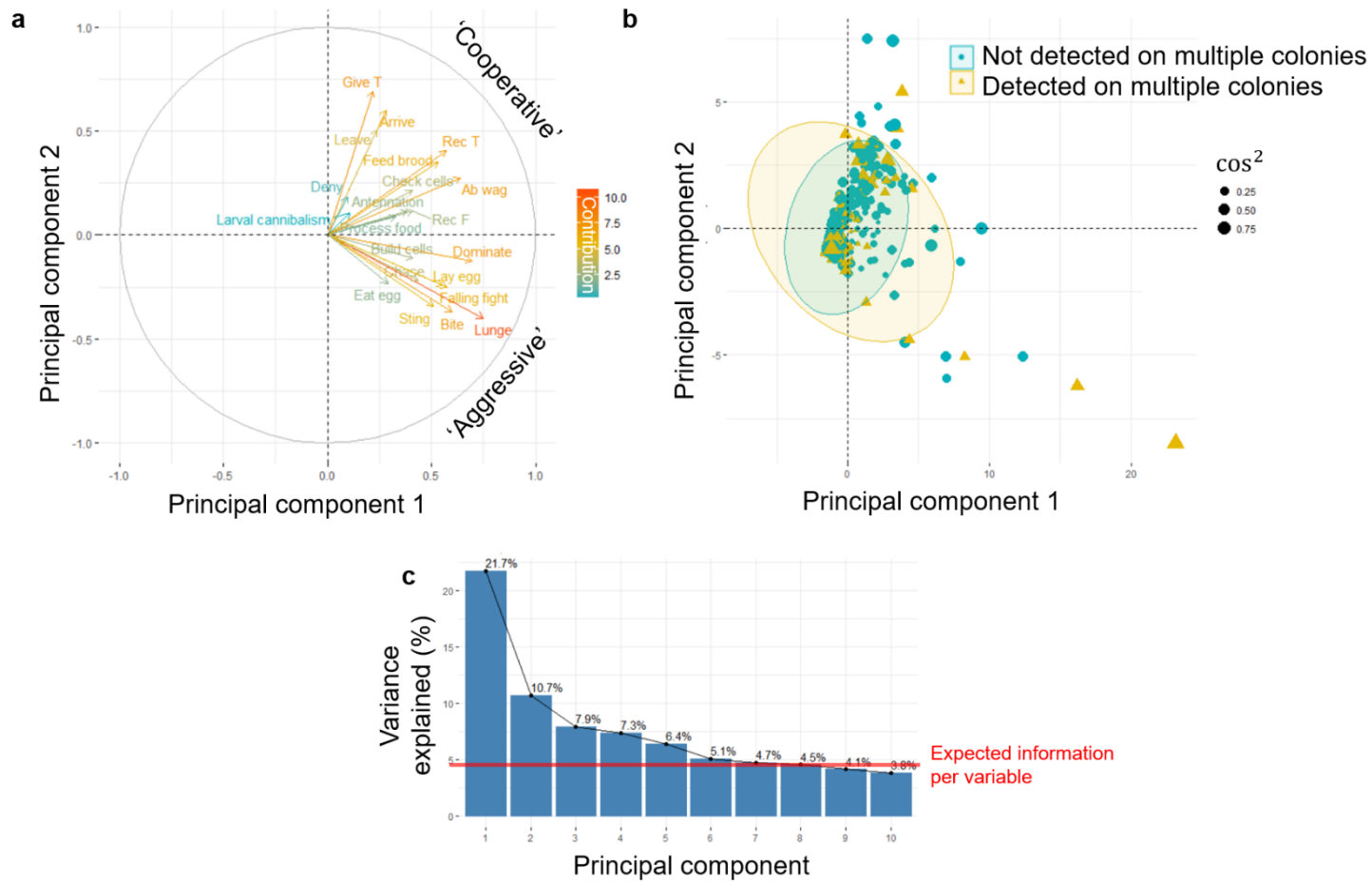


Figure 5.8 | **Principal components analysis (PCA) of *P. canadensis* behaviour.** (a) First and second principal components of total behavioural dataset (see Table 5.1 for description of each behaviour). (b) Drifters and non-drifters are not distinguishable by the first and second components. Observations are scaled by \cos^2 (a measure of the extent to which the components describe the observation). (c) The first and second components explain only 32.4% of the total variation, which is dispersed across multiple components.

Table 5.3 | Posterior estimates for mixed model of first principal component of *P. canadensis* behaviour (means parameterisation).
100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Non-drifter main effect ($g = 0.002$)	-0.145	3.154	0.070	-6.292	-0.176	5.922
In-drifter main effect ($g = 0.002$)	0.093	3.168	0.082	-5.958	0.0964	6.190
Out-drifter main effect ($g = 0.002$)	-0.260	3.179	0.078	-6.364	-0.239	5.892
Phase effect ($g = 0.123$)	-0.011	2.990	0.082	-6.067	0.068	6.018
Non-drifter/phase interaction ($g = 0.116$)	-0.050	2.939	0.057	-5.988	-0.004	6.088
In-drifter/phase interaction ($g = 0.116$)	-0.063	2.983	0.069	-5.865	-0.017	5.864
Out-drifter/phase interaction ($g = 0.116$)	-0.009	2.939	0.078	-5.905	0.157	5.949
Model precision	0.267	0.029	0.003	0.2162	0.265	0.326
Focal colony (random effect) ($g = 0.833$) precision	7.413	24.63	1.621	1.0E-5	1.833	64.390
Tagging colony (random effect) ($g = 0.187$) precision	14.100	32.23	2.292	0.0257	4.099	100.800
Bayesian R^2	0.160	0.096	0.012	-0.023	0.162	0.331
Posterior predictive p -value	0.496	0.500	0.010	0.000	0.000	1.000

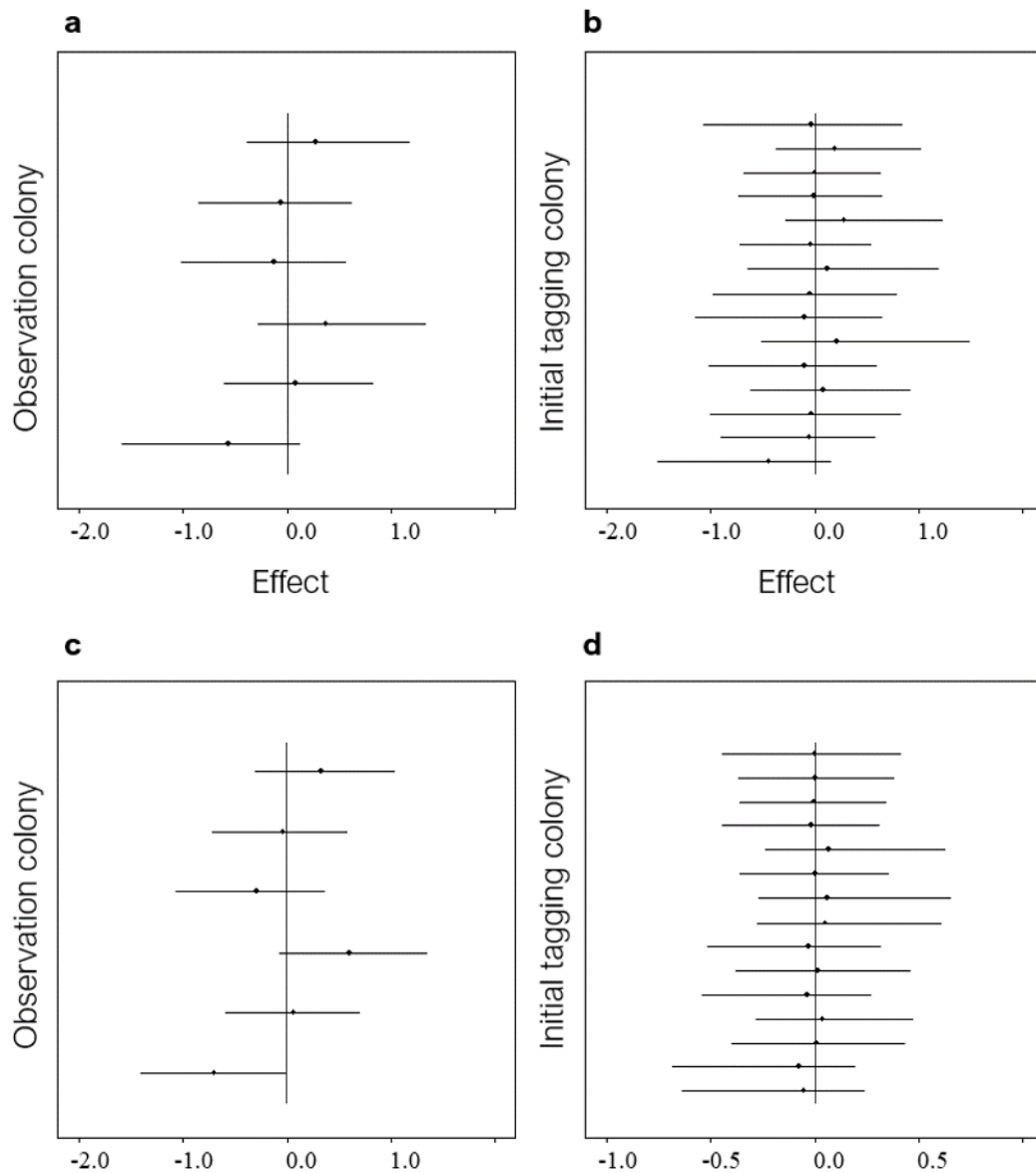


Figure 5.9 | No strong effect of colony on *P. canadensis* within-colony behaviour. (a) The effects for all six focal colonies' 95% credible intervals overlapped zero for the first principal component of wasp behaviour. **(b)** Similarly, no effect of tagging colony on the first principal component of behaviour. **(c)** One focal colony (numbered 6) showed a 95% credible interval not overlapping zero for the second principal component. **(d)** No effect of tagging colony on the second principal component. Medians are marked by dots.

Table 5.4 | Posterior estimates for mixed model of second principal component of *P. canadensis* behaviour (means parameterisation). 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Non-drifter main effect ($g = 0.000$)	0.0476	3.159	0.043	-6.219	0.054	6.243
In-drifter main effect ($g = 0.000$)	0.0084	3.175	0.044	-6.290	0.029	6.139
Out-drifter main effect ($g = 0.000$)	0.0159	3.166	0.044	-6.244	0.058	6.110
Phase effect ($g = 0.961$)	-0.457	0.628	0.010	-0.788	-0.463	-0.135
Non-drifter/phase interaction ($g = 0.006$)	0.0097	3.148	0.044	-6.193	0.011	6.162
In-drifter/phase interaction ($g = 0.006$)	0.058	3.188	0.045	-6.170	0.040	6.449
Out-drifter/phase interaction ($g = 0.006$)	0.027	3.125	0.047	-6.206	0.028	6.292
Model precision	0.501	0.033	5.4E-4	0.439	0.500	0.568
Focal colony (random effect) ($g = 1.000$) precision	3.065	2.215	0.057	0.554	2.600	8.326
Tagging colony (random effect) ($g = 0.061$) precision	8.474	33.44	2.430	4.3E-8	0.005	93.73
Bayesian R^2	0.128	0.058	9.6E-4	0.009	0.130	0.233
Posterior predictive p -value	0.493	0.500	0.007	0.000	0.000	1.000

Hypothesis 2: Do drifters and non-drifters differ in dominance during the nest inheritance struggle? In the post-manipulation dataset used for inferring dominance status, non-drifters, in-drifters (foreign wasps), and out-drifters (resident wasps) were all found throughout the inferred dominance hierarchy (Figure 5.10). Bayesian model averaging removed the drifter effect from the model ($g = 0.037$), and the 95% credible intervals were unchanged from the prior probabilities (Table 5.5). Similarly, there was no effect of drifting on the probability of being in the upper tenth dominance percentiles (Table 5.6).

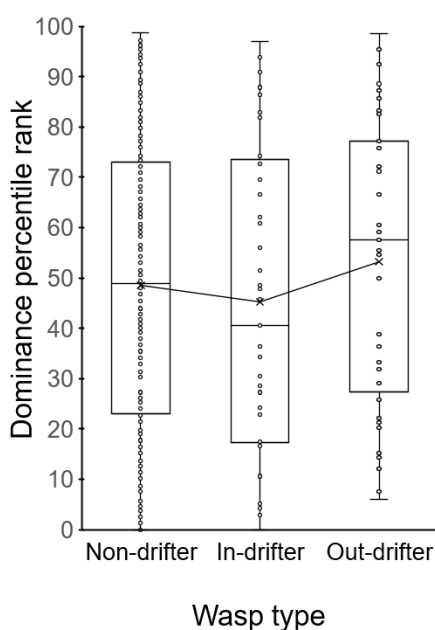


Figure 5.10 | In-drifters were found at all levels of the focal colony hierarchy during the nest inheritance competition. Contrary to prediction if drifters are all low-ranking indirect fitness maximisers, in-drifters and out-drifters are indistinguishable from non-drifting resident wasps in dominance percentile rank: high ranks are accessible to foreign wasps. Mean percentile ranks for each wasp type are shown by crosses.

Hypothesis 3: Do drifters target nest inheritance opportunities? There was no evidence that drifters targeted nest inheritance opportunities by switching to newly queenless colonies. RFID-detected drifters ($n = 98$) showed no change in proportional investment towards the focal (queenless) colonies after queen removal (Table 5.7). The identity of the colony that the drifter's invested most in had a credible effect on proportional investment and was fully retained by variable selection ($g = 1.000$). Likewise, restricting the analysis to the 44 drifters for whom simulated annealing estimates of dominance rank were available (see Hypothesis 2), showed no effect of queen removal on proportional investment as detected by RFID (Table 5.8). All predictors were removed as non-contributory by Bayesian model averaging (g close to zero) except for drifter's main colony, which was credible (95% credibility interval not overlapping zero) and fully retained ($g = 1.000$).

Table 5.5 | Posterior estimates for linear model of estimated within-colony dominance percentile. 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	48.20	4.237	0.043	42.65	48.60	52.48
Non-drifter effect ($g = 0.037$)	0.477	31.33	0.096	-61.54	0.789	61.61
In-drifter effect ($g = 0.037$)	0.400	31.34	0.101	-61.70	0.707	61.39
Out-drifter effect ($g = 0.037$)	0.656	31.31	0.116	-61.22	1.074	61.25
Linear model precision	0.001	1.0E-4	3.6E-7	9.8E-4	0.001	0.001

Table 5.6 | Posterior estimates for logistic model for probability of being in the upper tenth dominance percentile. 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	-2.380	0.234	0.002	-2.853	-2.373	-1.942
Non-drifter effect ($g = 0.001$)	-0.153	31.60	0.168	-61.94	-0.077	62.13
In-drifter effect ($g = 0.001$)	-0.252	31.64	0.171	-61.81	-0.098	61.96
Out-drifter effect ($g = 0.001$)	-0.174	31.81	0.162	-62.18	-0.251	62.42

Table 5.7 | Posterior estimates for logistic model for drifter change in investment in focal colonies (RFID visits). 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	-2.445	1.335	0.048	-4.659	-2.506	0.499
Phase effect ($g = 0.058$)	5.3E-4	3.064	0.010	-6.143	0.029	6.089
Worker-to-brood ratio ($g = 0.498$)	0.146	3.174	0.078	-6.234	0.239	6.109
Wasp random effect ($g = 0.123$) precision	34.17	679.4	18.04	0.011	0.044	40.76
Main colony random effect ($g = 1.000$) precision	0.079	0.033	4.2E-4	0.029	0.074	0.158

Table 5.8 | Posterior estimates for logistic model for drifter change in investment in focal colonies (RFID visits) for drifters with estimated dominance percentile ranks. 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	0.682	0.969	0.047	-1.336	0.695	2.565
Phase effect ($g = 0.038$)	0.020	9.694	0.062	-19.22	0.047	19.27
Main colony random effect ($g = 1.000$) precision	0.186	0.127	0.002	0.033	0.157	0.509
Rank effect ($g = 0.017$)	0.028	9.970	0.064	-19.52	-0.004	19.82
Phase/rank interaction ($g = 0.037$)	0.003	9.763	0.059	-19.30	-0.059	19.37

Hypothesis 4: Do drifters and non-drifters differ physically?

Ovary activation: Only four of the 76 dissected wasps showed C/D (active) or E (regressing) grade ovaries: 91.4% (32/35) of drifters and 97.6% (40/41) of non-drifters had inactive ovaries (Figure 5.11a). These ovary grades were all characterised by eggs under 1 mm in length (Figure 5.11b). Binary logistic regression found no credible difference between drifters and non-drifters in ovary activation (active or inactive; Table 5.10; Figure 5.11a), and no effect of colony. However, within the ovary-inactive wasps (A and B grade), drifters were credibly more likely to have B stage ovaries than non-drifters (Table 5.10; Figure 5.11a), meaning that ovaries contained at least some immature oocytes (B grade) as opposed to no oocytes (A grade).

Restricting the analysis to the 34 wasps with oocytes (*i.e.*, excluding A grade ovaries), there was no credible difference between drifters and non-drifters in egg size (Table 5.11; Figure 5.11b) or egg number (Table 5.12; Figure 5.11c). Note, however, that the small sample of oocyte-bearing wasps may obscure any true effect. Although there was superficially an effect of colony on egg size (*i.e.*, 95% credibility intervals for different colonies non-overlapping zero), colony random effect was removed from the optimum model by Bayesian model averaging ($g = 0.020$).

Wing length: Drifters and non-drifters did not differ in wing length (a proxy for body size) (Table 5.13). There was a credible effect of colony on wing length (for seven colonies, wing length effects showed 95% credible intervals nonoverlapping zero; Figure 5.12).

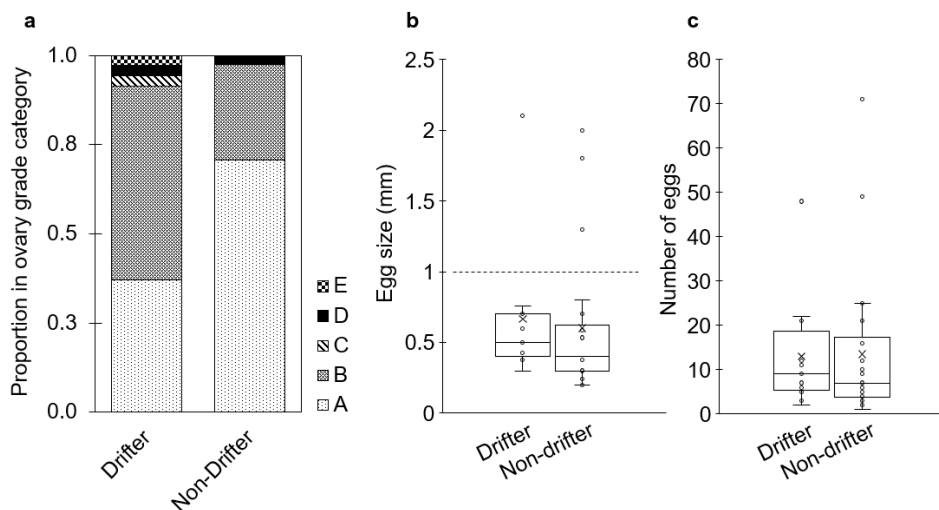


Figure 5.11 | **Ovary dissections showed no difference in total ovary activation between drifters and non-drifters.** (a) Grades of ovary development (see Figure 5.4). Drifters ($n = 35$) and non-drifters ($n = 41$) did not differ in ovary activation (A/B: inactive; C/D/E: active). However, ovary-inactive drifters (A or B grade) were more likely than ovary-inactive non-drifters to have B grade ovaries. (b) Drifters and non-drifters did not credibly differ in egg size. Only four wasps had eggs larger than 1 mm in length (dashed line). (c) Drifters and non-drifters did not differ in egg number.

Table 5.9 | Posterior estimates for binary logistic mixed model of ovary activation.
100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	-6.247	4.766	0.145	-19.23	-3.892	-2.196
Drifter regression slope ($g = 0.396$)	1.156	8.869	0.120	-18.10	1.935	17.89
Colony random effect precision ($g = 0.349$)	6.178	18.06	1.827	0.006	0.355	58.63

Table 5.10 | Posterior estimates for binary logistic mixed model of 'A' versus 'B' grade ovaries.
100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	-0.955	8.294	0.131	-17.74	-1.761	17.88
Drifter regression slope ($g = 0.340$)	0.938	8.261	0.118	-17.90	1.862	18.44
Colony random effect precision ($g = 0.401$)	13.28	31.73	2.960	0.004	0.719	107.3

Table 5.11 | Posterior estimates for linear mixed model of egg size. 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	0.621	0.086	3.0E-4	0.453	0.621	0.791
Drifter regression slope ($g = 0.000$)	2.119	1001	2.993	-1965	0.260	1966
Colony random effect ($g = 0.020$) precision	1.9E-8	2.4E-7	1.1E-8	0.000	3.0E-24	6.5E-10
Linear model precision	4.391	1.084	0.003	2.532	4.302	6.738
Posterior predictive p -value	0.500	0.500	0.002	0.000	1.000	1.000

Table 5.12 | Posterior estimates for linear mixed model of egg number. 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	12.72	248.8	0.795	-215.2	13.68	210.2
Drifter regression slope ($g = 0.015$)	2.466	992.7	3.055	-1957	5.551	1963
Colony random effect ($g = 0.158$) precision	22.80	148.6	3.282	0.000	7.2E-14	232.0
Linear model precision	0.004	0.001	2.9E-5	0.003	0.004	0.007
Posterior predictive p-value	0.500	0.500	0.002	0.000	1.000	1.000

Table 5.13 | Posterior estimates for mixed model of wing length. 100,000 iterations MCMC.

Variable	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	1937.0	6.999	0.0761	1923	1937	1951
Drifter regression slope ($g = 0.028$)	1.799	984.9	3.132	-1947	11.15	1951
Colony random effect precision ($g = 0.998$)	1.226	34.79	1.200	4.3E-4	8.6E-4	0.002
Linear model precision	9.7E-5	4.0E-6	1.2E-8	8.9E-5	9.6E-5	1.0E-4
Bayesian R^2	0.888	0.041	0.002	0.7951	0.8956	0.948

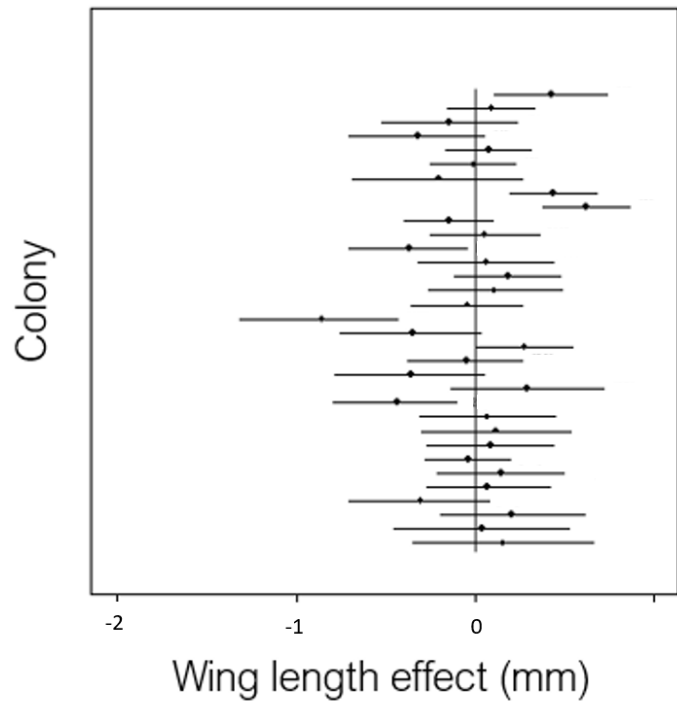


Figure 5.12 | **Wing length differed between colonies.** 95% credible intervals for the random effect 'colony' in a mixed model of wing length ($n = 33$ colonies, $n = 1,207$ wasps). Medians are marked by dots.

5.5 Discussion

By examining key phenotypic traits characterising *Polistes* wasps, I have found no evidence that drifters represent a distinct class of individual: there is no evidence that drifting is part of a specialist set of correlated behaviours. Instead, drifting may be a feature of *P. canadensis* life history that occurs with a given probability in the lives of all wasps.

What are drifting rates in *P. canadensis*? Drifters comprised 14.9% of the studied population. Different studies on *P. canadensis* populations have found varied rates of drifting using the same methods (Sumner *et al.*, 2007; Lengronne, 2013), reaching a maximum of 56% in one Panamanian population (Sumner *et al.*, 2007). From the small sample of RFID-tagged populations to date, it is too early to test potential reasons for inter-population variance in drifting rates. However, it is possible that there is a latitudinal gradient in drifting rates in *P. canadensis* from the Amazon latitudes to Central America; there is a latitudinal gradient in colony architecture over the same range (Jeanne, 1979) that may reflect an as-yet unidentified environmental gradient. Parasite pressure, resource scarcity, and optimum nesting seasons may all vary across the gradient, and each may influence drifting rates. Replicating RFID tagging across multiple aggregations along this gradient may be valuable.

Of the 216 total identified drifters, 66.2% (143/216) were detected on the seven focal colonies (either at tagging or during the experiment). This means that the intensively-observed 21.2% (7/33) of the colonies in the aggregation were visited by 66.2% of the identified drifters at some point in the study. Three potential explanations can be imagined for this apparent bias. First, sampling bias: drifters appearing on non-focal colonies, which did not receive the same intensity of observation as the focal colonies, are likely to have a lower rate of detection. Second, social crisis may have amplified either drifter detection probability or drifting rates on the focal colonies (although the second of these is unlikely, given the lack of a detectable change in drifter investment in the focal colonies). Third, drifters typically visit multiple colonies, so observing just a subset of colonies intensively may have led to detecting a large fraction of the population's drifters (*i.e.*, no sampling bias).

Why are drifters found at all levels of the dominance hierarchy? I found no evidence that drifters are drawn from a particular dominance stratum: (1) drifters occur at all levels of participation rate in the nest inheritance competition and are behaviourally indistinguishable from non-drifters (*Table 5.4*); (2) drifters do not differ from non-drifters in ovary activation following exposure to queen loss (*Table 5.9*); and (3) drifters do not adjust their visit rates to invest strategically in experimentally queenless colonies (*Table 5.7*). The lack of changes in investment preference either side of the manipulation suggests that

drifters do not show a shared response to the opportunity for nest inheritance. Instead, wasps with a history of drifting who invest heavily in competition for nest inheritance had already invested heavily in the focal colony during the pre-manipulation phase before the removal of the queen. Being a drifter does not predict the tendency to compete for the egg-laying position. Although high-ranking drifters can compete for nest inheritance on queenless nests (at a level indistinguishable from wasps who do not show drifting behaviour), there is no support for the hypothesis that they move between nests to maximise nest inheritance opportunities. Nonetheless, the presence of at least some highly-aggressive and competing foreign wasps in the colony during the nest inheritance struggle suggests that a subset of drifters may threaten both the indirect fitness interests of resident foragers and the direct fitness interests of resident high-ranking subordinates. Accepting drifters may be risky for the host colony. In Chapter 7, I ask whether host colonies possess the ability to discriminate and screen foreign arrivals.

Various authors have proposed that drifting is an indirect fitness maximising strategy in which workers redistribute themselves optimally across related colonies (Hamilton, 1964b; Sumner *et al.*, 2007; Lengronne, 2013). This indirect fitness hypothesis predicts that drifters are low-ranking, non-reproductive cooperators. The results here – drifters occur at all levels of social dominance – are consistent with two interpretations. First, drifting may not be a single strategy: in this hypothesis, cooperative drifting and aggressive drifting are separate inclusive fitness maximising strategies pursued by wasps at different levels of social dominance. Low-ranking wasps drift for indirect fitness; high-ranking wasps drift for direct fitness. In Chapter 6, I examine the viability of the indirect fitness hypothesis. Second, drifting may instead be a stochastic event that occurs with approximately equal frequency in the lives of most wasps, leading to ‘accidental’ drifting across the social hierarchy. Note, however, that a null hypothesis in which drifting is purely accidental should lead to higher rates of drifting amongst low-ranking foragers, who frequently depart the home nest (Blacher *et al.*, 2013). I have found no association between dominance rank and drifting within the dataset of 242 wasps for whom dominance status can be inferred on the focal colonies, but larger and replicated samples on numerous colonies are required before confident conclusions can be drawn.

Why did drifters generally lack active ovaries? The generally low levels of ovary activation amongst drifters support the conclusion of Sumner *et al.* (2007) that *P. canadensis* drifters are not predominantly parasitic egg-dumpers. These results are consistent with the different views of drifters as either (1) strategic indirect fitness maximisers or (2) lost foragers. However, although the majority of drifters and non-drifters lacked active ovaries (*i.e.*, C, D, or E grade ovaries), drifters were more likely to have B grade (oocyte-carrying) ovaries than non-drifters (*Figure 5.11*). A larger sample will be needed to confirm this effect. It is possible that egg-dumping opportunities arise only during the declining phase of the host colony, for which otherwise-benign drifters are primed for rapid ovary activation. Alternatively, the

association may be a sampling artefact, because we were forced to recover a pre-specified list of individuals for one sample (drifters) but not for the other sample (non-drifters): drifters with oocytes may be more easily sampled than drifters without oocytes, potentially because they are slightly less likely to be absent foraging or dead. The association should therefore be interpreted cautiously.

Why did future queens drift? No foreign drifters inherited any nest. However, three of the six resident wasps who subsequently inherited their nests had temporarily drifted outwards to foreign colonies at points in the experiment. A larger sample of queenless nests is needed to confirm that this is a general effect. If it proves to be a common behaviour amongst successful nest inheritors, why does it occur?

One possibility is that a high-ranking class of hopeful nest inheritors regularly scans the local aggregation for rare nest inheritance opportunities. However, if this is the sole explanation for movement by high-ranking wasps, the future queens should have only drifted in the pre-manipulation period. The three future queens who drifted all did so during the post-manipulation. An alternative explanation is that high-ranking wasps occasionally leave the nest because they are evicted, either by the other high-ranking wasps and the resident queen (when present) or by aggressive high-ranking rivals for nest inheritance (after the loss of the queen): before they successfully secured the queenship, the future queens were simply competitors. Brief eviction by rivals does occur: intense falling fights and stings, followed by immediate departures of one or both interactants, occurred throughout the post-manipulation. In principle, queenright neighbour nests are safe resource-rich refuges during the queen struggle, at which competing wasps may, temporarily, (1) avoid dangerous over-exposure to nestmate aggression and (2) obtain valuable energy by soliciting trophallaxis from the undisturbed influx of foragers. A third possibility is that drifting by high-ranking wasps is a means of deceiving nestmates: drifting by high-ranking wasps may be a form of temporary defection from the home colony, avoiding the personal costs of helping raise the brood whilst maximising the chances of direct fitness success. When triggered or forced to depart on foraging trips by ritualised aggression from nestmates, high-ranking wasps may superficially acquiesce but instead exploit the permeable borders of related neighbour colonies (at which they can avoid the high risks and energetic costs of foraging). In summary, the permeable nest network may accommodate sophisticated strategies by high-ranking wasps. However, high-ranking drifters were the minority: as is true amongst non-drifters, most drifters were low-ranking (*Figure 5.10*).

How robust are conclusions based on single animal social networks? Experimental manipulations of wild animal social networks at population scales have typically been performed on single large networks (*e.g.*, Firth and Sheldon 2015). Similarly, here I have experimentally manipulated a single large aggregation of 1,450 RFID-tagged wasps. Network observation is often a trade-off between maximising

within-network resolution and maximising between-colony replication (James *et al.*, 2009). This is also the case with RFID in wild populations, which requires that a high degree of monitoring infrastructure (antennae, readers, car batteries, wiring, etc.) be partially reconstructed daily (Lengronne, 2013). This approach allows us to make more robust within-network conclusions, but means that generalising across networks should be done with caution until additional whole network replications can be performed. Similarly, to maintain ecological realism by avoiding over-manipulating the network, here I restricted queen removal to a subset of seven colonies; future replications of queen removal are required to generalise reliably to the behaviour of all *P. canadensis* drifters in queenless colonies.

5.6 Conclusion

In this chapter, I used RFID-tagging, behavioural observation, and experimental queen removal to ask if drifting wasps show a distinct set of behaviours in comparison to non-drifting wasps. These results (1) find no evidence of drifter-specific behaviours within a large wild network, (2) suggest that drifting may not be a specific strategy pursued by a specific subset of wasps but rather an event that may occur in the lives of any wasp, and (3) provide the methods for future work in other *Polistes* aggregations to assess the extent to which drifting may correlate with behaviour.



Polistes canadensis post-emergence colony,
Fort Sherman, Panama.
Photograph: PK

6 | Drifting and diminishing returns to altruism in paper wasps

6.1 Chapter Summary

Hamilton's rule is a key principle of evolutionary biology: altruism evolves only if the benefits accruing to relatives are enough to justify the costs. However, in 1964 Hamilton highlighted an apparent anomaly to his own rule amongst the *Polistes* paper wasps of South America, which has recently received renewed interest. Recent results show large numbers of non-reproductive workers helping foreign colonies, seemingly undermining the advantage of altruism by approximately halving the relatedness of recipients. Hamilton proposed that helping related queens may allow wasps to avoid futile cooperation on colonies where the payoffs of altruism are diminished. Here, using a dataset of a quarter of a million repeat observations of brood cells, I quantify the extent of diminishing returns to altruism in *Polistes canadensis*. Multistate Markov models show that wild colonies suffer strong diminishing returns to cooperation at levels capable of explaining drifters divesting to neighbour colonies. I argue that two rival hypotheses for extreme drifting – bet-hedging and indirect reciprocity – are only feasible under complex ecological scenarios, whilst diminishing returns are sufficiently strong to provide a simple justification for drifting. However, social network analyses of wasp drifting show no consistent movement from hypothetically 'diminished' colonies to hypothetically 'undiminished' colonies, and suggest that additional influences on the payoffs of altruism and extreme drifting in *Polistes* remain to be discovered.

6.2 Introduction

Inclusive fitness theory explains altruism (self-sacrifice in the service of others) as attempts to maximise the evolutionary success of shared alleles (Hamilton, 1964ab; Gardner *et al.*, 2011). The theory is captured by a simple principle known as Hamilton's rule: perform any altruistic act only if the recipient's relatedness to yourself (r) multiplied by the fitness increase (B) is greater than your fitness decrease (C), *i.e.*, $rB > C$. However, in his seminal paper introducing inclusive fitness theory, Hamilton (1964b) annexed a section on 'anomalies' that appeared to violate his own theory. Among this list of anomalies are Hamilton's own observations of workers moving between colonies in the paper wasps of

South America. In Neotropical *Polistes*, non-reproductive workers continually move between colonies, raising the brood of distantly related recipients. Paradoxically, these workers appear to undermine their own inclusive fitness by diverting a finite amount of help from close relatives (high r) to neighbours (low r). Fifty years later, the paradox of between-colony worker traffic (known as ‘drifting’) in Neotropical *Polistes* wasps continues to pose a challenge to the logic of inclusive fitness theory.

The scale of drifting in some Neotropical *Polistes* has since become clear. From visual censuses of over ten thousand *Polistes canadensis* workers in Panama, Pickering (1980) identified more than a thousand drifters, and argued that *P. canadensis* forms close clusters of colonies that he termed ‘extended colonies’ (Figure 6.1). High-resolution radio-tagging by Sumner *et al.* (2007) in Panama subsequently detected 56% of workers trafficking between colonies, dissolving the boundaries between colonies much like supercolonies in highly eusocial ants (Helanterä *et al.*, 2009). Drifting is increasingly seen as an adaptive strategy across the social insects: in various taxa, drifters parasitise foreign colonies (Blacher, Yagound, *et al.*, 2013), succeed foreign queens (Seppä *et al.*, 2012), and enslave foreign workers (D’Ettorre and Heinze, 2001). However, between-colony cooperation by non-reproductive workers, who lack developed ovaries and perform standard worker tasks, has so far been observed only amongst primitively-eusocial *Polistes* wasps (*P. canadensis*: Sumner *et al.*, 2007; Lengronne, 2013; this thesis, Chapter 5) and highly-eusocial ants (Helanterä *et al.*, 2009), and is little understood.



Figure 6.1 | *Polistes canadensis* colonies often occur in clusters, allowing workers to move easily between colonies. (a) Tight cluster on Barro Colorado Island (Panama). Photograph: © Dr J. Pickering (1976), www.discoverlife.org. (b) Cluster at Fort Sherman (Panama). Photograph: PK. (c) Two colonies in a cluster at the same site. Photograph: PK. Colonies highlighted by asterisks.

We possess strong estimates of the relatedness of *P. canadensis* drifters to the brood they care for (r in Hamilton's rule; *Table 6.1*). Repeatedly across different drifter networks, drifters suffer a severe reduction in relatedness to recipients (from $r = 0.52 \pm 0.12$ towards home colonies to $r = 0.169 - 0.23$ towards new colonies; Sumner *et al.*, 2007; Lengronne *et al.*, unpublished). A simple solution to the drifting enigma is to suggest that drifters allocate investments in proportion to relatedness. A full sister queen ($r = 0.75$) on the natal nest should receive four times as much help as an aunt queen ($r = 0.1875$) on a neighbour nest. This common mistake – sometimes referred to as the 'proportional altruism' model – was identified by Altmann (1979) as a version of the 'gambler's fallacy'. Instead, rather than wasting effort on suboptimal recipients, it is always more profitable to invest entirely in the best recipient (Altmann, 1979; Dawkins, 1979; Weigel, 1981; Schulman and Rubenstein, 1983). Drifters helping colonies in proportion to relatedness would be a simple failure to maximise inclusive fitness.

Although we have estimates of relatedness (r), we currently lack any quantification of the fitness costs and benefits of changing worker allegiance (B and C). In order to overcome the over two-to-three-fold reduction in relatedness (*Table 6.1*), any adaptive hypothesis invoking an indirect fitness benefit (B) requires that drifting confers a two-to-three-fold greater benefit than non-drifting on recipients. Three indirect fitness hypotheses have been proposed to explain non-reproductive drifting in *Polistes*:

- (1) **Diminishing returns (Hamilton, 1964b)**: wasps seek new recipients when colony efficiency makes them increasingly redundant at home (Hamilton, 1964b; Page *et al.*, 1989; Sumner *et al.*, 2007; Lengronne, 2013).
- (2) **Bet-hedging (Sumner *et al.*, 2007)**: wasps help multiple related colonies in order to protect their inclusive fitness 'investment portfolio' against the destruction of any single colony by predators and parasites (Sumner *et al.*, 2007; Lengronne *et al.*, 2012; Lengronne, 2013).
- (3) **Indirect reciprocity (Nonacs, 2017)**: wasps help nonrelatives so that their home queens receive reciprocal help.

To explore these hypotheses, here I address the following questions:

- Question 1: **How might diminishing returns explain drifting?** Specifically, could the benefit provided by a worker to its host colony decline sufficiently as group size rises to justify workers switching to a lower-relatedness recipient? I collect longitudinal data on brood-rearing success on free-living colonies and ask how the number of workers affects the rate of brood development.
- Question 2: **Do workers move to colonies where the returns are greatest?** Specifically, do drifting wasps move from saturated colonies (where we expect little scope for providing benefits to the colony) to unsaturated colonies (where we expect a strong scope for

providing benefits to the colony), as predicted by the diminishing returns hypothesis? I use RFID data collected for this thesis and previous work in *P. canadensis* (Sumner *et al.*, 2007; Lengronne *et al.*, 2012; Lengronne, 2013).

Question 3: **How might indirect reciprocity explain drifting?** Specifically, does the indirect reciprocity hypothesis provide a route to drifting that can outcompete ‘free-riding’ (colonies that benefit from drifters without supplying them)?

Question 4: **How might bet-hedging explain drifting?** Specifically, under what conditions will wasps be selected to reduce the variance of their inclusive fitness ‘investment portfolios’?

In overview, I will argue that diminishing returns are simple and testable, whilst bet-hedging and indirect reciprocity require complex ecological scenarios.

Table 6.1 | Relatedness of drifters to recipients in P. canadensis (mean ± SE). Microsatellite data from Sumner et al. (2007) and T. Lengronne (2013).

	Sumner <i>et al.</i> (2007)	Lengronne <i>et al.</i> (unpublished)
r to home colony	0.52 ± 0.12 (n = 6 individual colonies)	0.561 ± 0.029 (n = 65 individual colonies)
r to visited colonies	0.23 ± 0.056 (n = 9 entire drifter networks, <i>i.e.</i> , colony aggregations)	0.169 ± 0.009 (n = 63 individual colonies)

6.3 Question 1: How might diminishing returns (Hamilton, 1964b) explain drifting?

The diminishing returns hypothesis predicts that wasps move to alternative, more distantly-related recipients when they are increasingly redundant on the natal nest. There are two forms of diminishing returns in social evolution:

- (1) **Short-term:** payoffs diminish due to the action of the focal altruist, so the altruist finds its recipient decreasingly valuable during its own investment. This should lead to altruists switching between recipients, as each recipient eventually becomes a suboptimal investment (Weigel, 1981; Schulman and Rubenstein, 1983).
- (2) **Long-term:** the focal altruist has a negligible effect on the payoff rate, but external factors mean that the payoff rate is already diminished for some recipients. This should lead to altruists investing solely in the best recipient, unless external factors cause payoff rates to diminish at that recipient.

Short-term diminishing returns are only plausible drivers of *Polistes* drifting if a single worker can provide a sufficiently large investment that the remaining opportunities to raise additional brood to adulthood are diminished on the focal colony. This might occur if (a) colonies are sufficiently small that

all larvae can be quickly provisioned, leaving the focal worker redundant, or (b) individual workers perform specialist tasks that are less valuable once completed (*e.g.*, foragers specialised on a particular prey item that is required by the colony only at intervals). The first may be unlikely in general, as post-emergence colonies range in size between 8 and 200 workers tending between 100 and 600 larvae in various stages of development. With a ‘conveyor belt’ of numerous larvae developing, it is arguably unlikely that a worker can increase the colony’s productivity sufficiently far to cause a large saturation in productivity rate. Likewise, the second situation does not match *Polistes* biology: high plasticity (Bell, 2014; this thesis, Chapter 5) implies little reason to expect drifters to provide specialist services. I do not consider short-term diminishing returns further here.

Long-term diminishing returns provide a plausible driver of drifting. Here, a worker may find her effect on the colony’s productivity to be negligible. As worker-to-brood ratio rises, individual workers may become increasingly redundant, and – all else being equal – should move to colonies with a small worker-to-brood ratio. This leads to two testable predictions: (1) payoffs saturate with workforce size at a sufficient rate to justify switching to lower-relatedness recipients; and (2) wasps move from saturated to unsaturated colonies. I next test these two predictions in turn.

Social insect colonies often suffer reduced per-capita productivity as they grow in size – an effect known as ‘Michener’s paradox’ (Michener, 1964; Karsai and Wenzel, 1998; Kramer *et al.*, 2014; Grinsted and Field, 2018). The diminishing returns hypothesis suggests that workers drift to escape Michener’s paradox: move to a new colony where you will have a larger effect on productivity. However, not all social insects show Michener’s paradox. In contrast, Shreeves and Field (2002) show linearly increasing per-capita productivity in *Liostenogaster flavolineata* foundress groups. Likewise, Jeanne and Nordheim (1996) argue that per-capita productivity increases with group size in *Polybia occidentalis* (a conclusion disputed by Karsai and Wenzel, 1998). In this section I use natural variation in brood number and worker number to quantify productivity in *P. canadensis* colonies with different numbers of workers and worker-to-brood ratios.

6.3.1 Methods

6.3.1.a *Brood development*

To obtain accurate measures of productivity, I tracked a cohort of developing brood on 91 free-living post-emergence colonies over a 56-day period (from 14th June to 8th August 2016). Colonies were clustered in six aggregations on the north coast of Panama (15.2 ± 7.7 colonies per aggregation, mean \pm S.D.) (*Figure 6.2*). Five aggregations were in clearings between lowland tropical forest and the Panama

Canal (former US Army Base Fort Sherman, San Lorenzo National Park, Colón Province) and one aggregation was in a clearing in a mangrove swamp (Galeta Point, Colón Province).

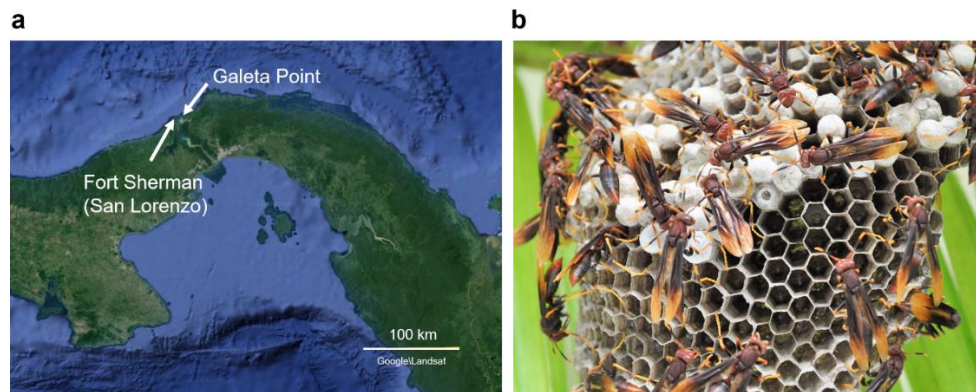


Figure 6.2 | Study site and species. (a) Aggregations were in two areas of Colón Province, Panama. **(b)** *Polistes canadensis* is a Neotropical social wasp with behavioural – but not morphological – castes, typically a single queen, and high rates of drifting. *Photograph: PK.*

Classification of brood development stages: In order to provide an accurate measure of how workers affect brood at different developmental stages, I split brood into 8 stereotypical developmental categories in a sequence through which all brood pass. Each category, and its notation, is listed in *Figure 6.3*. These categories match those used by Bell (2016), with the exception that Bell’s ‘small’ was split into S (immediately eclosed), A (early stomach developed), and C, while Bell’s ‘large’ is split into T and L, to generate a fine-grained picture of development. In analysis, I have merged states S and A to improve identifiability; henceforth, S/A is simply termed S. I examined each brood cell every 5 days, using a ladder to access colonies and a flashlight to illuminate each cell. The cell classification (*Figure 6.3*) was then dictated to a second observer, who recorded the specific cell’s current state on a hexagonal grid of the nest. Accordingly, brood classification was done by a single observer blind to the previous state of the cell. All extensions to the nest were annexed to the grid.

Quantifying workforce size: I censused group size by recording total adult numbers at night (8 pm–11 pm) using a red light to avoid disturbance (6–7 censuses per colony across the monitoring period). Nests that were difficult to observe were counted multiply to ensure the same total number in each count. Alongside the 91 colonies that provided brood development time data for the subsequent model, an additional 14 colonies were night-censused to provide additional data on colony survival. If group size changed between night-censuses, I assumed that any changes were smooth to avoid imposing artificial step changes in the model. I estimated group size as the mean (for each 5-day interval) of the fitted group sizes generated by a cubic spline through the night-censuses. Males were counted during daylight surveys during the brood surveys on 5-day intervals. Estimates of female number during each 5-day interval were obtained by subtracting interpolated male number from interpolated group size.

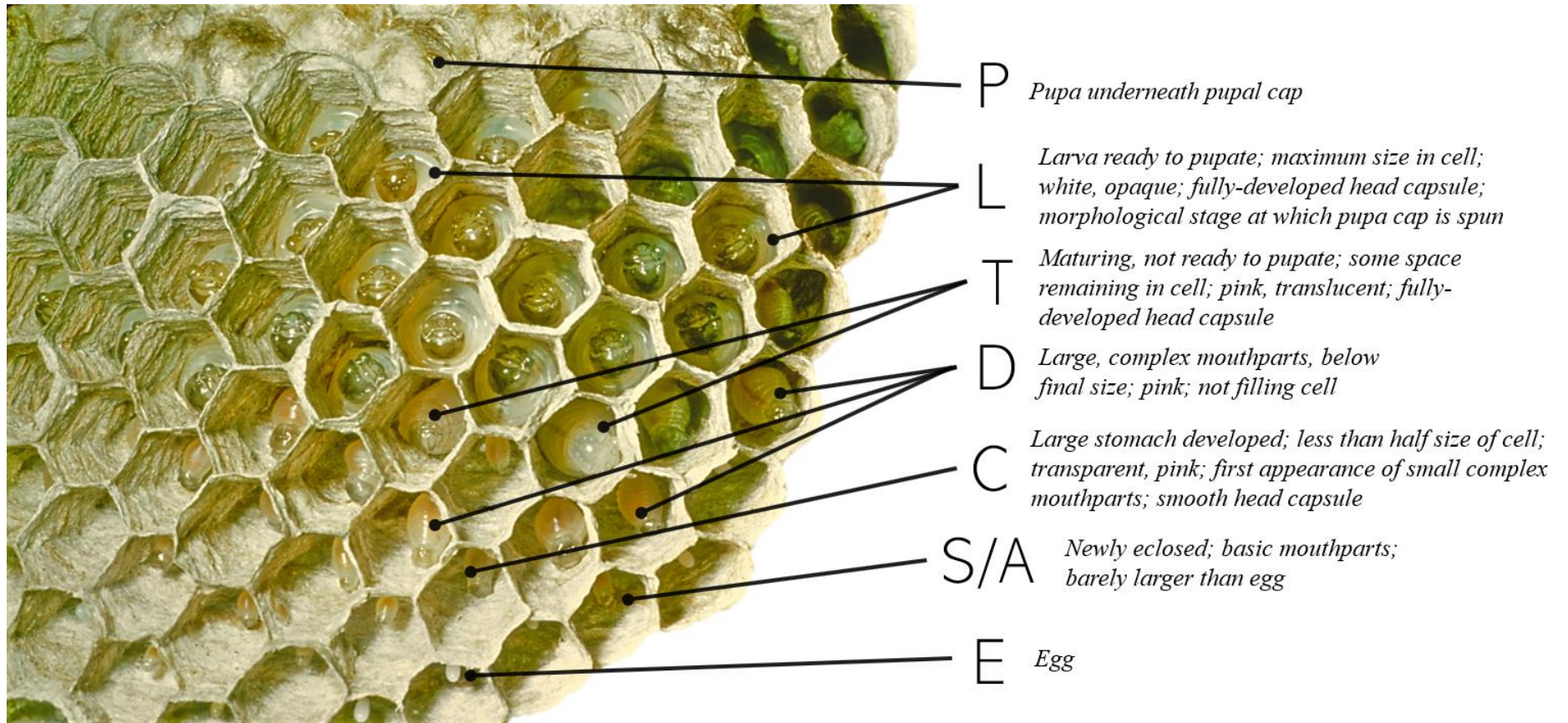


Figure 6.3 | 257,867 repeat observations were made of all cells on 91 post-emergence colonies over a 56-day period, recording 8 developmental states, empty cells, and death due to parasitism (sarcophagids and ichneumonids). To record the brood progress of the individual cells, larvae were split into stereotyped morphological categories. Over a period of weeks, eggs transition to pupae via larval stages. Brood pass through a clear developmental sequence of changing size, colour, and mouthpart complexity. Helping effort may affect these stages differently. *Photograph of P. canadensis nest: J. Pickering (1976) © www.discoverlife.org.*

6.3.1.b *Statistical methods*

The (relatedness-weighted) marginal effect of a worker on the development time of a larva is an incomplete measure of indirect fitness payoff. This is because *Polistes* nests experience a large amount of individual brood death (Sumner *et al.*, 2007), which returns the cell to the start of the developmental process (once the queen has redeposited an egg). A worker's major contribution might be to prevent inefficiency by minimising the rate of brood death. To accommodate both of these, I analysed brood development as a Markov chain, where the response variable is the expected time for a brood cell to produce a new adult ('time to absorption' of the Markov chain; Kemeny and Snell 1983). This is the measure relevant to inclusive fitness, and is distinct from the time taken for a single surviving brood to transition from an egg to an adult: the cell may cycle through repeat deaths before finally producing an adult. I treated the Markov transition matrix as a function of the predictor variables worker number, worker-to-brood ratio, and their interaction. To obtain the transition matrix, I used Bayesian mixed models with colony as a random effect: Bayesian Markov process models currently provide the most natural framework for incorporating random effects into longitudinal multistate models (Welton and Ades, 2005). Using the 'time to absorption' for *P. canadensis* colonies of different worker and brood sizes, I then obtained the predicted colony productivity rate, defined as the expected number of new adults produced per unit time. Because we are interested in the marginal effect of each additional worker on brood production, the most accurate measure of Hamiltonian benefit B is the partial derivative of this rate with respect to worker number, evaluated at the point in demographic parameter space characterising any focal colony.

I now describe the steps above in detail, in the following four sections (sections 6.3.1.c to 6.3.1.f).

6.3.1.c *Mixed model for brood development rates*

Because (1) brood states are categorical and (2) longitudinal data was observed in discrete time steps, I modelled the probability π_{ij} of a brood transition from developmental state i to each state j as multinomial logits. The self-transition $i \rightarrow i$ (the probability that the cell remains in the same state over the 5-day interval) provided the reference category ($\phi_{i \rightarrow i} = 1$) and all other transitions were described by log-linear functions of the covariates x_h in the vector \mathbf{x} (i.e., $\ln(\phi_{i \rightarrow (j \neq i)}) = \alpha_{ij} + \beta_{nij} \mathbf{x}_h$):

$$\pi_{ij} = \frac{\phi_{i \rightarrow j}}{1 + \sum_{j \neq i}^J \phi_{i \rightarrow j}} = \frac{e^{(\alpha_{ij} + \beta_{nij} \mathbf{x}_h)}}{1 + \sum_{j \neq i}^J e^{(\alpha_{ij} + \beta_{nij} \mathbf{x}_h)}} \quad (6.1)$$

I fitted the following log-linear regressions (note that the final two rows are adulthood (A) and death (F), respectively, and are absorbing, defined as a state from which no further transitions are possible):

$$\Phi = \begin{bmatrix} 1 & \phi_{E \rightarrow S} & \phi_{E \rightarrow C} & \phi_{E \rightarrow D} & \phi_{E \rightarrow T} & - & - & - & \phi_{E \rightarrow F} \\ - & 1 & \phi_{S \rightarrow C} & \phi_{S \rightarrow D} & \phi_{S \rightarrow T} & \phi_{S \rightarrow L} & - & - & \phi_{S \rightarrow F} \\ - & - & 1 & \phi_{C \rightarrow D} & \phi_{C \rightarrow T} & \phi_{C \rightarrow L} & - & - & \phi_{C \rightarrow F} \\ - & - & - & 1 & \phi_{D \rightarrow T} & \phi_{D \rightarrow L} & - & - & \phi_{D \rightarrow F} \\ - & - & - & - & 1 & \phi_{T \rightarrow L} & \phi_{T \rightarrow P} & - & \phi_{T \rightarrow F} \\ - & - & - & - & - & 1 & \phi_{L \rightarrow P} & - & \phi_{L \rightarrow F} \\ - & - & - & - & - & - & 1 & \phi_{P \rightarrow A} & \phi_{P \rightarrow F} \\ - & - & - & - & - & - & - & 1 & - \\ - & - & - & - & - & - & - & - & 1 \end{bmatrix} \quad (6.2)$$

The model is solved in discrete time, because brood were observed at fixed intervals. Accordingly, brood are free to transition from one state to a state further downstream than the next step in the sequence (effectively ‘skipping’ states in the Markov chain transition matrix); they have passed through the transitional states during the 5-day window, and are observed in a downstream state. Some transitions are not biologically possible during a 5-day window (such as E to L or C to P), so are not permitted in the Markov chain transition matrix (represented by a dash).

Below, I present three models with increasing complexity. ‘Model 1’ focuses on the baseline transition rates (*i.e.*, intercepts and random effects only) for the complete dataset of 168,811 observed transitions between live-brood-containing cells, which allows us to estimate the baseline productivity rate of *P. canadensis* colonies.

Next, I present two models (‘Model 2’ and ‘Model 3’) to identify the marginal change in productivity associated with each additional worker at different points in the parameter space typifying *P. canadensis* colonies. It is important to avoid confounding effects caused by a confusion between cause and effect. When a colony enters the declining phase, females may abscond the nest or deprioritise brood rearing. In principle, therefore, declining phase nests could introduce spurious correlations between worker number and colony productivity. To be strongly conservative in eliminating any confounding effects from declining-phase colonies, in ‘Model 2’ and ‘Model 3’ I therefore excluded all colony observations with more than 10% empty cells. Although this conservative step will remove a number of colonies at no risk of imminent decline, it is likely to exclude all declining-phase colonies. I also focused only on colony observations for which intra-colony variation through time in worker group sizes can be derived by cubic spline interpolation between night censuses. These steps focused the payoff models onto a core dataset of 67,106 observed live brood transitions on 289 colony observations on 64 colonies (from the total dataset of 168,811 observed live brood transitions on 1,027 colony observations on 91 colonies; see *Results* for the distribution of worker number and brood number at each observation).

I confirmed MCMC convergence by ensuring that the Gelman-Rubin diagnostic was below 1.1 on Gelman plots for 3 chains. I used a minimum of 20,000 iterations per chain for all models until convergence.

6.3.1.d *Indicator variable selection procedure (Model 3) to find the optimal model of brood development rates*

The optimum approach to Bayesian model selection is controversial (Gelman and Rubin, 1995; Ntzoufras, 2011; Kruschke, 2013; Gelman *et al.*, 2014; Hooten and Hobbs, 2015). Bayes factors are (1) often computationally intractable, (2) effectively impossible when comparing a large array of candidate models (Reich and Ghosh, 2006), and (3) have been criticised for paradoxical behaviour (Gelman *et al.*, 2014). Likewise, the standard ‘deviance information criterion’ (DIC) computed in *WinBUGS* (Spiegelhalter *et al.*, 2002) may perform inappropriately for hierarchical models (Kéry, 2010; Tenan *et al.*, 2014). A robust alternative approach – ‘indicator variable selection’ (Hooten and Hobbs, 2015) – is to allow the model to select itself. In an indicator variable selection procedure, we construct a saturated model, and introduce a series of binary indicator variables that ‘switch on’ or ‘switch off’ the predictor throughout MCMC (Hooten and Hobbs, 2015). The duration of MCMC time with each coefficient switched on is proportional to the coefficient’s marginal likelihood of contribution. For each predictor h ’s regression slope β_{hij} (within the vector $\boldsymbol{\beta}_{hij}$ in Equation 6.1), we can therefore annex a binary coefficient g_{hij} that switches between 0 and 1, and then track the mean of the posterior distribution for g_{hij} . If this mean is closer to 1, the corresponding regression slope β_{hij} is retained more frequently in the model.

The priors for g_{hij} and β_{hij} can be chosen to be independent (Kuo and Mallick, 1998) or joint (George and McCulloch 1997), and the decision is largely due to computational convenience: wide-variance vague priors may lead to problems in running MCMC when the priors are independent (Hooten and Hobbs, 2015). For the random effects, I used fully independent Bernoulli priors for g_{hij} to allow the Gibbs sampler to turn the specific random effect on or off directly. For fixed effects, I used a product of the independent priors for g_{hij} and β_{hij} , which can be written in the form of a mixture model ‘pseudoprior’ $f(\beta_{hij}|g_{hij})$ (Ntzoufras, 2002) known as a ‘slab and spike’ (Hooten and Hobbs, 2015):

$$f(\beta_{hij}|g_{hij}) = g_{hij}f(\beta_{hij}|g_{hij} = 1) + (1 - g_{hij})f(\beta_{hij}|g_{hij} = 0) \quad (6.3)$$

Following Ntzoufras (2002), I used normal priors for the conditional distribution of β_{hij} given g_{hij} within the slab and spike respectively:

$$f(\beta_{hij}|g_{hij} = 1) = N(0, \Sigma_{hij}) \quad (6.4)$$

$$f(\beta_{hij}|g_{hij} = 0) = N(0, S_{hij}) \quad (6.5)$$

with $S_{hij} = \frac{\Sigma_{hij}}{k^2}$ (with a default $k = 10$; Ntzoufras 2002). k can be tuned to assist MCMC in evaluating different models (Ntzoufras, 2002). The prior for $f(\beta_{hij}|g_{hij} = 0)$ can be parameterised with a potentially nonzero mean ($\bar{\mu}_{hij}$), and candidates for $\bar{\mu}_{hij}$ and S_{hij} are the values generated in the saturated model. For simplicity, I followed the recommendation by Ntzoufras (2002) to use $N\left(0, \frac{\Sigma_{hij}}{k^2}\right)$ with a sufficiently large k to drive the ‘spike’ prior to zero – a strategy advocated by the ‘stochastic search variable selection’ (SSVS) approach to indicator variable selection (George and McCulloch 1993), leading to β_{hij} being indistinguishable from zero when g_{hij} switches the predictor off. I modelled the indicators as Bernoulli random variables with a 50:50 prior ($g_{hij} \sim \text{Bernoulli}(0.5)$), representing our starting point of indifference between either including or dropping the slope β_{hij} . In interpreting the fitted model, I considered indicator variable selection to have ‘favoured’ retention of the associated predictor if $g_{hij} > 0.6$.

6.3.1.e *Expected time to adulthood*

To calculate the worker effect on the transition matrix for each model, controlling for oviposition rate, I submitted all estimated transition-to-death probabilities ($\phi_{i \rightarrow F} \forall i$) to the prediction matrices as transitions to new eggs. This isolates the potential effect of workers (as opposed to the egg-layer) to obtain per-cell efficiency without the confounding effect of variation between queens in the rate at which replacement eggs are laid following the death of larvae.

The expected ‘time to absorption’, in which a brood cell transitions from egg to adulthood ($\hat{m}_{E \rightarrow ADULT}$) via intermediate states, can be obtained using the linear algebra for a discrete Markov process via the ‘fundamental matrix’ method of Kemeny and Snell (1983). Following Grinstead & Snell (1997), I obtained the fundamental matrix \mathbf{N} by inverting the matrix $\mathbf{I}_t - \mathbf{Q}$, where \mathbf{I}_t is the identity matrix for the transient states and \mathbf{Q} is a square matrix of transition probabilities between each transient brood state with length equal to the number of transient states (*i.e.*, all states apart from adulthood and death)⁷. Accordingly:

$$\mathbf{N} = (\mathbf{I}_t - \mathbf{Q})^{-1} \quad (6.6)$$

⁷ The sum of each row in $\mathbf{I}_t - \mathbf{Q}$ must equal zero, with the exception of the row specifying transitions from pupae (from which it is possible to reach the one absorbing state, adulthood).

The element $n_{i,j}$ in \mathbf{N} is the frequency with which the chain is expected to visit state j given a current state i . The vector \mathbf{t} of times to absorption is then:

$$\mathbf{t} = \mathbf{N}\mathbf{1} \quad (6.7)$$

where $\mathbf{1}$ is a column vector of 1s. The i th element of \mathbf{t} is the duration (in step numbers) from state i to successful production of a new adult ($\hat{m}_{E \rightarrow ADULT} = \sum_{j=1}^J n_{E \rightarrow j}$).

$\mathbf{I}_t - \mathbf{Q}$ is not a symmetric positive-definite matrix (so cannot be inverted natively by *WinBUGS*). I therefore solved for \mathbf{N} in *Mathematica*. I derived the posterior predictive distribution for the passage from egg to adulthood ($\hat{m}_{E \rightarrow ADULT}$) for single brood cells as a function of the fixed effects; I included random effects in the MCMC to improve the estimation of the fixed effects (*i.e.*, fitting fixed effects whilst allowing for extraneous variation). I then derived the predicted whole-colony rate of brood production by converting the per-cell time to absorption to a productivity rate per unit time and scaling this rate to the number of active brood cells (containing brood from egg to large larva stages, inclusive) on the colony.

6.3.1.f *Indirect fitness payoff calculation*

To capture nonlinear returns to cooperation, Smith *et al.* (2010) propose a nonlinear form of Hamilton's rule. Here, neighbour-modulated fitness w is viewed as a polynomial linear regression on the frequency of cooperators amongst the focal individual's social partners. I obtained the equivalent polynomial function to estimate absolute fitness by fitting the polynomial interpolation of productivity q against worker number z and brood number y using the 1,000 simulated points in the posterior predictive distribution for whole colony productivity rate (in *Mathematica*): *i.e.*, to extract the shape of the posterior predictive distribution, I fit the smooth interpolation to 1,000 closely-packed samples monitored in MCMC. The diminishing returns hypothesis predicts that a worker can maximise inclusive fitness by shifting from a home colony H to a target colony T :

$$r_T \frac{\partial q(z, y)}{\partial z} \Big|_{\substack{z=z_T \\ y=y_T}} > r_H \frac{\partial q(z, y)}{\partial z} \Big|_{\substack{z=z_H \\ y=y_H}} \quad (6.8)$$

where she has a larger effect on the production rate q of offspring-equivalents by changing worker number x on T than she would have by changing q on H . The end result of 'Model 3' is a model of these partial derivatives (estimates of benefit B in Hamilton's rule) for colonies of different worker numbers and brood numbers.

6.3.2 Results

In total, 257,867 repeat observations were made of over 20,000 individually-tracked brood cells. Whole-colony failure was high: 105 post-emergence colonies were night-censused between 25th July 2016 and 18th August 2016, of which 25.7% (27 colonies) died. 8.3% (14,070/168,811) of live-brood transitions were to death.

Model 1 (intercepts-only): Baseline brood development rates of *P. canadensis* colonies: Using all observations on all 91 post-emergence colonies in all colony states (stable, declining, etc.), the intercepts-only model (Figure 6.4) showed that the probability of brood death falls with developmental stage, potentially reflecting reduced risk of mortality (due to disease, genetic defects, and cannibalism) rates for late-stage larvae. This may reflect workers prioritising re-cannibalising less valuable (*i.e.*, less-progressed) brood during temporary resource stress. Larvae spend the longest time in the ‘L’ stage. The high levels of brood failure generate an expected time for any specific egg-containing cell in the population to finally produce an adult (expected time to absorption) of 152 days, allowing for the possibility of multiple rounds of brood death. Note that this value is the average across developmental stages and is affected by falling brood productivity as colonies begin to decline.

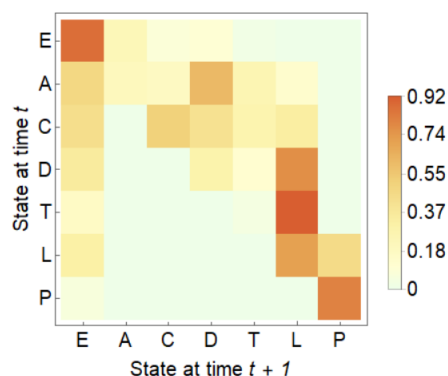


Figure 6.4 | **Baseline transition rates (intercepts-only) for *P. canadensis* brood-rearing (Model 1).** The Markov chain represents 168,811 observed live brood transitions across 91 colonies over 56 days. Shown are the transition rates (**Q** matrix) for Model 1 from a starting state (time t) to the next observation ($t + 1$), occurring 5 days later. High rates of brood death at all stages of development are represented by high reversions to the egg stage (state *E*): the first column shows that younger-stage brood are more likely to die than older-stage brood.

Model 2 (worker-to-brood ratio only): Model 2 is a simple model with only a single predictor (worker-to-brood ratio). The rates of progress changed substantially across the range of worker-to-brood ratios: brood failure declined with rising worker-to-brood ratio (Figure 6.5) and cells less frequently remained in the egg stage (Figure 6.5). Comparing transition matrices predicted by different worker-to-brood ratios reveals systematic changes: brood death rates fall, and faster progress is more likely (Figure 6.5).

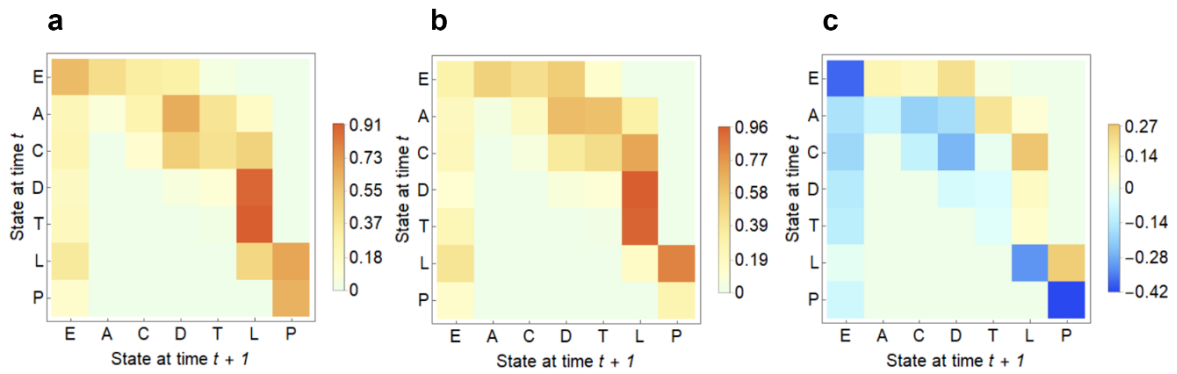


Figure 6.5 | Rates of state transitions change with worker-to-brood ratio (Model 2). (a) and (b) show are the probabilities of transitioning from each starting state at time t to the next observation ($t + 1$), occurring 5 days later. (a) The \mathbf{Q} matrix at the mean of posterior predictive distribution for a worker-to-brood ratio of 0.2. (b) The \mathbf{Q} matrix at the mean of the posterior predictive distribution for a worker-to-brood ratio of 0.3. (c) By subtracting (a) from (b), we see how brood development rates change within the Markov chain: death (represented by transitions to state 1 in the posterior predictive model) is less likely.

Model 3 (full model via indicator variable selection): Model 3 incorporated three predictors (worker number, worker-to-brood ratio, and their interaction) for each separate multinomial regression equation describing the Markov chain transition matrix for brood development. When selecting the optimum model of brood development, indicator variable selection favoured the retention of total worker number (Figure 6.6a), worker-to-brood ratio (Figure 6.6b), and their interactions (Figure 6.6c) as predictors for a number of brood transitions, which are shown as coloured arrows in Figure 6.6. In contrast, indicator variable selection only favoured retaining brood number as a predictor for a single brood transition (Figure 6.6c). For the subsection of colonies included in Model 3, brood numbers maintained by different worker numbers were close to linearly-predicted by worker group size (Table 6.2) over the range of most group sizes (Figure 6.7). Goodness-of-fit was calculated using McFadden’s pseudo- R^2 for multinomial logistic regression. An ‘excellent’ fit is considered if $R_{McFadden}^2$ lies between 0.2 and 0.4 (McFadden, 1977). The seven multinomial logistic regressions range in $R_{McFadden}^2$ from 0.194 to 0.342, reflecting high likelihoods for the fitted models over an intercepts-only model.

To obtain the predicted increment in brood production produced by the addition of a new worker to the colony, we can multiply brood number by per-brood Markov productivity rate at different points in parameter space, and take the partial derivative with respect to worker number. This represents an absolute fitness estimate of benefit B in Hamilton’s rule, because it is the marginal effect of an additional worker on the payoff rate. Following these steps to obtain B at different numbers of workers and brood reveals variation in the estimated benefits of altruism over the parameter space inhabited by *P. canadensis* colonies (Figure 6.8).

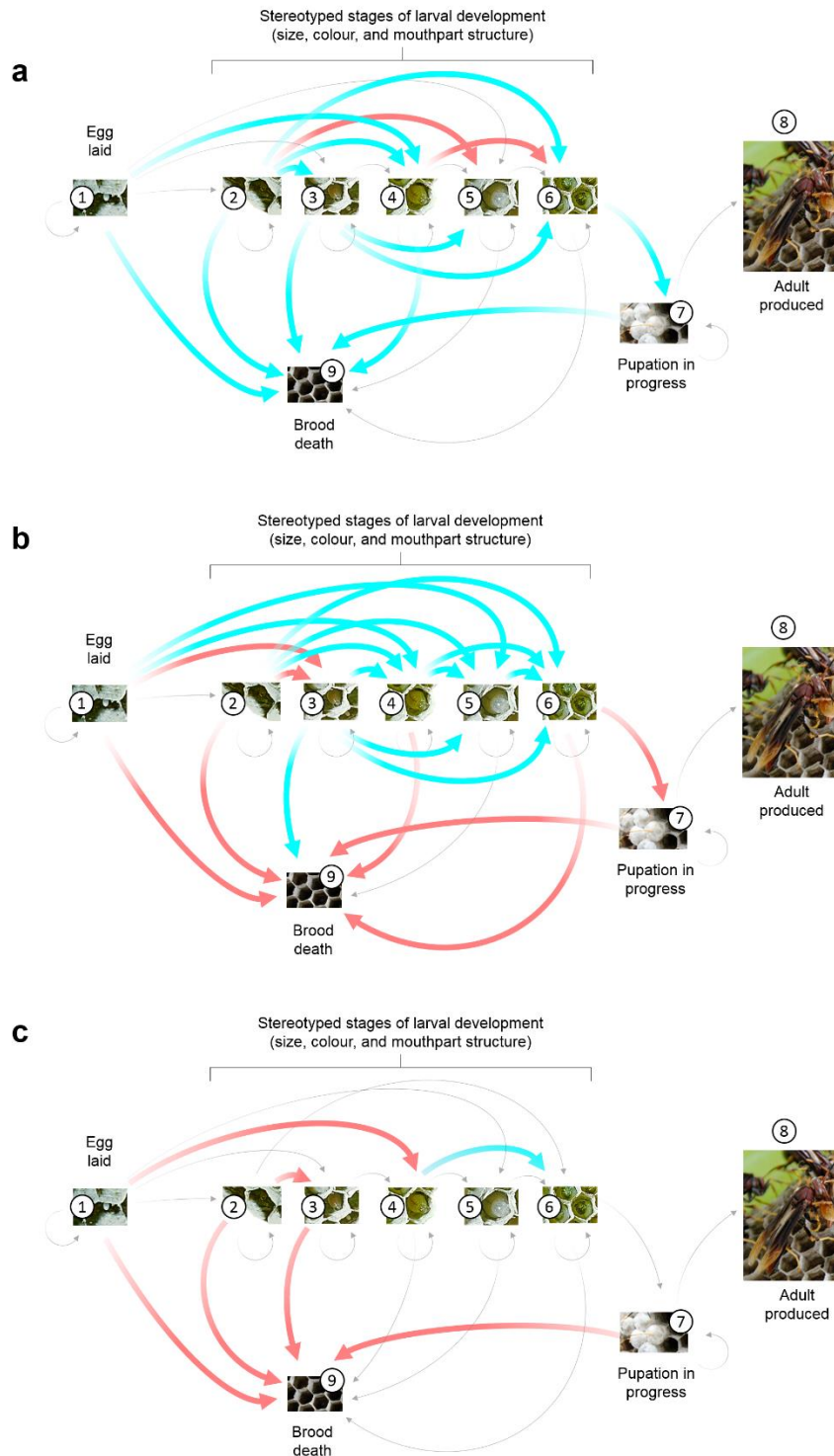


Figure 6.6 | Indicator variable selection results (Model 3). Shown are the positive and negative contributions of different predictors to separate brood transitions in Model 3. The predictors are: **(a)** number of workers (adult females). **(b)** Worker-to-brood ratio (brood defined as E to L). **(c)** Interactions between (a) and (b). If the transition arrow is blue, the predictor had a positive effect on the rate of the transition. If the transition arrow is red, the predictor had a negative effect on the rate of the transition. If the transition arrow is grey, the predictor had no effect on the rate of the transition. A positive or negative effect means, respectively, an increased or decreased transition rate relative to the rate at which the brood stays in the same state. For this reason, 'self-loops' representing staying in the same state (e.g., E to E, or L to L) are shown in grey by default.

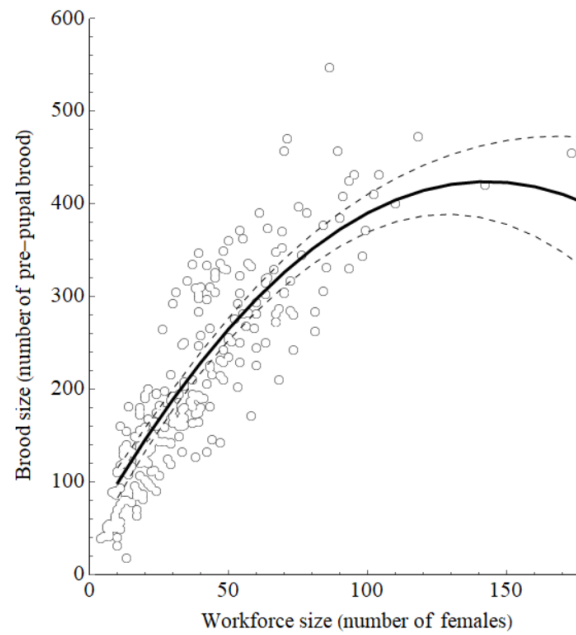


Figure 6.7 | Brood size maintained by workforces of different sizes is linear for most of the natural range of colony demographics. Solid black line denotes the mean of the posterior predictive distribution at each workforce size; dashed lines show 2.5% and 97.5% credible intervals. Points show colony state at the start of separate 5-day observation episodes; colony is a random effect.

Table 6.2 | Posteriors for parameters of brood size by workforce comparison. Quadratic model favoured by deviance information criterion (DIC).

	μ	σ	MC error	$q_{2.5}$	Median	$q_{97.5}$
Intercept	48.96	10.69	0.067	28.10	48.90	70.13
Worker number	5.263	0.347	0.002	4.580	5.264	5.941
Worker number squared	-0.018	0.002	0.000	-0.023	-0.018	-0.014
Whole model precision	0.001	0.000	0.000	0.001	0.001	0.001
Colony (random effect) precision	1.970	43.93	0.761	0.000	0.001	0.001

Summary of Question 1: In this section, I have asked whether *P. canadensis* colonies show diminishing returns to cooperation. Two simple models ('Model 1' and 'Model 2') were used to build towards a full fitted model of the benefit term in Hamilton's rule ('Model 3'), which used Bayesian indicator variable selection to select the optimum model. The results of Model 3, plotted in Figure 6.8, show that colonies gain improved productivity rates as (1) total worker group size increases and (2) the ratio of workers to brood increases. However, Figure 6.8 also shows that each additional worker is – on average – associated with a smaller increase in productivity rate. More formally, the rate improvements in the Markov chain governing brood production decelerate as worker number and the ratio of workers to brood rises (Figure 6.8), implying strong diminishing returns to cooperation. For workers on low-payoff colonies (in areas of Figure 6.8 represented by colder colours), a more than twofold increase in payoff

is possible by drifting to high pay-off colonies (in areas of *Figure 6.8* represented by warmer colours). In principle, this increase in the payoff rate of altruism would be sufficient to justify the approximately twofold reduction in relatedness to recipients (Sumner *et al.*, 2007). In the next section, I ask whether drifting wasps do indeed move across the parameter space as predicted by this diminishing returns model of the benefit term B in Hamilton's rule.

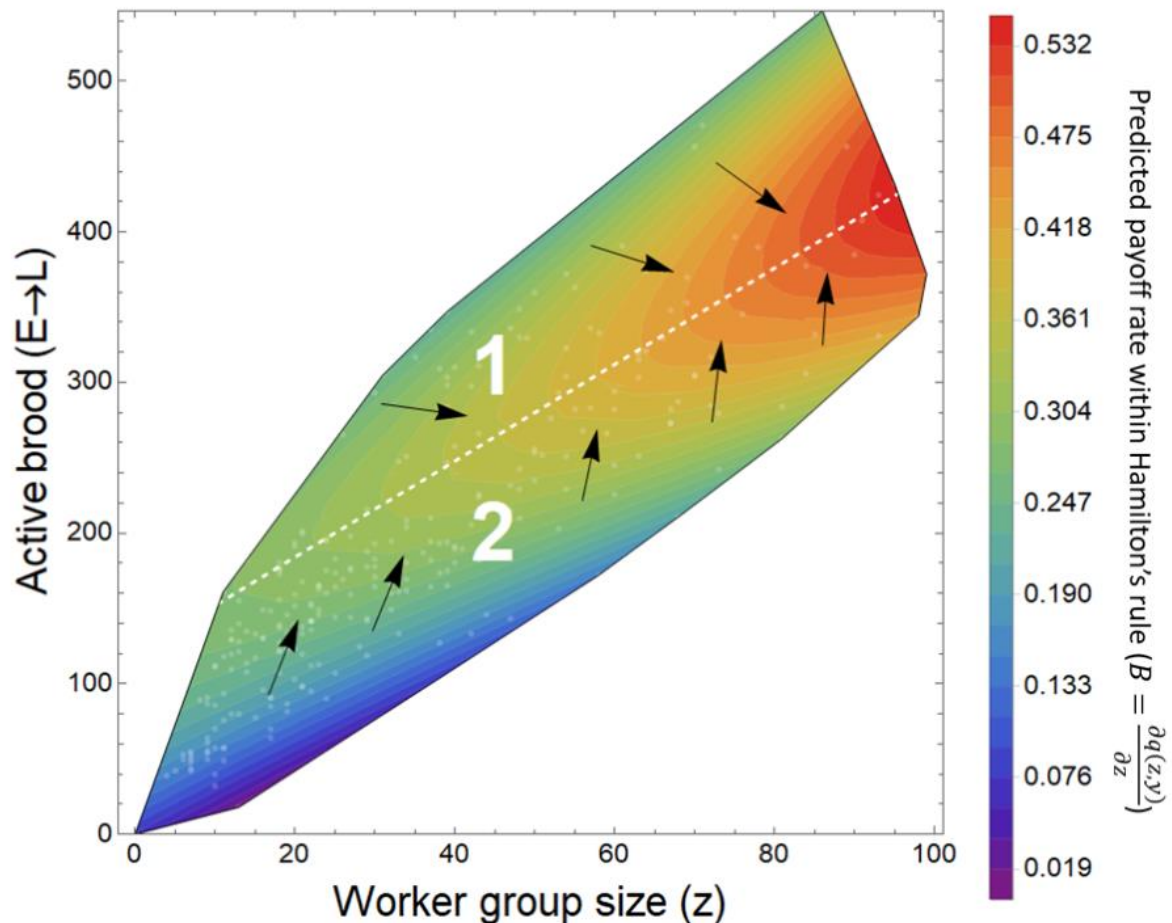


Figure 6.8 | Nonlinear returns to cooperation with additional workers: rate improvements in the Markov chain governing brood production decelerate as the ratio of workers to brood rises (descending from the dashed line) but accelerate once the colony has attained a high brood number (rising from the dashed line). For the zone occupied by most colonies (lower left of the space), colony productivity rate rises with worker group size (z) and number of active brood (y) but saturates as predicted by Michener's paradox. Shown is the inferred marginal contribution of an additional worker (calculated as the partial derivative of colony productivity rate (q), a function of total brood number and the time to absorption of the Markov process, with respect to worker group size (z)). Colony productivity rate q , as a function of worker group size (z), brood number (y), and worker-to-brood ratio ($z:y$) was obtained by fitting a polynomial interpolation to 1,000 simulated samples (representing simulated colonies in the natural range of *P. canadensis*) from the posterior predictive distribution monitored during MCMC. Separate 5-day colony observations (white dots) show the parameter space (worker group size and number of brood) inhabited by non-declining-phase colonies during the 56 days of monitoring.

6.4 Question 2: Do workers move to colonies where the productivity returns are greatest?

In this section, I test the second prediction of the diminishing returns hypothesis: wasps move from saturated to unsaturated colonies to maximise their marginal effect on colony productivity (Hamilton, 1964b; Lengronne, 2013). To test this prediction, I collated available radio-frequency identification (RFID) data from unmanipulated *P. canadensis* populations, both from my own fieldwork and from previous fieldwork by the Sumner Lab Group. This comprised six populations in five separate field seasons, from French Guiana (2015 data: PK, Chapter 5, this thesis) and Panama (2016 data: PK, this chapter; 2005 data (first five days only): Sumner *et al.* 2007; 2009-2010 data: Lengronne 2013). Any data collected by others were used by permission of Dr S. Sumner and Dr T. Lengronne. I collected the 2016 Panama RFID data in the field following identical methods to those described in Chapter 5, using 691 RFID-tagged wasps on 26 colonies monitored over a six-day period, during which 331 wasps were detected by RFID.

I removed from analysis any repeat detections occurring within 120 seconds of a first appearance, which typically represent movement of the wasp around the antennae before passing through the detection radius. Following this step, the total dataset of all available RFID studies on *P. canadensis* comprised 23,968 separate RFID-detections of 1,828 detected wasps.

6.4.1 Social network analysis (SNA)

To test whether drifters within this dataset tended to move in a particular direction across the demographic parameter space defining *P. canadensis* colonies, I used social network analyses (SNA). Analyses of network data are typically complicated by the difficulty of specifying appropriate random effects (*i.e.*, inter-node dependencies are often complex functions of network structure). To avoid this problem, network analyses normally use MR-QAPs (multiple regression quadratic assignment procedures; Hirsch *et al.*, 2012; Firth and Sheldon, 2015), also known as 'QAP regressions', which randomly permute the response variable (here, directional drifter links between colonies) across the matrix defining the network (colony aggregation).

For the five RFID studies that consisted of single aggregations that can be analysed as single networks, I used MR-QAP in the networks package *UCINET* (Borgatti *et al.*, 1992, 2013), treating individual colonies as nodes and number of drifting events as directional edges. All analyses used 10,000 permutations. I included between-colony relatedness data (microsatellites) as independent variables for the Panama 2005 aggregation (genotyped by Sumner *et al.* 2007) and the Panama 2009 aggregation (genotyped by

Lengronne 2013); details of genotyping in each case can be found in Sumner *et al.* (2007) and Lengronne (2013). If data were available, I used the difference between pairs of colonies in worker number, brood number, and worker-to-brood ratio as independent variables in MR-QAP. The diminishing returns hypothesis predicts that high-payoff colonies should receive drifters and low-payoff colonies should emit them (*Figure 6.8*). If this prediction holds, MR-QAP should show negative coefficients for worker number and worker-to-brood ratio: wasps will be moving from colonies with many workers and saturated productivity rates to colonies with few workers and unsaturated productivity rates.

6.4.2 Results

Across the dataset of 1,828 RFID-detected wasps (drifters and non-drifters), 22.6% (413/1,828) were identified as drifters, where drifters are defined as any wasp detected on more than one colony. This includes, for instance, wasps who were detected only on one colony by RFID but this colony was not where they had been during the tagging phase preceding RFID monitoring (denoted as ‘tagging-only drifters’ in *Figure 6.9*). 16.1% (295/1,828) of the RFID-detected wasps were detected on more than one colony by RFID during the RFID monitoring (‘RFID-phase drifters’ in *Figure 6.9*). Because it provides a standardised and identical method in each population, RFID allows us to compare drifting rates directly across *P. canadensis* populations, and reveals large variation between populations in drifting rates (*Figure 6.9*). Most drifters invested predominantly in a main colony and supplemented that colony with additional colonies visited less often (*Figure 6.10*). The initial tagging colony was the most visited colony for 53.3% of drifters.

Figure 6.11 plots the trajectories of wasp drifting on the same axes as *Figure 6.8*, and shows no clear direction of movement from nests predicted to be ‘diminished’ to nests predicted to be ‘undiminished’. Similarly, social network analysis revealed no clear direction of wasp movement across the parameter space defining *P. canadensis* colonies (*Table 6.3*). I do not show Panama 2009 (Lengronne *et al.*, 2012) in *Table 6.3*, because the model yielded a negative adjusted R^2 , which implies insufficient power in the sample size to test the predictors in that aggregation. . Relatedness and had no effect on drifting in the two genotyped populations (Panama 2005 is shown in *Table 6.3b*; Panama 2009 is not shown). Likewise, MR-QAP found no significant effect of the difference in worker-to-brood ratio between colonies in any aggregation (*Table 6.3*). In general, MR-QAP shows very low adjusted R^2 values (0.00484–0.10479), which implies a biologically meaningless effect size of the various significant predictors; nonetheless, inter-colony distance was significant in 3 of the 4 populations and there was a significant effect of worker number in two populations (*Table 6.3b* and *Table 6.3c*), although in opposite directions.

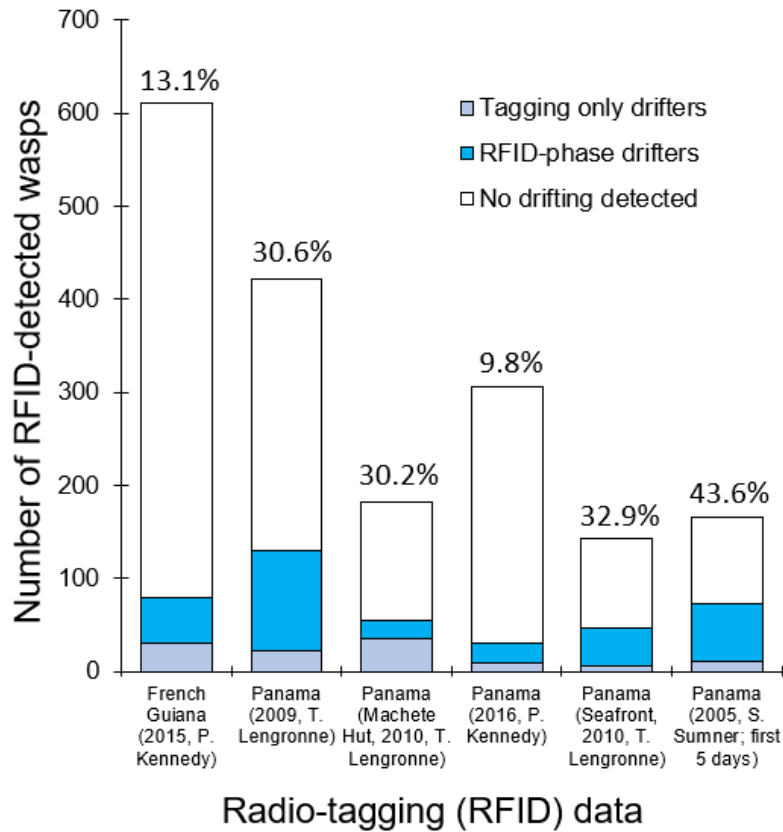


Figure 6.9 | RFID-detected drifting rates vary across *P. canadensis* populations. Shown are RFID data from six studies in different sites and years. ‘Tagging-only drifters’ are wasps who were detected by RFID on a single colony during RFID monitoring in which the colony that differed from their tagging colony. ‘RFID-phase’ drifters are wasps detected on more than one colony during RFID monitoring. ‘No drifting detected’ wasps are wasps never detected by RFID on foreign colonies. The percentage of RFID-detected drifters (‘tagging-only’ plus ‘RFID-phase’) is shown for each population.

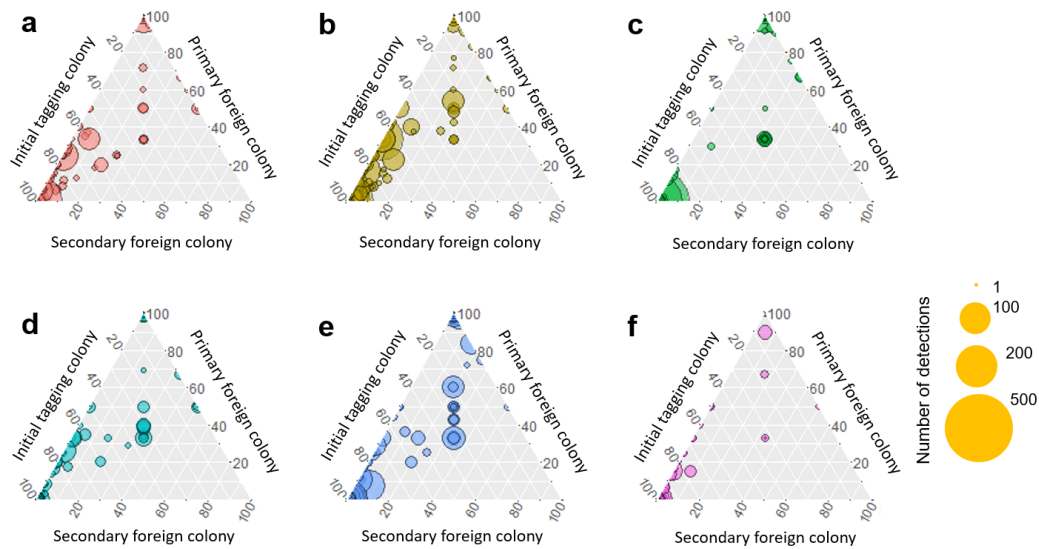


Figure 6.10 | Most drifters invest mainly in a single colony, and supplement that investment with other colonies. Shown are between-colony investment ratios by RFID-detected *P. canadensis* workers ($n = 1,828$ wasps) across six populations. Each axis denotes the proportional time investment (number of separate RFID detection bouts) in the colony on which the wasp was first collected and tagged ('initial tagging colony') and the first and second most visited colonies other than the initial tagging colony (denoted 'primary foreign colony' and 'secondary foreign colony', respectively). Points are individual wasps, scaled in proportion to the total number of RFID detections of a minimum 120-second duration. Populations were sampled in multiple sites and years: **(a)** data collected by Sumner *et al.* (2007) at Hospital Nacional (Panama, 2005); **(b)** data collected by T. Lengronne (unpublished) at Galeta Point Field Station (Panama, 2009); **(c)** data collected by T. Lengronne (unpublished) at Galeta Point Field Station aggregation 1 (Panama, 2010); **(d)** data collected by T. Lengronne (unpublished) at Galeta Point Field Station aggregation 2 (Panama, 2010); **(e)** data collected by P. Kennedy (this thesis) in Sinnamary (French Guiana, 2015); **(f)** data collected by P. Kennedy (this thesis) at Fort Sherman (Panama, 2016).

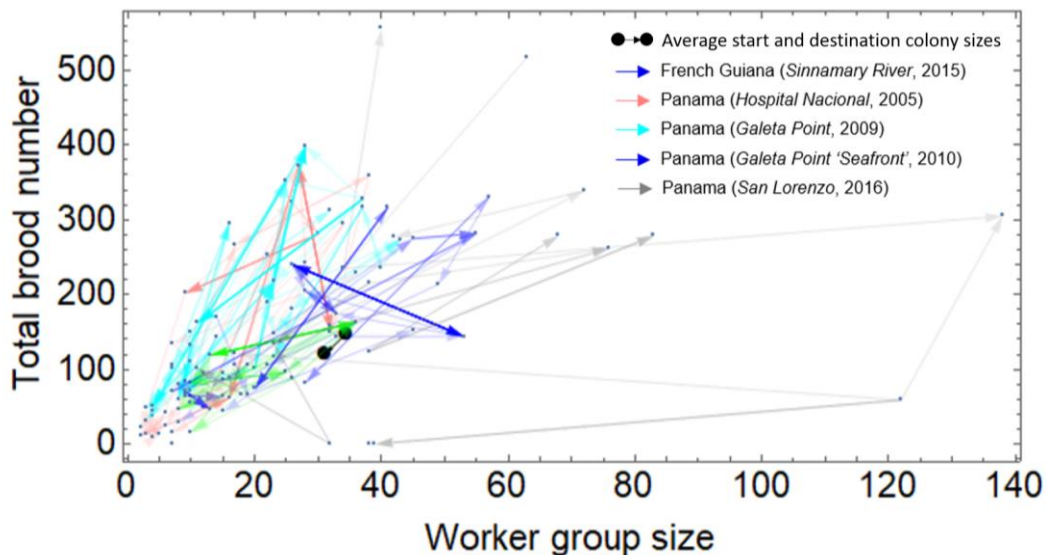


Figure 6.11 | RFID-tracked wasps from multiple sites and years show no detectably consistent preferences for demographic features (group size and brood number) in their target colonies. Small points represent colonies; arrows represent drifter connections from a starting colony to a new colony; the mean values for worker group size and total brood number for start and destination colonies are shown in large black points, connected by an arrow. Brood counts were unavailable for the Panama 2010 'Machete Hut' cohort (Lengronne, 2013). If wasps move from 'diminished' to 'undiminished' colonies, *Figure 6.8* predicts that most trajectories should be from right to left (i.e. from cold to warm areas in *Figure 6.8*).

Table 6.3 | Social network analyses of RFID-tagged wasp populations using MR-QAP. (a) French Guiana 2015; (b) Panama 2005; (c) Panama (Machete Hut) 2010; (d) Panama (Seafront) 2010. For Panama 2005 (Sumner *et al.*, 2007), brood and worker counts were not available for 6 of the 33 colonies, and inter-colony relatednesses were not available for 12 of the 33 colonies; for Panama 2010 ‘Seafront’ (Lengronne, 2013), brood counts were not available for 3 of the 12 colonies. Missing values were supplied to UCINET as ‘n’. Brood data were not available for Panama ‘Machete Hut’.

(a) French Guiana (River Sinnamary, 2015); 7 days, 33 colonies, fieldwork: P. Kennedy. Adjusted R ² =0.01435			
Variable	Unstandardised coefficient	Standardised coefficient	p-value
Intercept	0.28554	–	–
Distance between colonies	-0.00033	-0.13349	0.00040*
Difference in brood (E→L) number	-0.00011	-0.01777	0.33507
Difference in worker number	0.00008	0.00534	0.45325
Difference in worker-to-brood ratio	0.00981	0.00446	0.43766
(b) Panama (Hospital Nacional, 2005); 5 days, 33 colonies, fieldwork: Sumner <i>et al.</i> (2007) Adjusted R ² =0.00484			
Variable	Unstandardised coefficient	Standardised coefficient	p-value
Intercept	0.57794	–	–
Distance between colonies	-0.00009	-0.16243	0.00340*
Difference in brood (E→L) number	-0.00092	-0.08269	0.0018*
Difference in worker number	0.00400	0.04339	0.02680*
Difference in worker-to-brood ratio	-0.16634	-0.02418	0.05599
Relatedness	-0.28105	-0.03514	0.34327
(c) Panama (Machete Hut, 2010); 5 days, 16 colonies, fieldwork: T. Lengronne. Adjusted R ² =0.01648.			
Variable	Unstandardised coefficient	Standardised coefficient	p-value
Intercept	3.66122	–	–
Distance between colonies	-0.00159	-0.00527	0.49125
Difference in worker number	-0.35462	-0.15709	0.00160*

(d) **Panama (Seafront, 2010)**; 5 days, 12 colonies, fieldwork: T. Lengronne. Adjusted $R^2=0.10479$.

Variable	Unstandardised coefficient	Standardised coefficient	p-value
Intercept	1.10340	–	–
Distance between colonies	-0.00136	-0.32063	0.00020*
Difference in worker number	0.01414	0.14952	0.22278
Difference in brood (E→L) number	-0.01081	-0.42640	0.06759
Difference in worker-to-brood ratio	-0.54586	-0.23042	0.13829

Summary of Question 3: In this section, social network analysis found no evidence that wasps move from low-payoff colonies towards high-payoff colonies: drifting trajectories shown in *Figure 6.11* are not in the consistent direction predicted by *Figure 6.8*. Moreover, drifters did not invest in just a single high-payoff colony, but rather invested in several colonies (*Figure 6.10*). Taken together, the answers to Question 2 and Question 3 are equivocal on the diminishing returns hypothesis for drifting: *P. canadensis* does show strong diminishing returns to cooperation (Question 2), but there is no evidence – from social network analyses of RFID networks – that wasps move in the direction predicted by the diminishing returns hypothesis (Question 3). Nonetheless, it is important to highlight that the analyses in this section (Question 3) are not a definitive test of the role of diminishing returns: they are restricted by representing only a small sample of wild aggregations (four networks), for which only two have relatedness data. An immediate priority will be to extend such analyses to additional variables that may influence payoff rates, including parasitism and queen fecundity (see *Discussion*).

6.5 Question 3: How might indirect reciprocity (Nonacs, 2017) explain drifting?

The indirect reciprocity hypothesis for drifting was proposed by Nonacs (2017) in reference to *Polistes canadensis* and other social insect species with high levels of cooperative drifting, including the supercolonial ants (Helanterä, 2009). It involves the following two hypothetical effects. First, cooperation between distant relatives or non-relatives generates disproportionately higher fecundity payoffs than cooperation between close relatives ('social heterosis'; Nonacs and Kapheim 2007). Second, drifter-emitting colonies provide these 'socially heterotic' benefits to unrelated neighbours in order to increase the probability that they themselves receive similar help as a 'reward' from unrelated

third parties ('indirect reciprocity'). These indirect-reciprocator third parties successfully identify the drifter-emitting colonies by the fact it has an honest and recognisable tag. Thus, drifter-emitting colonies are rewarded by receiving social heterotic benefits from the arrival of drifters from third party colonies.

There are two elements to this hypothesis: 'social heterosis' and 'indirect reciprocity'. At present, there is limited evidence for social heterosis in wasps: Hoggard *et al.* (2013) show that antimicrobial compounds in *Polistes humilis* are more effective in genetically diverse colonies. There is clear evidence that intra-colony genetic diversity in ants provides disease resistance (Ugelvig *et al.*, 2010) and even results in patriline-specific behavioural castes ('genetic polyethism'; Evison and Hughes 2011; Waddington *et al.* 2010). In contrast, indirect reciprocity has never been found outside humans, where it is sustained by cognitively-complex image-scoring (Yoeli *et al.*, 2013), and even amongst humans its existence is disputed (Bshary and Raihani, 2017). Accordingly, the claim that it could explain cooperation in a social insect is exciting. However, contrary to Nonacs (2017), here I argue that this complex combination of social heterosis and indirect reciprocity may be implausible as an explanation of drifting in *Polistes*.

The conditions for drifting to evolve by indirect reciprocity can be captured in a simple scenario. Let a *Polistes* worker be related by r_1 to her home queen and r_2 to a neighbour queen. Let drifting confer a fecundity benefit x on the neighbour queen, multiplied by a putative social heterosis effect k . Helping the home queen confers the fecundity benefit x without any amplifying effect of social heterosis. To allow for indirect reciprocity, assume that providing help to neighbour queens increases the probability (from P_0 to P_1 , where $q = P_1 - P_0$) that the home queen receives the fecundity benefit kx from indirect-reciprocator third parties, who may be workers on other colonies (as envisioned by Nonacs, 2017) or worker offspring of the recipient neighbour queen. Accordingly, drifting in this scenario increases the worker's inclusive fitness if $r_2 kx + r_1 q kx > r_1 x$, or, more simply:

$$q + \frac{r_2}{r_1} > \frac{1}{k} \quad (6.9)$$

When $r_2 = 0$ (as proposed by Nonacs 2017; see black region in *Figure 6.12*), this resembles the well-known rule $q > c/b$ for the evolution of indirect reciprocity in the absence of kin selection (Nowak 2005), where c/b is the cost-to-benefit ratio. Because Nonacs's (2017) hypothesis invokes social heterosis, the recipient kin should in general be distantly related ($0 < r_2 \ll 1$); otherwise, there can be no social heterotic benefit due to cooperating with distant relatives. However, if some level of social heterosis benefit k can be conferred on more closely-related kin ($r_1 > r_2 \gg 0$), the requirement for third-party reciprocation (q) decreases (*Figure 6.12*).

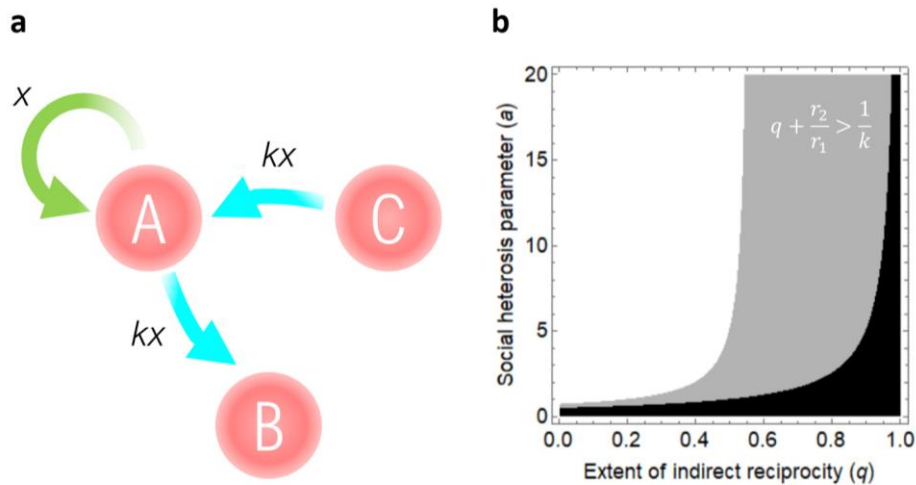


Figure 6.12 | The indirect reciprocity hypothesis is implausible as an explanation for drifting in *P. canadensis*. (a) The hypothesis argues that a worker from the focal colony (A) can confer a benefit x on a neighbour colony (B), with the payoff amplified by a factor k due to complementarity between unrelated or distantly-related workers (known as ‘social heterosis’). Drifting to colony B increases the probability that colony A receives similar social heterosis benefits due to the arrival of workers from a third-party colony (C). (b) Indirect reciprocity between non-kin evolves when the cost (c) to benefit (b) ratio is less than the probability of reciprocation ($q > \frac{c}{b}$; Nowak and Sigmund 2005). Adjusted for additional indirect fitness benefits from helping distant kin, this rule is $q + \frac{r_2}{r_1} > \frac{1}{k}$ (see main text), where r_1 is the worker’s relatedness to the home colony and r_2 is inter-colony relatedness in social interactions. Here, I set $k = \frac{1-r_2/a}{1-r_1/a}$, where a is a scaling factor (smaller values of a result in higher values of social heterosis). The black region represents parameters that favour drifting by indirect reciprocity when targeting non-relatives ($r_2 = 0$). The grey region represents targeting related colonies ($r_2 = 0.23$): the extension from the black region arises from standard indirect fitness benefits of helping kin, rather than social heterosis. $r_1 = 0.52$.

For acts of cooperation to be rewarded by indirect-reciprocator third parties ($q > 0$), third parties must have access to reliable information about actor behaviour (Nowak and Sigmund, 2005; Santos *et al.*, 2018), based either on reputation or honest tags (Milinski *et al.*, 2001). If cooperators are unable to direct costly cooperation to other cooperators at the exclusion of others, cooperation will be unable to outcompete free-riders. In the context of wasp drifting, free-rider colonies would accept foreign cooperative drifters without contributing drifters to neighbour colonies. Indeed, the potential existence of ‘parasitic’ satellite nests, strategically positioned close to large nests in order to absorb drifters, has been proposed in *Polistes fuscatus* (Page *et al.*, 1989). To explain how indirect reciprocity could evolve against free-riding, Nonacs (2017) suggests that an honest tag exists for cooperative (*i.e.*, drifter-emitting) colonies:

‘...the tag in this case is simple and honest: a willingness to accept drifters. Reciprocating nests would be evident in the population by their relaxed acceptance threshold levels... There would

be no need to evolve specific phenotypic markers, learn to recognize reciprocators, or to punish cheaters.' (Nonacs, 2017)

However, contrary to Nonacs (2017), '*willingness to accept drifters*' is not an honest signal that a colony is a drifter-emitter. By definition, free-riding colonies will also have '*relaxed acceptance thresholds*', because they will readily accept foreign help without reciprocating. The opportunity to free-ride drives q to zero, as there is no longer an expectation of reciprocal help. The failure of free-riders to evolve in Nonacs (2017) may instead be due to elements of the simulation: the two relevant traits in question – namely, (1) willingness to drift and (2) willingness to accept drifters – may be unable to evolve independently in the model.

Contrary to the quotation above – but in line with a large literature on the stringent conditions for indirect reciprocity (Nowak and Sigmund, 1998; Leimar and Hammerstein, 2001; Bshary and Raihani, 2017) – it is not possible for drifting to evolve by indirect reciprocity without invoking complex stabilising mechanisms for which there is currently no evidence in any social insect. These include colony-level reputation, honest colony phenotypic markers, or punishment of defector colonies by cooperator colonies. The proposed assortment process underlying the indirect reciprocity hypothesis, which does not invoke these mechanisms, does not allow for the evolution of drifting in *P. canadensis*. Equivalent objections would apply to a 'generalised reciprocity' explanation (in which recipients of cooperation 'pay it forward' by cooperating with a random third party; van Doorn *et al.*, 2011). In the context of drifting wasps, there is no stable mechanism by which reciprocators will assort with one another to the exclusion of non-reciprocators.

6.6 Question 4: How might bet-hedging (Sumner *et al.*, 2007) explain drifting?

The bet-hedging hypothesis for drifting, proposed by Sumner *et al.* (2007), argues that non-reproductive workers diversify their helping effort across multiple related queens on different colonies to minimise the risk that their inclusive fitness portfolio is destroyed by the chance destruction of their home colony. Neotropical *Polistes* colonies inhabit a volatile environment, with extreme aggregation-wide brood loss to army ants (Young, 1979), sudden colony destruction by birds (McCann *et al.*, 2014), and assaults by lepidopteran, dipteran, and hymenopteran parasites (Jeanne, 1979).

Here, I show that the key premise of the Sumner *et al.* (2007) hypothesis is correct – inclusive fitness maximisation does involve an overlooked mean-variance trade-off – but that the hypothesis may not offer a general solution to between-colony cooperation in *P. canadensis*. From the selection covariance of the Price equation under uncertainty (Equation 5 in Grafen, 2006b), we can write:

$$\mathbb{E}_\pi[\Delta\bar{G}] = \mathbb{C}_i \left(G_i, \mathbb{E}_\pi \left[\frac{c_\pi + \sum_j^J r_j b_{j,\pi}}{\bar{w}_\pi} \right] \right) \quad (6.10)$$

where G_i denotes the breeding value of the i th individual, c_π denotes the additive effect of individual i on its own reproductive success in environmental-demographic state π and $\sum_{j=1}^J r_j b_{j,\pi}$ denotes the sum of the additive effects on the reproductive success of each recipient $j \in J$ in environmental-demographic state π (weighted by relatedness r_j). Population average reproductive success \bar{w} is free to fluctuate between states. The expectation covarying with breeding value is referred to as ‘expected relative inclusive fitness’ by (Grafen, 2006b).

Following a similar step in Chapter 3, I take the first-order Taylor approximation of expected relative inclusive fitness, and rearrange Equation 6.1 to extract the coefficient of variation in \bar{w} (denoted v) and the correlations (denoted ρ_c and ρ_b respectively) between population average reproductive success \bar{w} and c_μ and $I = \sum_{j=1}^J r_j b_{j,\pi}$ respectively as they fluctuate across environmental-demographic states:

$$\mathbb{E}_\pi[\Delta\bar{G}] = \mathbb{C}_i \left(G_i, \frac{1}{\mathbb{E}_\pi[\bar{w}_\pi]} \left(\mathbb{E}_\pi[c_\pi] + \mathbb{E}_\pi \left[\sum_{j=1}^J r_j b_{j,\pi} \right] + v \left(\rho_{c,\bar{w}} \sigma_\pi [c] + \rho_{I,\bar{w}} \sigma_\pi \left[\sum_{j=1}^J r_j b_{j,\pi} \right] \right) \right) \right) \quad (6.11)$$

Grafen (2006b) and Batty *et al.* (2014) argue that the maximand of selection at the level of individual organisms is the quantity covarying with breeding value in the selection covariance. The extent to which this is generally true is currently under debate (Ewens, 2014; Birch, 2016b; see Chapter 1, this thesis). However, the bet-hedging hypothesis of Sumner *et al.* (2007) does not invoke synergistic fitness effects, heterozygote advantage, transmission biases, or other effects that are likely to restrict the generality of the maximand view, so I extract the hypothesised maximand with the caveat that I assume fitness effects to be strictly additive or (more plausibly) selection to be δ -weak (during selection for propensity to drift, mutants and wild-type differ only marginally; Birch 2017).

Sumner *et al.* (2007) argue for no direct fitness effects of between-colony cooperation ($\mathbb{E}_\pi[c_\pi] = 0$). The total additive effects of the actor on the reproductive success of others defines the entire inclusive fitness payoff:

$$\max \frac{1}{\mathbb{E}_\pi[\bar{w}_\pi]} \left(\mathbb{E}_\pi \left[\sum_{j=1}^J r_j b_{j,\pi} \right] + v \left(\rho_{I,\bar{w}} \sigma_\pi \left[\sum_{j=1}^J r_j b_{j,\pi} \right] \right) \right) \quad (6.12)$$

Multiplying a maximand by a constant does not change the optimum strategy, so we multiply the whole maximand by $\mathbb{E}_\pi[\bar{w}_\pi]$. Denote the expected absolute inclusive fitness payoff (expected number of surviving offspring equivalents) $\mu = \mathbb{E}_\pi[\sum_{j=1}^J r_j b_{j,\pi}]$ and the standard deviation in absolute inclusive fitness payoff $\sigma = \sigma_\pi[\sum_{j=1}^J r_j b_{j,\pi}]$:

$$\max \mu - v \rho_{I,\bar{w}} \sigma \quad (6.13)$$

This trade-off in inclusive fitness is analogous to the mean-variance trade-off in investment portfolios familiar to economists and investment bankers as the ‘Markowitz programme’ (Markowitz, 1952; Way *et al.*, 2017):

$$\max \mu' - v' \sigma' \quad (6.14)$$

where μ' is the expected profit of an investment portfolio, σ' is its risk (standard deviation) and v' is the subjective risk-aversion of the investor. For an inclusive fitness maximiser, risk-aversion is exactly equal to the product $v \rho_{I,\bar{w}}$, which captures the intuition that an inclusive fitness portfolio that is resilient to downside fluctuations (occurring when population average reproductive success is poor) gains a bet-hedging benefit. Following the approach standard in economics (Zivot, 2011), we can express Equation 6.13 in matrix form:

$$\begin{aligned} \max \mathbf{g}^T \mathbb{E}[\mathbf{q}] - v \cdot \rho_{I,\bar{w}} \cdot \mathbf{g}^T \mathbf{C} \mathbf{g} \\ \text{s. t.} \quad \mathbf{g}^T \mathbf{1} = 1 \end{aligned} \quad (6.15)$$

where \mathbf{g} is the vector of investment weights (helping efforts) placed on the various recipients (including itself), \mathbf{q} is the vector of payoff rates (number of offspring-equivalents produced per unit invested), $\mathbf{1}$ is a vector of 1s, and \mathbf{C} is the variance-covariance matrix for the payoff rates of the various investments. The bet-hedging hypothesis therefore implies that an optimisation trade-off exists within \mathbf{g} , balancing the expectation and the variance in inclusive fitness profit (measured in the number of offspring-equivalents produced).

Environmental stochasticity is the most powerful source of high- v fluctuations (Chapter 3, this thesis). For instance, a wasp who invests equally in two distinct classes of recipient or two distinct categories of behaviour – X and Y –, in the knowledge that, due to fluctuating external factors, *either* X or Y will prove to be a good investment but not both, hedges her inclusive fitness by minimising σ . Equation 6.15 shows that, counter-intuitively, maximising the total expected number of offspring-equivalents is not always the optimum strategy: in fluctuating environments (high v), it pays to minimise fluctuations in the production of offspring-equivalents, even at the partial expense of expected success. However, Equation 6.15 also shows that the bet-hedging hypothesis may be unable to explain the specific case of

drifting in *P. canadensis* without complex ecological effects, due to the appearance of v and $\rho_{I,\bar{w}}$ in the maximand. I describe each term separately.

First, the scenario proposed by the bet-hedging hypothesis may be unlikely to generate high v . The source of stochasticity is demographic rather than environmental: workers are proposed to hedge against chance failures of the home colony (Sumner *et al.*, 2007; Lengronne *et al.*, 2012; Lengronne, 2013). Accordingly, unless wasps compete against a very small competitive population (intense local competition), v will show only negligible fluctuation ($v \approx 0$, due to the law of large numbers). This occurs even if the risk of complete failure is extremely high for any colony. Now, recalibrating \mathbf{g} to secure even a major reduction in σ cannot increase the value of the maximand: selection cannot favour accepting even a slight reduction in relatedness in order to diversify helping effort across recipients in a normal (*i.e.*, not extremely small or subdivided) population, even if it provides a huge reduction in the risk σ associated with the actor's inclusive fitness portfolio. Unlike environmental stochasticity (Chapter 3), demographic stochasticity is a weak force in the evolution of bet-hedging⁸.

Second, even if the population does show $v > 0$, diversification of altruism to distant relatives is only favoured if competitors (non-drifting wasps) suffer poor absolute indirect fitness returns I in states in which \bar{w} is low. In other words, there must be a pre-existing correlation $\rho_{I,\bar{w}}$ between I and \bar{w} as they each fluctuate across states. However, if colony loss to natural enemies occurs randomly, this correlation is already zero even for a non-drifting allele: in any one state, some workers gain a high I by chance, others a low I , so there is no aggregate fluctuation. Accordingly, drifters may reduce their individual σ , but gain no benefit from doing so: their competitors have – by default – already hedged the risk ($v\rho_{I,\bar{w}} = 0$).

I confirmed this effect with an asexual individual-based simulation in *MATLAB*. I let obligately-reproductive recipients inhabit a square lattice in a fixed-size population undergoing a Moran process. At each time step, each reproductive i produces n_i obligately-nonreproductive altruists, sampled independently from an identical normal distribution. Altruists 'drift' with probability d_i specified by the focal allele: a proportion $1 - d_i$ of altruists remain with the focal recipient i . With probability α , drifting altruists encounter recipients who are identical to themselves at the focal locus. The remaining $1 - \alpha$

⁸In general, demographic stochasticity only generates meaningfully nonzero v values if the population is either (a) subdivided into miniature demes with intense local competition and high individual-level stochastic failure (Chapter 4) or (b) punctuated by selectively-intense bottlenecks that favour risk-minimisation. Both scenarios reduce N_d (effective population size of focal deme d). For high v_d , N_d must be sufficiently small that chance colony-level destruction can lead to non-negligible fluctuation in \bar{w}_d (intra-demic average reproductive success). Effective population size is small for eusocial organisms, because reproductives represent a very small proportion of the total population (Nomura and Takahashi, 2012). Nonetheless, even for a 'small' population with $N_d = 100$, stochasticity is essentially invisible if dependent on independent individual-level failures (Schreiber, 2015).

recipients are distributed at random across recipients, such that relatedness $r = \alpha$ (Gardner *et al.*, 2011). Offspring inherit the parent phenotype clonally. Stochastic colony failures mean that individual drifters have lower variances σ in their absolute inclusive fitness portfolios, but the lack of correlations ρ and whole-population fluctuation ν means this reduction offers no selective advantage, and drifters fail to invade.

In principle, one form of bet-hedging is possible as a driver of drifting. In this case, two conditions result in high ν and high pre-existing $\rho_{I,\bar{w}}$: (1) stochasticity is driven by an unpredictable environmental source (and so the whole population fluctuates in risk exposure) and (2) the non-drifter genotype is not already diversified across investments by default. To see this, let colonies be split into two or more hypothetical ‘types’ (e.g. *A* versus *B*). These might be ‘large’ versus ‘small’, or ‘foraging-specialist’ versus ‘nursing-specialist’, etc. Let colonies of each type perform best in different states, where different generations may experience different states. If the non-drifter genotype tends to invest a larger proportion of its work effort in one type over the other (*i.e.*, it is not diversified across types by default), the genotype will experience intergenerational fluctuations in whole-genotype reproductive success. In contrast, by spreading workers more equitably across colony types (at the cost of accidentally diverting a proportion of help to nonrelatives), the drifter genotype can avoid these fluctuations, and so gain a bet-hedging benefit by securing a disproportionately higher relative fitness when the non-drifter genotype suffers bad years. There is no reason, however, to predict that a non-drifter genotype would invest more heavily in a certain colony ‘type’ – and, if it did so, equilibrating the genotype’s investment between colony types may easily be achieved by simply founding different types, without the necessity of wasting a proportion of work effort on weakly-related neighbours by drifting.

6.7 Discussion

Can indirect fitness explain *Polistes* drifting? Between-colony cooperation in *Polistes* has posed an outstanding problem in social evolution since Hamilton (1964b). Three indirect fitness hypotheses have so far been proposed. In this chapter, I have argued that although the two most recently-proposed hypotheses – bet-hedging (Sumner *et al.*, 2007; Lengronne, 2013) and indirect reciprocity (Nonacs 2017) – offer clever solutions, they may be unlikely to explain between-colony cooperation without invoking complex ecological scenarios. The remaining hypothesis – diminishing returns to cooperation (Hamilton, 1964b) – makes two predictions that I test empirically: (1) colonies show sufficiently saturating productivity with worker group size to justify switching to a lower-relatedness recipient and (2) wasps move in the direction predicted by this payoff gradient.

I show that prediction (1) is met in *P. canadensis*. Specifically, drawing on a large longitudinal dataset of 20,000 developing brood, I demonstrate that the relationship between the slope of productivity with respect to worker number varies strongly and systematically across the parameter space characterising *P. canadensis* colonies (Figure 6.8) – quantifying Michener’s (1964) paradox using longitudinal data. Remarkably, this partial derivative shows a several-fold increase over some routes through the parameter space inhabited by *P. canadensis*: the marginal benefit of an additional worker drops substantially as the worker-to-brood ratio rises. Accordingly, Figure 6.8b quantifies the indirect fitness returns accruing to workers on mature (*i.e.*, post-emergence) colonies, and suggests that wasps can – in principle – increase their indirect fitness by diverting help to related colonies with lower worker-to-brood ratios.

However, I do not find support for prediction (2). Using RFID data from multiple populations, I find no evidence that wasps move in the direction predicted to maximise indirect fitness. Instead, only between-colony distance is a reliable predictor of between-colony cooperation (Table 6.3). Importantly, the proportion of variance explained was extremely low in all populations, suggesting that – at least with respect to obvious predictors – wasps move near-randomly between local colonies. *P. canadensis* workers invest large amounts of helping effort in neighbour colonies (up to 56% of the population’s workforce drifts; Sumner *et al.* 2007). The results presented here imply that, rather than targeting high-payoff colonies, these large numbers of drifting workers appear to neglect a lucrative inclusive fitness opportunity by diffusing from the natal colony to neighbours close to randomly (Figure 6.11; Table 6.3).

The near-random movement of wasps amongst colonies (Question 3) should be taken as a provisional result: it will be crucial to analyse additional variables that may explain wasp movement by altering the payoff rate on different colonies. For instance, the presence of parasites or disease in the colony (Strassmann and Thomas, 1980) may make further helping effort redundant at home. Similarly, a detectable decline in the queen’s fecundity (through behaviour or chemical cues; Dapporto *et al.*, 2007) may allow workers to anticipate the imminent onset of social crisis (challenges to the queen) or the declining phase of the colony’s life, in which frequent cannibalism of the larvae and subordinate egg-laying are likely to reduce the expected indirect payoff of continued cooperation.

RFID tagging reveals large and unexplained variation in drifting rates between *P. canadensis* aggregations (Figure 6.9). As the RFID system performs similarly in different populations (see Chapter 5), this suggests that there may be genuine differences in drifting rates between populations. Detailed monitoring of a large number of aggregations will be necessary to explore correlates of this variation. Drifting rate might conceivably be affected by season, average relatedness, average between-colony distance, average parasite load, between-colony variation in parasite load, between-colony synchrony

in worker and brood number, El Niño cycles, nesting substrate, the spatial structure of colony networks, latitudinal differences in nest architecture (e.g., Jeanne, 1979), aggregation disturbance level, the number of flight paths from the aggregation to main foraging grounds, food availability, and nest predation frequency, amongst other ecological factors. Since *P. canadensis* extends over a large tropical and subtropical latitudinal range, progress in understanding variation in drifting rates might be made by replicating RFID monitoring on a large number of *P. canadensis* aggregations distributed along large-scale ecological gradients.

Progress will be made by imminent advances in technology: At present, a constraint in RFID analyses of drifter movement is the potential confounding effect of ‘prospecting’ behaviour (sensu Pöysä, 2006), in which individuals survey the population to identify the best investment opportunities. A ‘prospecting’ wasp would visit colonies only to assess whether recipients are high-payoff opportunities, but would appear on RFID records as apparently making investments in the colony. Although passive RFID tags can provide remarkable insights into *Polistes* behaviour (Sumner *et al.*, 2007), it may be necessary to move beyond passive RFID tags to make progress on quantifying drifting. Passive tags have a small detection radius (Nunes-Silva *et al.*, 2018) and antennae typically can only detect wasps one at a time as they pass through the flight path to the nest. Instead, it will be advantageous to move towards methods that provide complete and unbroken censuses of the colony at all points in time. These techniques are now on the horizon: RFID tags with anti-collision technology (which allow multiple tags to be read simultaneously) are almost small enough to replace current passive RFID tags for use on free-flying insects. Likewise, ongoing developments in RFID antennae (Jones and Chung, 2016) will soon allow large detection radii that cover the entire nest comb, rather than just covering flight paths. In *Polistes*, where wasps can approach and enter the colony from any trajectory, this will be a substantial advance.

Longitudinal data allow us to quantify the payoffs of cooperation: In this chapter, I have used a purely observational approach to quantify productivity. Key parameters of brood-rearing can be quantified effectively in unmanipulated colonies, including natural rates of stochastic failure, predation, parasitism, queen turnover, workforce fluctuation, and male production. In principle, two forms of experimental intervention might be used to quantify the relationship between worker-to-brood ratio and brood rearing success: remove workers or remove brood. However, in both cases, manipulation risks introducing (rather than controlling) a series of confounding variables, which can be largely avoided by taking an observational approach: (1) drifting within aggregations mean that experimental manipulations on a single colony may ramify between colonies, so colony-level interventions are not independent (Croft *et al.*, 2011) and therefore of ambiguous scope; (2) worker removal is likely to trigger the activation of auxiliary ‘lazy workers’ (Lengronne, 2013; Charbonneau *et al.*, 2017), leading

to short-term masking of per-worker effects; (3) worker removal may trigger switching of inactive high-ranking wasps to helping behaviour (Cant and Field, 2005), changing both on-nest dynamics and leading to similar masking effects; (4) if workers respond to colony state, worker removal may trigger inflow (or outflow) of workers to elsewhere within the aggregation, masking or amplifying the per-worker effect; (5) brood removal can be perceived by workers as a decline in queen fecundity (Liebig *et al.*, 2005), or may be mistaken for brood death (and the potential presence of parasites or disease), and so change workers' inclusive fitness priorities (Jandt *et al.*, 2013); (6) fluctuations in colony membership (due to drifting and pupation) mean that worker-to-brood ratios cannot be held at a fixed experimental level without continued manipulation. In contrast, a fully observational (un-manipulated) longitudinal dataset, as used here, more directly captures the unconfounded association between workforce size and productivity rate, and thus provides a direct approach to quantifying the payoffs of cooperation.

Can bet-hedging and indirect reciprocity be tested empirically? Although I have argued in this chapter that the bet-hedging hypothesis and indirect reciprocity hypotheses may be unlikely as general explanations of cooperative drifting (Question 4 and Question 5, above), they are still both testable empirically. To test the bet-hedging hypothesis, it will be necessary to quantify the parameter v (the level of stochasticity in average reproductive success experienced by the whole population), ideally using long-term datasets. I argue above that inclusive fitness diversification bet-hedging will only pay when the entities being diversified across (*i.e.*, investments in different colonies) fluctuate in uncorrelated or anticorrelated ways. In principle, this suggests a testable prediction: identify colony types that do best under different environmental conditions. A variable of interest might be colony size: large colonies might do better than small colonies in years of high parasite load (they are potentially 'too big to fail') but do worse than small colonies in years of low food availability, and so on. In this case, a cooperative drifter might hedge her bets by investing in both small and large colonies. In short, the bet-hedging hypothesis may in principle be made to work by environmental rather than demographic stochasticity.

The indirect reciprocity hypothesis (Nonacs, 2017) requires a number of strict conditions to hold, each of which can be tested empirically. The two most important are: (1) whether social heterosis exists within *P. canadensis* colonies and (2) whether a stable mechanism by which reciprocating nests can associate can be observed. Although I have presented a sceptical argument for the existence of indirect reciprocity amongst *P. canadensis* drifters, I am less sceptical about social heterosis. Social heterosis may be a potentially important effect in understanding *Polistes* societies more generally (beyond the problem of drifting).

6.8 Conclusion

In this Chapter, I have critically examined proposed hypotheses for high levels of between-colony cooperation in *P. canadensis*. By quantifying the benefit term B in Hamilton's rule, I show that diminishing returns to cooperation are fundamental to *P. canadensis* societies, which suggests an adaptive context in which between-colony cooperation can evolve to maximise indirect fitness. However, using RFID data from 1,828 wasps over several studies, I find no evidence that drifters strategically target colonies predicted to have the highest indirect fitness payoffs; instead, wasps appear to diffuse near-randomly within local colony networks. Confirming this possibility will now require detailed analysis of drifting rates in relation to additional colony variables, including parasitism, queen fecundity, foraging rate, and the extent to which would-be drifters can anticipate the imminent failure of the nest. Future studies of *P. canadensis* drifting will benefit from a new wave of technological innovations in animal behaviour.



Polistes satan, Pedregulho, Brazil. Photograph: PK

Chapter 7

7 | Drifting in *Polistes satan*: the host colony response

7.1 Chapter Summary

In many social insect species, infiltration of the colony by non-nestmates can be severely deleterious, leaving host colonies vulnerable to parasitism, usurpation, theft, and disease. Paradoxically, however, some social insects show high rates of between-colony movement (known as 'drifting'). Are colonies in these species prevented from repelling intruders by an inability to recognise non-nestmates? Drifting has been detected in various *Polistes* wasp species. In Neotropical *Polistes* paper wasps, drifting has been detected at extreme levels, suggesting that colony boundaries may be more permeable than in any other social insect outside of the supercolonial ants. However, the nestmate recognition abilities of Neotropical *Polistes* remain almost completely unknown. In this chapter, I use radio-tagging to show for the first time that drifting occurs in the Neotropical paper wasp *Polistes satan*, and that the rates of drifting are relatively high (17.7% of workers). Most drifters lacked active ovaries, but drifters were more likely than non-drifters to have active ovaries. I then show that members of *P. satan* colonies can recognise non-nestmates from neighbour colonies, treating them differently in recognition assays from nestmates and non-nestmates from further afield. Despite this ability to recognise non-nestmates, *P. satan* colonies showed high levels of non-nestmate acceptance. Moreover, recent drifters were no more likely to be accepted than recent non-drifters. Unusually amongst social insects, deliberately accepting non-nestmates may be strategically advantageous: the benefits of augmenting the workforce may outweigh any elevated risks of subversion by outsiders.

Social insects should – and generally do – exhibit intense aggression towards conspecific intruders (Reeve, 1989; Couvillon *et al.*, 2008). Preserving the integrity of the nest against threats from outsiders may often be crucial to maintaining the benefits of cooperation (Queller and Strassmann, 2009; Sturgis and Gordon, 2012). Successful infiltration can undermine the fitness interests of resident workers: intruders may lay parasitic ‘cuckoo’ eggs (Blacher, Yagound, *et al.*, 2013), challenge or usurp the queen (Klahn, 1988), steal resources (Couvillon *et al.*, 2008), or seize the egg-laying position after the death of the resident queen (Monnin *et al.*, 2009). These risks suggest that there should be strong selection against a permeable nest boundary in social insect societies (Johnson *et al.*, 2011).

Despite the clear prediction that intruders should be resisted, between-nest movement (‘drifting’) is now known to occur at high levels in some social insect species. ‘Drifters’ are individuals who (temporarily or permanently) leave their natal colony’s nest and enter foreign nests (Blacher *et al.*, 2013; Nonacs, 2017). Drifting is especially prevalent amongst ‘unicolonial’ ants (Helanterä, 2009) and simple eusocial wasps (Sumner *et al.*, 2007; Lengronne, 2013); in one large nest aggregation of the Neotropical paper wasp *Polistes canadensis*, over half the worker population was observed drifting (Sumner *et al.*, 2007). Whilst the surprisingly high levels of drifting in Neotropical paper wasps have been noted by multiple authors over the past five decades (Hamilton, 1964b; Pickering, 1980; Sumner *et al.*, 2007; Lengronne, 2013), these studies have generally focused on just the single best-studied species (*Polistes canadensis*) and on potential motivations of the drifters themselves. Our understanding of the extent of drifting behaviour and the host colony response is therefore limited.

To distinguish between different hypotheses for drifting behaviour, empirical work on recognition of non-nestmates and levels of non-nestmate acceptance by members of host nests is needed. If high levels of drifting are associated with a lack of effective nestmate recognition, two potential explanations for drifting may be plausible: (1) drifting may be a simple result of recognition errors (by both drifters and members of the nests they visit); or (2) drifting may evolve as an adaptive strategy by selfish drifters to exploit the inability of nest members to detect non-nestmates. In Chapter 5, I showed that some drifters in *P. canadensis* can and do compete for nest inheritance on foreign nests, implying that at least some drifters pose a potential threat to the indirect fitness interests of non-reproductive resident subordinates and the direct fitness interests of high-ranking resident subordinates (who would otherwise have been next in line to inherit the position as egg-layer). Conversely, if high levels of drifting occur in species with the capacity to discriminate effectively between nestmates and non-nestmates, members of the host nest may be interpreted as making a choice to accept drifters. In this case, foreign drifters may be accepted because (1) evicting them would simply be too costly or (2) incoming drifters are, on average, beneficial to nest members (at least at some points in the nest’s life) (Chapter 6; Mora-Kepfer, 2014).

Careful experimentation is needed to separate non-nestmate recognition and non-nestmate acceptance. Members of the nest may be aware that a new arrival is a non-nestmate (showing recognition) but fail to reject her from the nest (showing acceptance). An observation of differential aggression towards nestmates and non-nestmates when, for instance, presented on forceps does not necessarily imply an attempt at non-nestmate rejection. Although presentation trials in which wasps are introduced on forceps are widely used in *Polistes* recognition tests (e.g., Signorotti *et al.*, 2014) forceps introductions represent an unusual social context: social behaviours directed at forceps-presented wasps do not necessarily reflect social behaviours that would be observed were the wasp to arrive naturally and interact freely with residents. This is not a problem for inferring recognition, which requires only a clear differential response directed to nestmates versus non-nestmates. However, it would pose a problem for inferring non-nestmate acceptance. Acceptance can be tested by freely releasing focal wasps onto host nests, permitting them to interact freely with resident wasps without restraint, and confirming after a period of time that focal wasps are permitted to remain without eviction or harassment. By using separate assays for recognition and acceptance, we can detect recognition without mistaking it for rejection.

Existing work suggests the potential for both differential recognition and acceptance in Neotropical *Polistes* species, but empirical testing is rare. Sophisticated knowledge about the social and chemical mechanisms of recognition in *Polistes* comes from experimental tests in seven temperate species (Fishwild and Gamboa, 1992; Gamboa, 2004; Bruschini *et al.*, 2011; Signorotti *et al.*, 2014). However, only 3.5% of *Polistes* species are found in temperate zones, and the highest detected rates of drifting in paper wasps occur in the tropics (Sumner *et al.*, 2007; Lengronne, 2013). Since a landmark review by Gamboa (2004) highlighted that *Polistes* nestmate recognition remained to be studied in any tropical member of the genus, only one study has looked for and found evidence of nestmate recognition in the Neotropics (*Polistes lanio* in Brazil; Braun *et al.*, 2008), but those conclusions were based on a sample of only three nests at unspecified stages in the nest cycle. Clarity as to nest stage is valuable as foundress nests may be more or less discriminatory than post-emergence nests. Testing whether nestmate recognition and discrimination occurs in tropical *Polistes* is therefore a crucial next step in solving the paradox of drifting behaviour.

In this chapter, I examine drifting behaviour in the Neotropical paper wasp *Polistes satan*, broadening knowledge of polistine drifting beyond the well-studied *Polistes canadensis*, and experimentally test recognition and acceptance of non-nestmates on post-emergence nests. Combining radio-frequency identification (RFID) tagging, behavioural observations, and field experimental manipulations, I ask the following questions:

- (1) Does drifting occur in *P. satan*?
- (2) Do drifters and non-drifters in *P. satan* differ in behaviour and ovary development level? Non-nestmates in pursuit of direct fitness should show active ovaries, and potentially less cooperative behaviour than nestmates.
- (3) Does *P. satan* have the capacity for nestmate recognition?
- (4) Does *P. satan* show non-nestmate acceptance?
- (5) Does *P. satan* preferentially accept drifters over non-drifters?

Answering Questions 1 and 2 provides preliminary characterisations of drifters (in terms of behaviour and reproductive status) in a second Neotropical *Polistes* species, complementing previous work on *P. canadensis*. Cuticular hydrocarbons show a nest-specific signal in *Polistes satan* (Tannure-Nascimento *et al.*, 2007) suggesting that informational cues are hypothetically available for resident wasps to discriminate nestmates from non-nestmates. To distinguish between recognition (Question 3) and acceptance (Question 4), I use two different assays. First, to test recognition, I present wasps restricted on forceps, and ask whether focal nests show differential behavioural responses to nestmates versus non-nestmates. Second, to test acceptance, I release wasps freely onto the nest, and monitor whether resident wasps attempt to evict the new arrival. To answer Question 5, I first identify drifters using RFID-tagging and then monitor whether resident wasps attempt to evict drifters and non-drifters that have been freely released onto focal nests.

7.2 Materials and Methods

7.2.1 Species background

Polistes satan Bequaert is an independent-founding simple eusocial wasp, with a distribution restricted to central subtropical Brazil (Carpenter, 1996; Raw, 2018). *P. satan* nests are typically found in shaded places, including the interior of buildings (Raw, 1998; Kudô *et al.*, 2013). Nest foundation is more likely at the end of the dry season (early September), and dry season female aggregations are known to occur during colder periods (Tannure-Nascimento *et al.*, 2005). Nest architecture in *P. satan* resembles that of the southern range of *P. canadensis* described in Chapter 5: each nest is split into multiple brood-carrying combs. Combs lack a covering envelope, which allows non-invasive observation. *P. satan* nests are generally dominated by one singly-mated egg-layer (a monogynous 'queen'), with evidence of some supplementary egg-laying by inseminated subordinates (Gaspar *et al.*, 2007). Facial colour varies widely between individuals (black colour has been linked to dominance status, at least in the foundress stage; Tannure-Nascimento *et al.*, 2008).

7.2.2 Study site

This study took place in the Pedregulho-Rifaina area of São Paulo State, which contains ‘floristically distinct’ remnants of the fragmented cerrado biome (Durigan *et al.*, 2007; Sasaki and De Mello-Silva, 2008) interspersed with coffee plantations and grazed pasture. I studied all 46 nests of a *P. satan* population in the Pedregulho valley at the start of the wet season (November 2016). The population consisted of two aggregations 0.73 km apart (Figure 7.1a), interspersed predominantly by open farmland (Figure 7.1b) and a small forest fragment. Aggregation 1 comprised 14 post-emergence nests in an abandoned farmhouse (20°09'45.8"S 47°30'02.5"W); Aggregation 2 comprised 32 pre- and post-emergence nests on a working farm (Fazenda Pimenta, 20°09'54.0"S 47°29'38.1"W). All nests were founded on anthropogenic substrates (walls, wooden beams, and wooden frames; Figure 7.1c). Previous surveys suggest a density of 1–1.6 *P. satan* nests per hectare in the cerrado (Santos *et al.*, 2007). Aggregations of *P. satan* in northern São Paulo State are sparse (F. Nascimento, *pers. comm.*), and cerrado remnants in the Pedregulho-Rifaina region may provide valuable habitat both for *P. satan* and social wasps in general (Zucchi *et al.*, 1995).

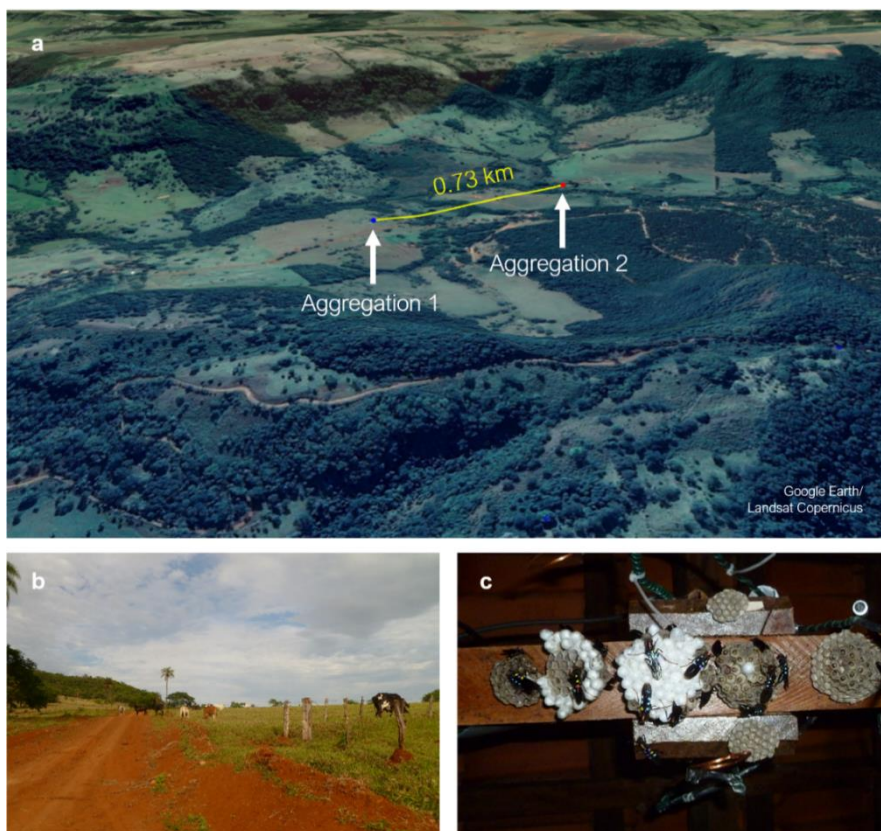


Figure 7.1 | **Study site and species.** (a) Nests used in this study were from neighbour aggregations in the Pedregulho valley (São Paulo State, Brazil). (b) The valley floor is a mosaic of grazed pasture and forest fragments. (c) A single *P. satan* nest suspended from a wooden beam in the Aggregation 1 farmhouse. This nest consisted of seven independent combs with brood at different stages.

7.2.3 Question 1: Does drifting occur in *P. satan*?

I used a combination of RFID tagging and visual observation (as described in Chapter 5) on all wasps in Aggregation 1. A total of 515 wasps were both RFID tagged and colour coded (using Posca pens; Yagound *et al.*, 2017); an additional 33 wasps were colour coded without RFID tags. For RFID tagging, I used low-frequency passive tags (GiS BeeTags, 2 x 6 mm, 18 mg; *Figure 7.2*). Tags were attached to the thorax using Loctite cyanoacrylate glue. I applied a three-colour nest-specific code (*i.e.*, the code of the nest on which the wasp was initially collected for tagging) to the upper half of the left wing and a three-colour wasp-specific code to the upper half of the right wing, which enabled individual wasps to be quickly identifiable in the field. To minimise disturbance of nests during the tagging procedure, each wasp was removed from their nest individually with forceps, tagged and paint marked, placed in a small plastic container for a few minutes to allow the glue to fix, and then individually returned to the nest with forceps. Because face colour has been associated with dominance in *P. satan* (Tannure-Nascimento *et al.*, 2008), wasps were categorised according to face colour based on the predominant colour determined by a single observer (black versus red), and eye colour (newly-emerged wasps have black eyes, which turn red with maturity).

To provide approximately equal RFID coverage by edge area across nests, each nest received 2–7 *in situ* RFID-antennae (GiS TS-A37, 3 cm diameter). Antennae were connected to antenna-specific readers (GiS TS-R64), which were powered by 12-volt car batteries (Moura) via electrical cords. I arranged RFID antennae in a circular array around the comb cluster. Where possible, I attached readers to solid material (walls of the farmhouse) using Velcro pads glued to the substrate; where this was not possible, I suspended readers by metal wires from the farmhouse ceiling. Mesh nets channelled flight paths over the antennal detection range. I monitored the nest network using RFID for 11 h per day (8.30 am – 7.30 pm) for six days, and collated data each evening from readers onto a field laptop. *Ad libitum* visual observations of drifting during the RFID period were also recorded: drifters could be readily identified in the field by their nest-specific colour codes. The number of active brood (eggs, larvae, and pupae) were counted on all nests at the end of the RFID monitoring period, and all observable brood parasites were recorded (*Figure 7.3*).



Figure 7.2 | RFID-tags (indicated by arrow) provide a small and lightweight method of tracking *P. satan* movement.



Figure 7.3 | Parasitic larvae (*Sarcophagidae*) in a *P. satan* nest experiencing ongoing brood loss in Aggregation 1. The loss of brood to parasites may compromise the indirect fitness returns of continued cooperation, providing a 'diminishing returns' justification for drifting (see Chapter 6).

7.2.4 Classifying drifters and non-drifters

To answer Questions 2 and 6 above, the combination of RFID monitoring and visual records were used to allocate wasps to either the 'drifter' or the 'non-drifter' category. Some individuals may have drifted before the six-day RFID monitoring phase and then never drifted within the RFID-monitoring period. These wasps would then be categorised as non-drifters for the purposes of this experiment (*i.e.*, 'drifters' are individuals who had recently drifted). In addition, some individuals may have avoided detection during the RFID monitoring phase, and thus been categorised as false negatives ('non-drifters' who are drifters). However, the high resolution of RFID-tagging (Sumner *et al.*, 2007) combined with visual observations means that false negatives are likely to be rare.

7.2.5 Question 2: Do drifters differ from non-drifters in behaviour and ovary development level?

Behaviour: To provide a preliminary picture of drifter behaviour and compare that behaviour with non-drifters, I observed a random sample of eight post-emergence nests in Aggregation 1 ($n = 293$ wasps). Behavioural data were collected in 34 hour-long observation sessions (mean = 4.25 h per nest, range 1–7 h) during the six-day RFID monitoring period ($n = 2,082$ behavioural observations) using the ethogram in *Table 7.1*. This short and unequal sampling was not intended to be comprehensive, but rather to provide a preliminary measure of drifter activity. Of the behaviourally-observed wasps, 21.8%

(64/293) were known drifters, identified according to the methods described in Question 1. The behaviours for a subset of known drifters ($n = 19$) were observed on more than one nest.

I classified drifters as ‘in-drifters’ to a focal nest if they were initially tagged on a different nest, and ‘out-drifters’ from a given focal nest if the focal nest was the tagging nest and they visit different nests during the monitoring period. Here, I make the broad assumption that tagging nests are natal nests. Some wasps may have been drifting when initially tagged, meaning that a minority of wasps categorised as in-drifters may in fact be returning to the natal nest. However, drifting Neotropical *Polistes* have previously been shown to (1) invest the most effort in the natal nest and (2) typically be nestmates on the nest they were tagged on (Sumner *et al.*, 2007).

As drifter behaviour may differ across nests, I parsed the data into rates per hour at which each behaviour was initiated by each wasp on each separate nest ($n = 312$ wasp-on-nest combinations across $n = 293$ wasps). I used principal components analysis (PCA) on the standardised variables to extract the main axes of variation from the wasp-on-nest dataset, using the *R* package *FactoMineR* (Lê *et al.*, 2008), and visualised PCA plots using the *R* package *factoextra* (Kassambara and Mundt, 2017). I treated the first principal component of the PCA as the response variable, with focal nest and wasp as random effects, and drifter status (*i.e.*, non-drifter, in-drifter, or out-drifter) and face colour (*i.e.*, red, black, or unrecorded) as categorical fixed effects. Unless otherwise stated, all models in this chapter used Gibbs sampling Markov Chain Monte Carlo (MCMC); Gibbs chains were run for a minimum of 100,000 iterations. I confirmed convergence via trace plots. Following the standard approach in *WinBUGS*, I present posterior predictions for error terms using the precision (*i.e.*, the reciprocal of the variance). The term ‘credible’ is used to denote parameters whose 95% credible intervals do not overlap zero. For model selection, I follow the same methods as in Chapters 5 and 6 by using binary indicator variables g_i for indicator variable selection (Ntzoufras, 2002), and present the posterior inclusion probability for effects.

Ovary development level: To ask whether drifters differ from non-drifters in ovary development level, I collected all available drifters present on nests ($n = 32$ drifters, 33% of detected drifters), and an associated sample of non-drifters ($n = 39$), one day after completion of RFID monitoring; collected wasps were placed in 80% ethanol. Aggregations of *P. satan* are rare and difficult to locate in Sao Paulo State (A. de Souza, *pers. comm.*); therefore, to preserve this aggregation for future research by the University of São Paulo (Prof. F. Nascimento) and protect a viable wasp population in the Pedregulho valley, I collected a subset of the population for ovary dissection as opposed to killing all wasps on all nests. I dissected out and photographed ovaries via a Leica IC80 HD camera on a Leica M165C stereomicroscope and measured the largest oocyte to the nearest hundredth of a millimetre in *ImageJ*.

Ovaries were categorised according to the four visual development categories (A–D) described in Chapter 4, following Gobbi *et al.* (2006). All dissections and measurements were conducted blind to drifter status.

To analyse the ovary data, I used two multiple membership (MM) mixed models, in which (1) egg size and (2) total egg number were predicted by two random effects (tagging nest and foreign nest), given MM weightings that sum to 1 (Durrant *et al.*, 2018), and one fixed effect (the dummy variable ‘drifter’ or ‘non-drifter’). To accommodate the multiple nest membership of drifters, I used equal weightings (0.5) for the two nests visited by each drifter and a full weighting (1) for the single nest visited by non-drifters, following a similar procedure in Durrant *et al.* (2018). To ask whether drifters differ in ovary activation, I used a logistic mixed model of ‘active’ (‘C’ or ‘D’ grade) versus ‘inactive’ (‘A’ or ‘B’ grade). Categorical independent variables were ‘drifter’ and ‘non-drifter’, with weighted random effects specifying the natal nest (for non-drifters) and visited nest (for drifters).

Table 7.1 | Ethogram of key monitored behaviours

Interaction	Code	Description
Antennation	ANT	Antennal inspection of a social partner
Receive trophallaxis/give trophallaxis	REC T/GIVE T	Transfer of liquid food by regurgitation
Receive food/give food	REC F/GIVE F	Transfer of solid food from large food ball
Bite	BITE	Bite to wings, legs, head, or thorax of a social partner. To quantify escalation in the behavioural trials, bites are split into ‘small bite’ and ‘sustained biting’: the former is a quick bite, immediately released; the latter is a continued bite or a series of continued bites without immediate release.
Lunge	LUNGE	Sudden fast approach towards a social partner without walking or moving tarsi placement
Chase	CHASE	Fast pursuit of a social partner across the comb surface
Sting	STING	Attempted sting of a social partner, accompanied by abdomen twisted underneath thorax
Dominate	DOMINATE	Submission posture (flattened body, pressed to nest surface) adopted post-antennation or due to the close approach of a social partner
Falling fight	FALLING FIGHT	Jointly falling from the nest during a struggle, with one or both individuals grasping the other
Behaviour	Code	Description
Check cells	CC	Inspection of multiple cells (brood-containing or empty)
Feed brood	FB	Transferring water or foodstuff to larva; head fully within a brood-containing cell for a minimum of 5 s
Build cells	BUILD	Layering pulp to build a new cell or add to an existing cell
Process food	PROC F	Manipulation of a solid food ball by mandibles
Abdominal wagging	AW	Rapid horizontal vibration of abdomen
Arrival/departure	ARRIVE/LEAVE	Arrival or departure from the nest
Arrive with food	ARRIVE F	Arrival at the nest carrying a food ball (insect prey)
Larval cannibalism	EAT LARVA	Consuming live brood
Egg-laying	LAY EGG	Production of a new egg in an empty cell
Fan	FAN	Rapid wing movements whilst stationary to cool down the nest
Parasite alarm	PARASITE ALARM	Frenetic, abrupt movement across the comb surface, occurring as a group behaviour

7.2.6 Question 3: Does *P. satan* have the capacity for nestmate recognition?

To investigate whether *P. satan* can distinguish nestmates from non-nestmates, I conducted a presentation experiment. I followed established methods (presentation of wasps on forceps) used extensively in temperate *Polistes* (Signorotti *et al.*, 2014). In Aggregation 2, nests were grouped together into nine 'clusters', defined as a closely-packed nests within the wider aggregation; clusters were a minimum of 7 m apart. Twenty-five free-living undisturbed focal nests in Aggregation 2 each received four treatments in a repeated-measures design: presentation of (1) a nestmate wasp, (2) a 'local' non-nestmate (from within the same cluster), (3) a 'distant' non-nestmate (from a different cluster in the same general aggregation), and (4) a 'complete foreigner' non-nestmate from Aggregation 1. Wasps used in presentations were from 42 source nests across the two aggregations. Each wasp was only used in one trial.



Figure 7.4 | Aggregation 2 was a single farm; within the aggregation were nine nest clusters (marked by circles). Non-nestmates from the same cluster are denoted 'local'; non-nestmates from other clusters are denoted 'distant'; and non-nestmates from the other aggregation (Aggregation 1; see *Figure 7.1a*) are denoted 'complete' foreigners.

Focal wasps were removed from their nests and isolated in small plastic containers for a minimum of 2 h. Black-eyed wasps (newly emerged) were not used as focal wasps in behavioural trials. All containers were cleaned with hexane to ensure that no hydrocarbon residues from the previous occupant were present. In each trial ($n = 100$), a wasp was removed from the container and held close to the focal nest, 1.5–2 cm from residents, on forceps for 2 m. By being held on the forceps, the presented wasp was unable to move freely, to avoid interactants, or to depart the nest. I recorded all interactions with the presented wasp during each two-minute trial, blind to treatment: I dictated all observed behaviours to a second observer, who transcribed the behaviours in writing. To prevent interference between trials,

each nest was only used once per day. I used a fully counterbalanced allocation of treatment order to nests. The second observer used the counterbalancing list to identify which trial to perform next in sequence, so that the primary observer (observing the nest and dictating behaviours) was completely blind to treatment. Each wasp interaction was weighted according to intensity on a five-step scale (0: antennation; 1: lunge; 2: small bite; 3: sustained bite; 4: sting). This provided an ‘aggression score’ (sum of all aggressive acts received by the presented wasp) and an ‘escalation score’ (the weight of the most aggressive act received by the presented wasp). I recorded both the facial colour and head width of all presented wasps (measurements were made using digital callipers to the nearest 0.1 mm).

To test the effect of treatment on aggression score, I used a linear mixed model with the following covariates characterising each trial: focal nest group size, head size of the presented wasp, and adult-to-brood ratio of the focal nest. I included the ratio of adults to brood (*i.e.*, number of small to large sized larvae) because, in principle, nests may invest less effort in identifying non-nestmates when the nest is in greater need of additional workers (Mora-Kepfer, 2013). Only six wasps had black facial colours as opposed to non-black, so face colour was not analysed. Lastly, I included focal nest and source nest (defined as a nest from which the focal wasp was taken) as random effects with vague (wide variance) priors centred on zero.

Since escalation score is an ordinal variable, I used a Bayesian ordered logit model to test for a treatment effect on escalation, implemented in *RStan* via the package *brms* (Burkner, 2015). As the syntax and capabilities of *brms* differ from *WinBUGS*, I used leave-one-out cross-validation (LOO) for model selection instead of indicator variable selection; the model that minimised the LOO score is presented. As *RStan* uses a more efficient MCMC sampler than *WinBUGS*, I followed the default (Burkner, 2015) of using four chains each with only 2,000 iterations. I confirmed convergence by $\hat{R} = 1$.

7.2.7 Question 4: Does *P. satan* show non-nestmate acceptance?

To investigate whether nests are more likely to evict non-nestmates than nestmates when exposed to wasps arriving at the nest, I used an ‘acceptance’ experiment. This second experiment involved gently placing wasps on post-emergence nests directly using forceps, observing whether wasps are evicted by individuals from the home nest, and comparing the acceptance of non-nestmates (derived from the same aggregation) and nestmates. Acceptance may be context dependent: in principle, foreigners that have made an expensive investment in nest productivity may be more trustworthy (‘partner screening’; Archetti *et al.*, 2011). To simulate the arrival of food-bearing foreigners, I therefore introduced a third

treatment by providing a subset of local foreigners with carbohydrate resources (honey), which was dabbed onto the mandibles immediately before presentation.

Focal wasps were removed from their nests and stored overnight in plastic containers with a small quantity of sugar-water. This procedure was for two reasons: (1) separation guarantees that wasps did not have recent familiarity with the target nest by same-day drifting that might have already established acceptance levels; and (2) pilot tests had confirmed that confinement renders wasps placid, passive and prepared to remain on foreign nests without leaving. This minimises the likelihood that experimental wasps reject the foreign nest, as opposed to vice versa, and allows a focus on the behaviour of the focal nest's individuals. Each nest ($n = 23$) was used as both source and focal nest. Releasing trials ($n = 64$) were conducted in a counterbalanced order by an observer blind to treatment ($n = 21$ non-nestmates without honey, $n = 23$ non-nestmates with honey, $n = 20$ nestmates); note that five trials were not possible due to logistical constraints. All focal wasps were placed on combs where resident wasps were present. I recorded three outcomes: 'acceptance' (present on the nest after two minutes without harassment), 'rejection' (evicted from the nest by aggression from resident wasps), and 'self-exit' (wasp left without aggressive harassment). For all releasing trials, aggressive acts were scored as in Question 2 (0: antennation; 1: lunge; 2: small bite; 3: sustained biting; 4: sting), and an aggression score and an escalation score were generated for each trial. I also recorded all aggressive acts performed by the focal wasp, which provided a focal-wasp specific aggression score. If the focal wasp walked off the nest onto the surrounding substrate after being introduced/released, the trial was repeated by replacing the wasp back on the focal nest.

For analysis of the releasing trials, I used three tests: (1) logistic regression on the probability that wasps were accepted into the focal nest at the end of the two-minute period; (2) a mixed model on aggression score received; and (3) an ordered logit mixed model on escalation score received. Source nest and focal nest were included as random effects. Fixed effects were: focal nest group size, aggression score of the focal wasp (*i.e.*, how the introduced wasp treats the residents it encounters), and facial colour (coded as predominantly black or predominantly not black following a visual categorisation in the field). The ordered logit model was conducted in *brms* as described for the ordered logit model in the previous section.

7.2.8 Question 5: Does *P. satan* preferentially accept drifters over non-drifters?

To investigate whether nests are more likely to admit foreign wasps who have recently drifted, I conducted a third repeated-measures experiment. I first used the RFID data to identify which nests were included in the drifting network of each individual. Twenty-seven focal nests were then each

presented with three treatments, in random order, at the completion of the RFID-monitoring period: (1) an RFID-detected non-nestmate drifter; (2) an RFID-confirmed non-nestmate non-drifter (wasps never detected drifting in the RFID monitoring period) from the same source nest as each RFID-detected drifter; and (3) a nestmate (control) wasp from the focal nest. Focal wasps were removed from their nest and gently released directly onto a brood-carrying comb of the focal nest. I recorded the outcome of the release (acceptance, rejection, self-exit, as in Question 4) at the end of two minutes, and also the frequency of each aggressive interaction experienced by the focal wasp (interactions received and interactions given) during that period, by dictating to a second observer.

For analysis of drifter releasing trials I used three tests as in Question 4: (1) logistic regression on the probability that wasps were accepted into the focal nest at the end of the two-minute period; (2) a mixed model on aggression score received; and (3) an ordered logits mixed model (in *brms*) on escalation score received. All three analyses used treatment type (drifter, non-drifter, or nestmate), focal nest group size and aggression score of the presented wasp as fixed effects, with focal nest and source nest as random effects.

7.3 Results

7.3.1 Question 1: Does drifting occur in *P. satan*?

Using both methods combined (RFID and visual observation), 17.7% (97/548) of the marked wasps were identified as drifting. Of the RFID-tagged wasps, 61.7% (318/515) were detected at least once by the antennae (*Figure 7.5*). Of these, 11.3% (36/318) were recorded by RFID-antennae on two or more nests (including the one on which they had been tagged) during the monitoring phase; a further 25 wasps were detected by RFID visiting a nest other than the nest they had been tagged on, and were also classified as 'drifters'. Of the identified drifters, 23.7% (23/97) moved between two nests that were under visible stress (*Figure 7.5*): one nest was suffering apparent queen succession fights (behavioural data revealed high levels of aggression between multiple high dominants) and the other was suffering ongoing brood destruction by parasitic sarcophagid larvae. Drifters were active across the social network used for subsequent analysis (*Figure 7.6*). Nests differed in the total wasp populations revealed by RFID-detected visitations (range: 1–23 RFID-detected drifters).

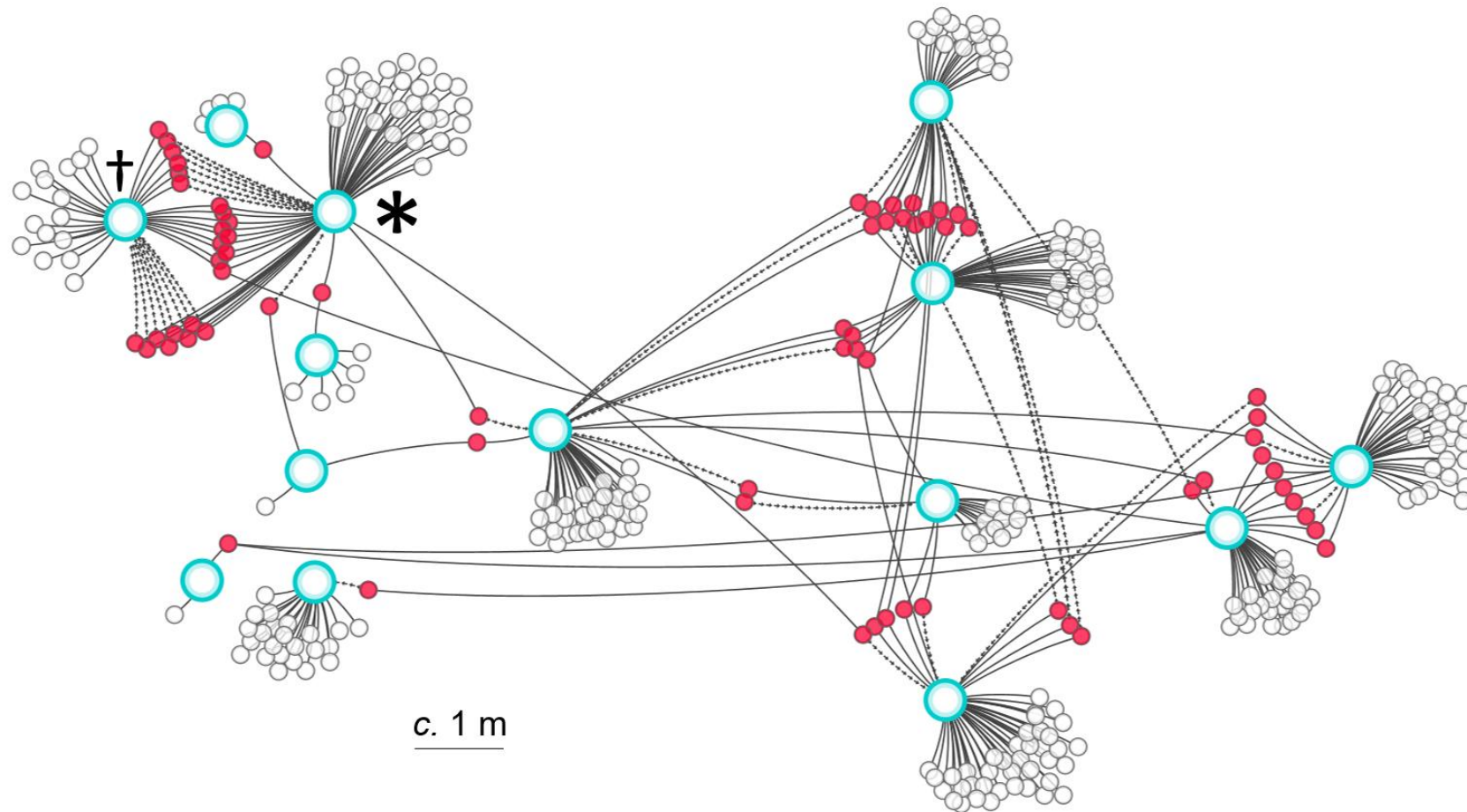


Figure 7.5 | RFID-tag-generated spatial drifter network for wasps ($n = 318$) visiting nests ($n = 14$) over a six-day period. Nest layout reflects approximate spatial relationships. Nests are marked by blue circles. Drifters are shown in red. RFID-detected wasps only visiting a single nest are shown in white. RFID-detected wasps known to be drifting based on visual observations (including at tagging) on nests other than their RFID-detected targets are included in red: for these wasps, the visually-observed nest is indicated by dashed edges. The nest marked '*' was in a natural state of queen indeterminacy (multiple aggressive dominants); the neighbouring nest marked '+' was suffering brood destruction by sarcophagid parasites.

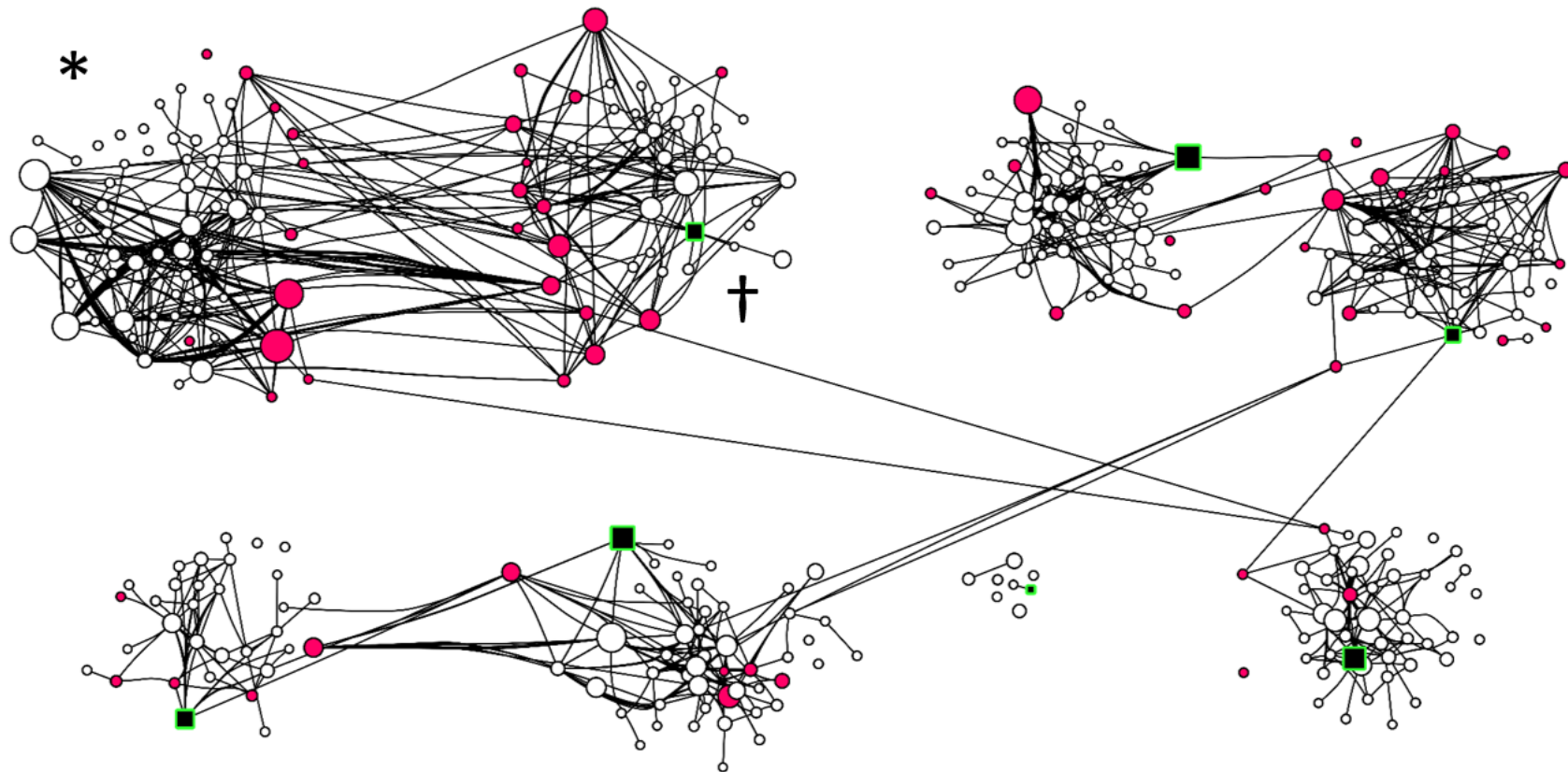


Figure 7.6 | **Drifters participate in colony behavioural social networks.** Cross-nest behavioural social network showing all recorded behaviours on the focal subset of eight colonies in Aggregation 1. Drifters (red circles) interact with residents (white circles) on separate nests. Wasps are scaled in size by their number of connections to other wasps (out-degree). Inferred queens (the dominant individual on each nest) are highlighted as green-edged squares for all nests except one nest (marked by ‘*’) that was in a natural state of queen indeterminacy (multiple aggressive dominants). A nest with sarcophagid parasites is marked by ‘+’.

7.3.2 Question 2: Do drifters differ from non-drifters in behaviour and ovary development level?

Behaviour: PCA on the total social network (Figure 7.6) found that individual principal components of *P. satan* behaviour explained relatively small percentages of behavioural variation (Figure 7.7–Figure 7.9). Inter-behaviour correlation was low: the first component, which can loosely be interpreted as general level of within-nest activity, explains only 12.2% of the variance. There was a weak clustering of behaviours typically interpreted as dominant (bite, sting, lunge) and behaviours typically interpreted as cooperative (foraging and processing food) on the second principal component (Figure 7.8), but this axis of variation explains only 8.7% of the total variance. This echoes similar results in *P. canadensis* (Chapter 5; Bell, 2014): most individuals performed a wide range of behaviours.

There was no evidence that drifters differ from non-drifters in behaviour. There was full overlap in the 95% confidence ellipses of non-drifters, in-drifters, and out-drifters (Figure 7.9). Likewise, in the corresponding mixed model, there was no effect of drifter status or facial colour on the first or second principal component: 95% credible intervals for each category overlapped zero (Table 7.2; Table 7.3).

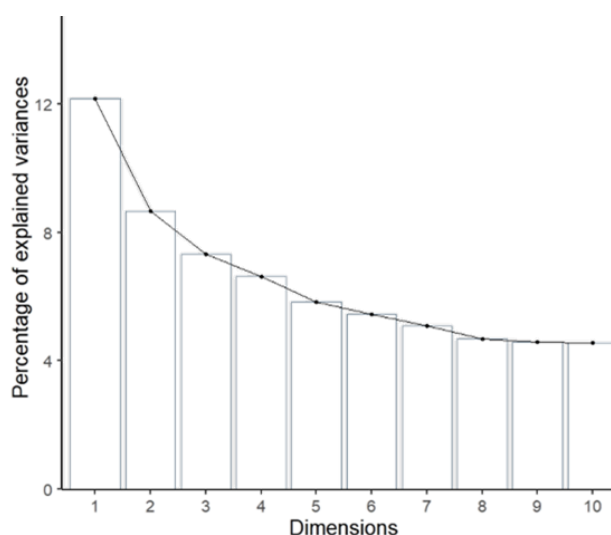


Figure 7.7 | Percentage of variation explained by different principal components in standardised PCA. The low percentages of variation explained by the principal components implies that *P. satan* individuals do not show major consistent differences between individuals in behavioural profiles for the measured behaviours.

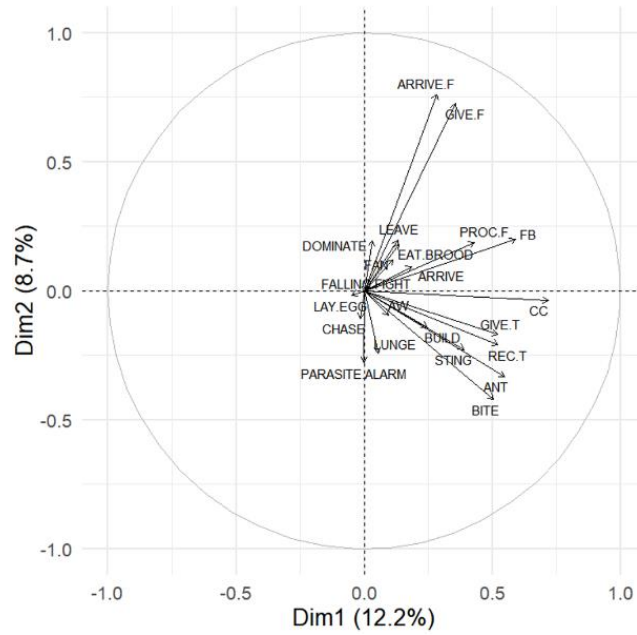


Figure 7.8 | The contributions of individual behaviour to standardised PCA. The first and second components ('Dim1' and 'Dim2') are shown. See Table 7.1 for description of behaviours.

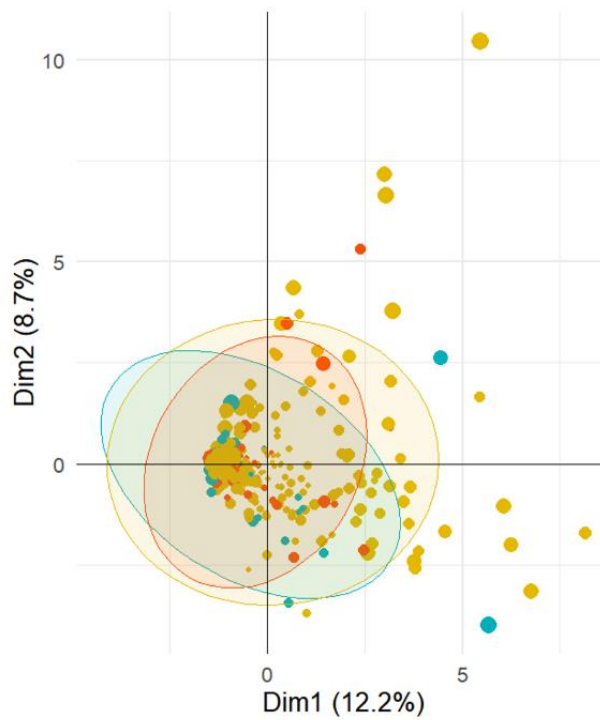


Figure 7.9 | Individual principal components scores. Each point ($n = 312$) represents a set of behavioural observations for a specific wasp on a specific nest. Points are scaled in proportion to \cos^2 scores (the contribution of the point to the principal components categorisation). Ellipses show the 95% confidence regions for each wasp type (non-drifters, in-drifters, and out-drifters). Points and associated confidence ellipses are categorised by colour: non-drifters (orange), in-drifters (blue), and out-drifters (red). The first and second components ('Dim1' and 'Dim2') are plotted.

Table 7.2 | Posterior estimates for model of first principal component of *P. satan* behaviour. 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Status: Non-drifter ($g = 0.010$)	-0.003	3.158	0.009	-6.213	0.015	6.200
Status: In-drifter ($g = 0.010$)	-0.007	3.152	0.010	-6.165	-0.021	6.211
Status: Out-drifter ($g = 0.010$)	-0.002	3.160	0.010	-6.176	-0.003	6.214
Face colour ($g = 0.083$)	7.3E-4	3.028	0.010	-6.092	0.086	6.055
Intercept	0.128	0.359	0.006	-0.500	0.114	0.855
Total model precision	0.598	0.290	0.030	0.369	0.454	1.376
Focal nest random effect ($g = 1.000$) precision	2.464	1.942	0.053	0.436	1.955	7.569
Wasp random effect ($g = 0.422$) precision	15.31	34.38	3.616	0.488	2.646	130.7
Bayesian R^2	0.222	0.194	0.009	-0.020	0.161	0.710
Posterior predictive p -value	0.502	0.500	0.002	0.000	1.000	1.000

Table 7.3 | Posterior estimates for model of second principal component of *P. satan* behaviour. 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Status: Non-drifter ($g = 0.005$)	-0.006	3.168	0.009	-6.216	0.012	6.209
Status: In-drifter ($g = 0.005$)	-0.005	3.160	0.009	-6.194	-0.014	6.211
Status: Out-drifter ($g = 0.005$)	-5.5E-4	3.163	0.010	-6.181	0.003	6.214
Face colour ($g = 0.056$)	-0.013	3.071	0.009	-6.139	0.004	6.098
Intercept	0.148	0.295	0.006	-0.285	0.090	0.835
Total model precision	0.555	0.061	0.002	0.461	0.550	0.670
Focal nest random effect ($g = 0.740$) precision	5.427	15.88	0.216	2.7E-15	1.831	35.99
Wasp random effect ($g = 0.068$) precision	3.496	16.57	0.725	1.4E-11	4.9E-6	42.80
Bayesian R^2	0.049	0.093	0.002	-0.134	0.050	0.220
Posterior predictive p -value	0.501	0.500	0.001	0.000	1.000	1.000

Ovary development level: Developed ovaries were found among both drifters and non-drifters. Drifters (9/32 wasps, 28.1%) were credibly more likely than non-drifters (3/39 wasps, 7.7%) to possess active ('C' or 'D') grade ovaries (Table 7.4) over inactive ('A' or 'B' grade), although no dissected wasps had 'D' stage (*i.e.*, maximally active (egg-layer)) ovaries (Figure 7.10a). There was no credible effect of nest on the probability of ovary activation: all nests effects showed 95% credible intervals overlapping zero. Excluding all 'A' stage wasps (*i.e.*, focusing only on wasps with oocytes, $n = 50$), the multiple membership model for egg size showed that, although egg size ranged widely from 0.24 mm to 2.40 mm, sampled drifters had larger eggs on average than non-drifters (Table 7.5; Figure 7.10b). The random effects terms (home and foreign nest) all had 95% credible intervals for nest-specific parameter estimates overlapping zero. Drifters and non-drifters did not differ in the multiple membership model for total egg number, and the relevant coefficient of determination was very low ($R^2 = 0.026$; Table 7.6; Figure 7.10c).

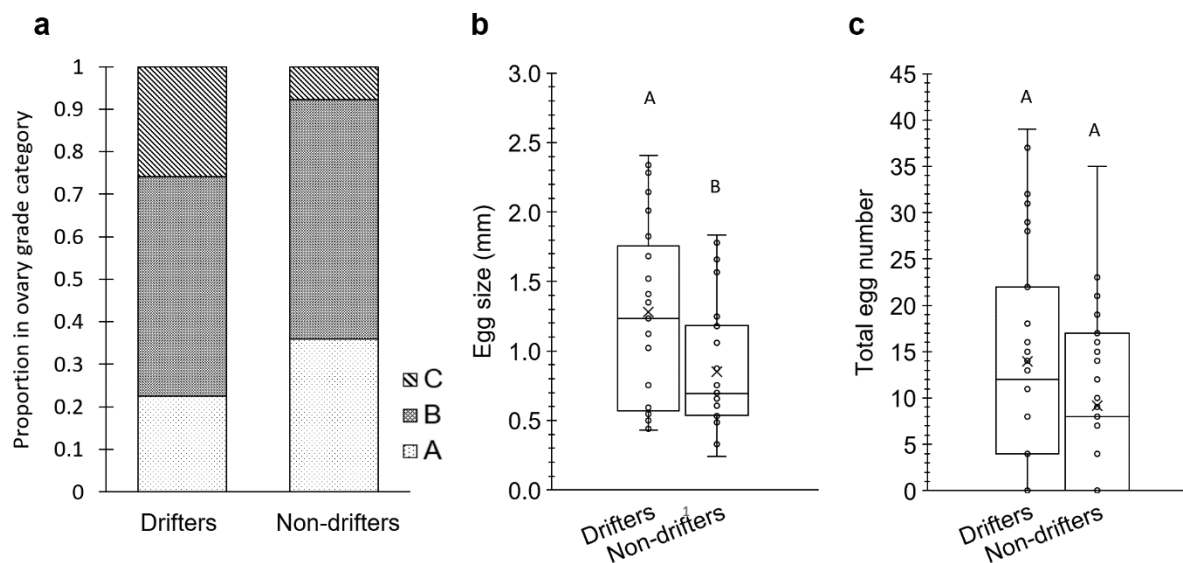


Figure 7.10 | *P. satan* drifters show higher rates of ovary activation than non-drifters. (a) Ovary grade categories. (b) Egg size. (c) Total egg number. Medians shown by mid-bars; means shown by crosses; individual tests show by circles; interquartile ranges shown by boxes.

Table 7.4 | Posterior estimates for logistic mixed model of ovary activation. 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: drifter	3.711	3.153	0.172	0.574	2.618	13.02
Intercept	-4.534	3.000	0.162	-13.62	-3.503	-1.568
Foreign nest random effect precision	25.28	44.68	1.634	0.086	7.484	158.5
Home nest random effect precision	10.84	38.07	1.780	0.007	0.390	113.0

Table 7.5 | Posterior estimates for model of egg size. 100,000 iterations MCMC. Effects with 95% credible intervals not overlapping zero are highlighted in bold.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: drifter	0.497	0.220	0.002	0.077	0.494	0.937
Intercept	0.826	0.144	9.4E-4	0.538	0.827	1.107
Total model precision	3.652	0.833	0.005	2.238	3.580	5.479
Foreign nest random effect precision	14.53	32.94	0.439	0.389	3.613	106.2
Home nest random effect precision	43.47	52.48	0.530	3.283	25.46	192.2
Bayesian R ²	0.198	0.190	0.001	-0.241	0.224	0.492
Posterior predictive <i>p</i> -value	0.506	0.500	0.002	0.000	1.000	1.000

Table 7.6 | Posterior estimates for model of egg number. 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: drifter	4.212	2.688	0.016	-1.174	4.246	9.400
Intercept	9.466	1.880	0.009	5.790	9.459	13.18
Total model precision	0.009	0.002	1.1E-5	0.006	0.009	0.013
Foreign nest random effect precision	81.92	262.4	6.007	0.006	1.649	820.5
Home nest random effect precision	92.17	297.6	6.026	0.023	2.272	889.9
Bayesian R ²	0.026	0.175	0.001	-0.371	0.045	0.314
Posterior predictive <i>p</i> -value	0.502	0.500	0.002	0.000	1.000	1.000

7.3.3 Question 3: Does *P. satan* have the capacity for nestmate recognition?

All presented wasps received interactions from resident wasps: 14.7 ± 7.9 (mean \pm S.D.) interactions per trial. The mixed model for aggression score showed that wasps on the focal nest were most strongly aggressive towards 'local' non-nestmates (*i.e.*, non-nestmates from the same cluster as the focal nest), with a credibly greater level of aggression elicited by these individuals than nestmates of the resident wasps (*Table 7.7; Figure 7.11a*). 'Distant' non-nestmates (non-nestmates from other clusters within the same aggregation) and 'complete foreigners' (non-nestmates from the other aggregation, 0.73 km away) did not receive credibly different levels of aggression compared with resident wasps, but did receive credibly less aggression than 'local' non-nestmates (*Table 7.7; Figure 7.11a*).

The mixed model for escalation score showed that nestmates were less likely than all three categories of non-nestmate to experience high escalation scores (*Figure 7.11b-c*). The fitted model after leave-one-out cross validation is shown in *Table 7.8*.

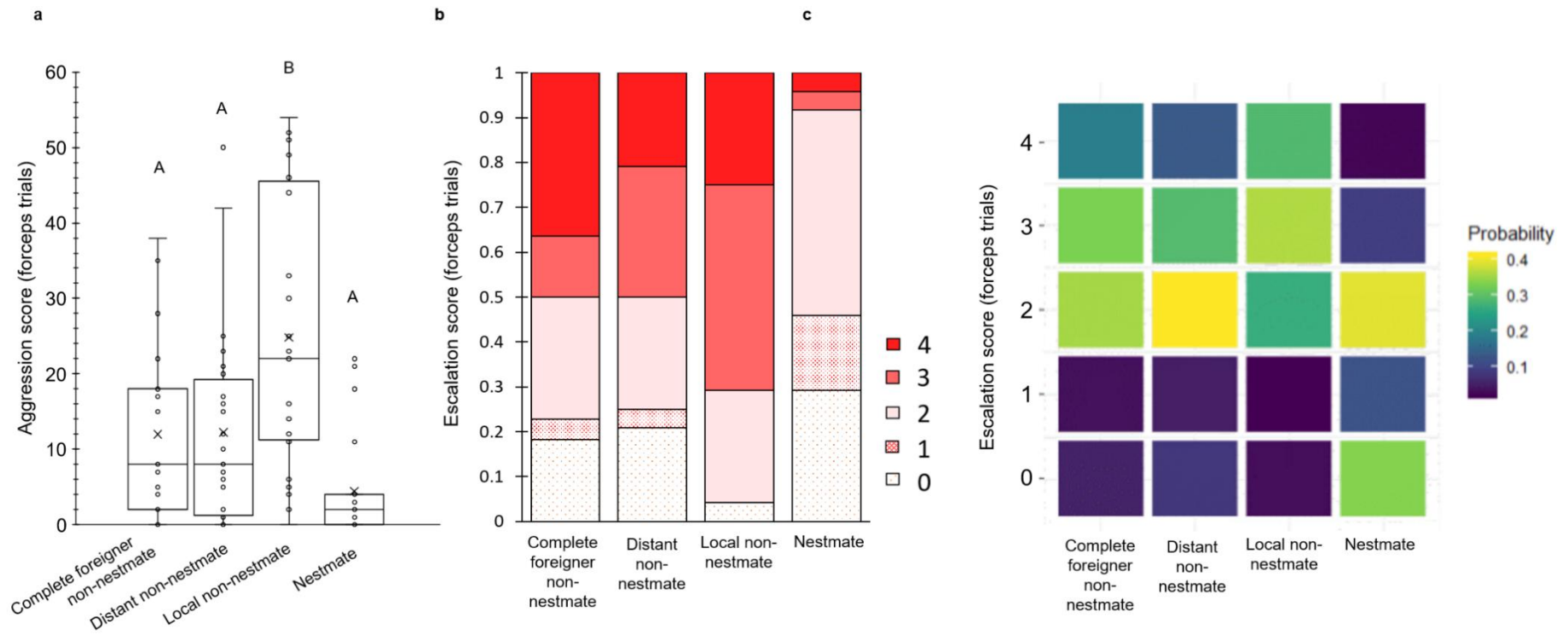


Figure 7.11 | *P. satan* nests showed differential responses towards nestmates and non-nestmates. (a) Aggression scores observed; there is a credible difference between treatments highlighted 'A' and the treatment highlighted 'B'. Medians shown by mid-bars; means shown by crosses; individual tests show by circles; interquartile ranges shown by boxes. (b) Escalation scores observed. (c) Probability of each escalation score for each treatment, as identified by the fitted model for escalation score. High escalation scores (scores 3 and 4) occurred with low probability (dark purple) for nestmates but with higher probability (green) for non-nestmates (local, distant, and complete foreigner non-nestmate treatments).

Table 7.7 | Posterior estimates for mixed model of aggression score (forceps-based recognition trials). 100,000 iterations MCMC. Pairwise comparisons are labelled 'Contrast'. Effects with 95% credible intervals not overlapping zero are highlighted in bold.

Effect (with indicator mean)	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: Nestmate ($g = 0.998$)	-5.087	2.395	0.017	-9.705	-5.105	-0.312
Wasp: Local non-nestmate ($g = 0.998$)	7.104	2.425	0.021	2.269	7.135	11.77
Wasp: Distant non-nestmate ($g = 0.998$)	-0.383	2.334	0.008	-4.982	-0.385	4.183
Wasp: Complete foreigner non-nestmate ($g = 0.998$)	-0.349	2.377	0.008	-5.030	-0.352	4.293
Focal nest group size ($g = 0.027$)	0.012	9.841	0.032	-19.44	0.092	19.54
Head size ($g = 0.123$)	-0.012	9.395	0.028	-19.07	-0.001	19.07
Intercept	12.91	2.344	0.015	8.140	12.96	17.34
Focal nest worker-to-brood ratio ($g = 0.221$)	-0.411	8.905	0.029	-18.57	-1.127	18.52
Total model precision	0.006	8.7E-4	1.2E-5	0.004	0.006	0.008
Focal nest random effect ($g = 0.489$) precision	2.7E-20	1.0E-10	1.4E-12	9.4E-35	2.5E-27	2.2E-19
Source nest random effect ($g = 0.284$) precision	129.6	334.8	30.72	0.032	9.709	1204
Bayesian R^2	0.269	0.159	0.005	-0.062	0.274	0.544
Contrast: Complete versus Distant	0.045	2.993	0.039	-5.825	-0.003	6.014
Contrast: Local versus Complete	7.074	3.036	0.048	0.961	7.100	12.96
Contrast: Local versus Distant	7.119	3.005	0.046	1.164	7.145	12.92
Contrast: Local versus Resident	11.56	3.077	0.053	5.565	11.59	17.37
Contrast: Resident versus Complete	-4.490	2.931	0.040	-10.14	-4.493	1.304
Contrast: Resident versus Distant	-4.445	2.949	0.041	-10.18	-4.476	1.366
Posterior predictive p -value	0.499	0.500	0.002	0.000	0.000	1.000

Table 7.8 | Posterior estimates for ordered logit model of escalation score (forceps-based recognition trials).
4 chains of 2,000 iterations NUTS-MCMC.

Effect	μ	σ	$q_{2.5}$	$q_{97.5}$
Intercept: Escalation Score 0	-2.81	0.62	-4.04	-1.63
Intercept: Escalation Score 1	-2.24	0.60	-3.42	-1.07
Intercept: Escalation Score 2	-0.15	0.54	-1.18	0.92
Intercept: Escalation Score 3	1.46	0.56	0.39	2.61
<i>Intercept: Escalation Score 4 is the reference category.</i>				
Treatment: Nestmate	-2.13	0.61	-3.34	-0.97
Treatment: Local non-nestmate	0.55	0.59	-0.58	1.68
Treatment: Distant non-nestmate	-0.41	0.59	-1.57	0.76
<i>Treatment: Complete foreigner is the reference category</i>				
Host colony (random effect) standard deviation	1.26	0.40	0.54	2.08

7.3.4 Question 4: Does *P. satan* show non-nestmate acceptance?

P. satan showed a high degree of non-nestmate acceptance. Acceptance of wasps freely released onto nests was high in all treatment groups: at the end of each two-minute trial, 85% of nestmates (17/20), 66.7% (14/21) of non-nestmates without honey, and 60.9% (14/23) of non-nestmates with honey resources were accepted on the nest. Bayesian logistic regression found no credible differences between treatment groups in the probability of acceptance (*Table 7.9*). Aggression score of the released wasp had a positive effect on probability of acceptance (median regression slope on logit = 22.36, $g = 1.000$; *Table 7.9*). This last effect should be interpreted cautiously, as a wasp is inevitably more able to aggress the host nest if permitted to remain for the whole trial.

Mixed models showed that neither total aggression score (*Table 7.10*) nor escalation score (*Table 7.11*) were credibly affected by treatment type (nestmate, non-nestmate without honey, and non-nestmate with honey resources; *Figure 7.12a*), face colour, focal nest group size, or mean aggression score shown by the released wasp, which were removed by indicator variable selection in the model for aggression score and leave-one-out cross validation in the model for escalation score.

Only six wasps were aggressively rejected by individuals on the focal nest (zero nestmates, four non-nestmates without honey, and two non-nestmates with honey resources); the remaining thirteen wasps who were absent at the end of the two-minute trial left voluntarily without obvious eviction. Accepted wasps received 10.7 ± 6.2 (mean \pm S.D.) interactions during the two minutes (*Figure 7.12b*); only one accepted wasp (a non-nestmate without honey) received no interactions from any resident.

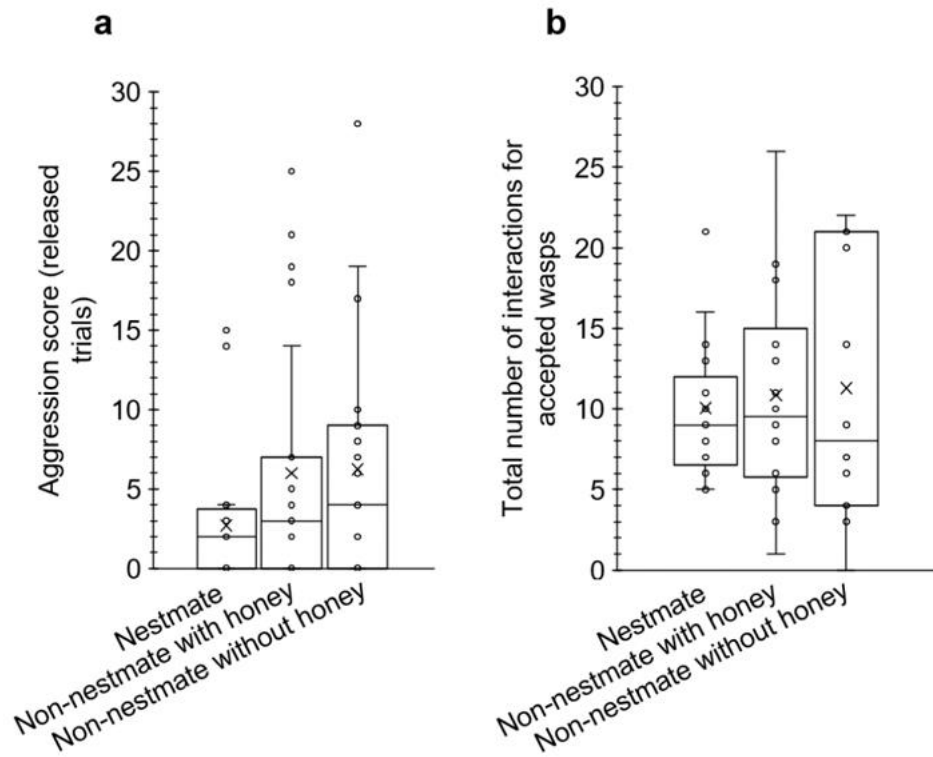


Figure 7.12 | **Wasps freely released onto nests.** (a) An apparently lower aggression directed towards recipients was not credibly different (see Table 7.10). (b) High levels of acceptance were not due to an absence of interactions; only one accepted wasp received no interactions. Medians shown by mid-bars; means shown by crosses; individual tests show by circles; interquartile ranges shown by boxes.

Table 7.9 | Posterior estimates for logistic mixed model of probability of being stably on the nest after two minutes (wasps released onto nests). 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: Nestmate ($g = 0.000$)	-0.397	31.60	0.235	-61.82	-0.351	60.89
Wasp: Non-nestmate with honey ($g = 0.000$)	0.423	31.52	0.204	-61.61	0.506	61.79
Wasp: Non-nestmate without honey ($g = 0.000$)	0.259	31.98	0.233	-61.83	0.321	62.66
Focal wasp's aggression score ($g = 1.000$)	26.40	18.92	0.169	2.330	22.36	71.35
Facial colour ($g = 0.875$)	23.60	22.69	0.230	-26.86	21.57	71.82
Focal nest group size ($g = 0.000$)	0.127	31.38	0.222	-61.30	0.050	61.96
Intercept	0.278	0.788	0.026	-1.223	0.256	1.818
Focal nest random effect ($g = 0.629$) precision	217.5	950.4	50.66	6.5E-4	0.520	2388
Source nest random effect ($g = 0.153$) precision	0.062	0.150	0.008	4.0E-8	0.002	0.389

Table 7.10 | Posterior estimates for aggression score received by introduced wasps (wasps released onto nests). 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: Nestmate ($g = 0.382$)	-0.699	2.942	0.016	-6.158	-0.856	5.507
Wasp: Non-nestmate with honey ($g = 0.382$)	0.237	2.817	0.013	-5.560	0.297	5.649
Wasp: Non-nestmate without honey ($g = 0.382$)	0.365	2.851	0.014	-5.582	0.463	5.726
Focal wasp's aggression score ($g = 0.113$)	-0.027	2.974	0.009	-6.000	-0.139	6.030
Facial colour ($g = 0.518$)	-1.039	2.865	0.010	-6.185	-1.235	5.179
Focal nest group size ($g = 0.016$)	0.003	3.122	0.010	-6.157	0.0106	6.154
Intercept	5.172	1.439	0.012	2.069	5.170	8.269
Total model precision	0.022	0.004	1.8E-5	0.015	0.022	0.030
Focal nest random effect ($g = 0.046$) precision	29.77	363.7	10.63	0.000	8.1E-29	89.19
Source nest ($g = 0.121$) random effect precision	210.3	1385	40.43	4.2E-45	2.8E-9	2123
Posterior predictive p -value	0.499	0.500	0.002	0.000	0.000	1.000

Table 7.11 | Posterior estimates for ordered logit model of escalation score (wasps released onto nests). Four chains of 2,000 iterations NUTS-MCMC.

Effect	μ	σ	$q_{2.5}$	$q_{97.5}$
Intercept: Escalation Score 0	-1.27	0.69	-2.75	-0.01
Intercept: Escalation Score 1	-1.00	0.69	-2.44	0.28
Intercept: Escalation Score 2	1.05	0.69	-0.26	2.24
Intercept: Escalation Score 3	2.96	0.83	1.49	4.70
Intercept: Escalation Score 4	3.72	0.93	2.09	5.77
<i>Intercept: Escalation Score 5 (falling fight) is the reference category</i>				
Treatment: Nestmate	-0.91	0.64	-2.21	0.37
Treatment: Non-nestmate without honey	0.31	0.62	-0.93	1.52
<i>Treatment: Non-nestmate with honey is the reference category</i>				
Host colony (random effect) standard deviation	2.15	0.65	1.08	3.63

7.3.5 Question 5: Does *P. satan* preferentially accept drifters over non-drifters?

There was no evidence that nests preferentially accepted recent non-nestmate drifters over recent non-nestmate non-drifters. First, logistic regression showed no evidence that nestmates were more likely than non-nestmates to still be on the nest after two minutes (Table 7.12). In the acceptance experiment (releasing drifters, non-drifters and nestmates freely onto the focal nest), very few wasps (5/81; one drifter, three non-drifters and one nestmate) were aggressively evicted during the two minutes of interaction after experimental introduction. Nine wasps left voluntarily ('self-exit') during the two-minute period without being aggressively evicted (six drifters and three non-drifters); conversely, 75.0% of presented drifters (21/28), 77.8% of presented non-drifters (21/27), and 96.2% of nestmates (25/26) were integrated with the nest after two minutes of interactions (interpreted as 'acceptance'). One presented drifter absconded the nest immediately, before behavioural interactions, and was therefore removed from all subsequent analyses. Neither aggression score (Table 7.13) nor escalation score (Table 7.14) received by introduced wasps were predicted by treatment (drifter, non-drifter, or nestmate): all released wasps received similar levels of aggression (Figure 7.13a). Accepted wasps received 9.3 ± 6.0 (mean \pm S.D.) interactions during the two minutes (Figure 7.13b); two accepted wasps (both non-nestmate non-drifters) received no interactions. Six wasps (two drifters, one non-drifter and three nestmates) interacted with the brood during the two minutes, either by cell checking or brood feeding.

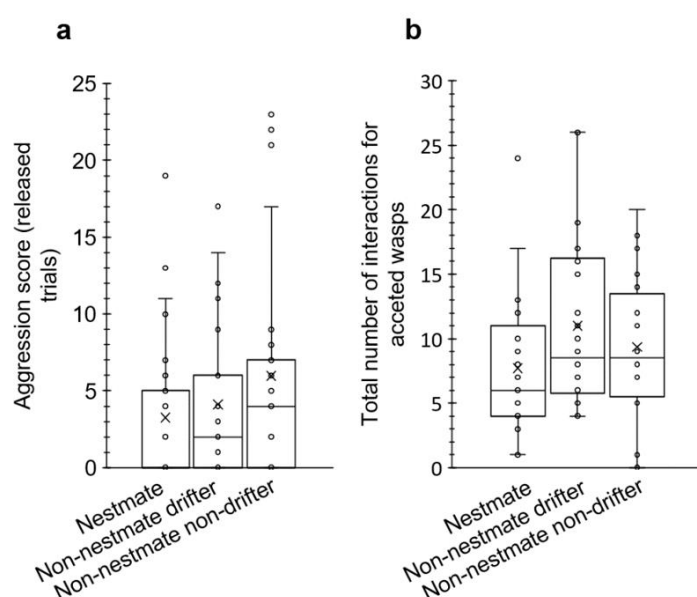


Figure 7.13 | No credible difference in aggression between nestmates, RFID-detected drifters, and non-drifters. (a) Aggression score (see Table 7.13). (b) High levels of acceptance were not due to an absence of interactions. Two accepted wasps received no interactions. Medians shown by mid-bars; means shown by crosses; individual tests show by circles; interquartile ranges shown by boxes.

Table 7.12 | Posterior estimates for mixed model logistic regression for probability of being stably on the nest after two minutes (wasps released onto nests). 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: Nestmate ($g = 0.001$)	-0.362	31.59	0.244	-62.07	-0.213	61.71
Wasp: Non-nestmate drifter ($g = 0.001$)	0.141	31.55	0.235	-61.51	0.397	62.17
Wasp: Non-nestmate non-drifter ($g = 0.001$)	0.195	31.46	0.226	-61.01	-0.079	62.51
Focal wasp's aggression score ($g = 0.003$)	0.171	31.69	0.233	-61.80	-0.017	62.25
Focal nest group size ($g = 0.001$)	0.152	31.55	0.214	-61.51	0.069	62.61
Intercept	1.397	0.324	0.003	0.787	1.389	2.050
Focal nest random effect ($g = 0.162$) precision	456.5	2154.	65.93	9.4E-4	0.021	5108
Source nest random effect ($g = 0.000$) precision	4.1E-5	3.1E-4	1.3E-5	1.5E-12	1.1E-10	3.5E-4

Table 7.13 | Posterior estimates for aggression score received by introduced wasps (wasps released onto nests). 100,000 iterations MCMC.

Effect	μ	σ	MCMC error	$q_{2.5}$	Median	$q_{97.5}$
Wasp: Nestmate ($g = 0.037$)	-0.068	9.892	0.038	-19.57	-0.140	19.57
Wasp: Non-nestmate drifter ($g = 0.037$)	-0.040	9.843	0.039	-19.57	-0.072	19.31
Wasp: Non-nestmate non-drifter ($g = 0.037$)	0.032	9.857	0.037	-19.68	0.091	19.44
Focal's aggression score ($g = 0.045$)	0.041	9.747	0.032	-19.29	0.179	19.32
Focal nest group size ($g = 0.005$)	0.035	9.971	0.030	-19.44	0.030	19.64
Intercept	4.493	0.963	0.020	2.963	4.469	6.005
Total model precision	0.030	0.005	1.5E-5	0.022	0.030	0.040
Focal nest random effect ($g = 0.015$) precision	33.23	581.4	11.55	0.000	0.000	4.859
Tagging nest random effect ($g = 0.007$) precision	4.605	146.3	2.435	0.000	0.000	7.2E-5
Posterior predictive p -value	0.499	0.500	0.002	0.000	0.000	1.000

Table 7.14 | Posterior estimates for ordered logit model of escalation score (wasps released onto nest).
Four chains of 2,000 iterations NUTS-MCMC.

Effect	μ	σ	$q_{2.5}$	$q_{97.5}$
Intercept: Escalation Score 0	-0.40	0.43	-1.28	0.43
Intercept: Escalation Score 1	-0.29	0.43	-1.15	0.53
Intercept: Escalation Score 2	1.32	0.45	0.44	2.21
Intercept: Escalation Score 3	2.85	0.57	1.77	4.03
Intercept: Escalation Score 4	4.72	0.91	3.10	6.67
<i>Intercept: Escalation Score 5 (falling fight) is the reference category</i>				
Treatment: Non-nestmate non-drifter	0.83	0.52	-0.18	1.82
Treatment: Resident	-0.59	0.53	-1.64	0.45
<i>Treatment: Non-nestmate drifter is the reference category</i>				
Host colony (random effect) standard deviation	0.39	0.33	0.01	1.25

7.4 Discussion

Drifting in *Polistes* is a paradoxical behaviour in which workers divest from their natal colony and appear on foreign colonies, seemingly reducing their indirect fitness by doing so (Hamilton, 1964b; Sumner *et al.*, 2007). So far, drifting in Neotropical *Polistes* has been investigated only in the well-studied species *P. canadensis*, and the responses of host colony members to drifting remains unknown. In this chapter, I show high levels of drifting (17.7% of individuals) in a second paper wasp in the Neotropics, and find high levels of non-nestmate acceptance by host colonies despite non-nestmate recognition.

Why does drifting occur in *Polistes satan*? Drifters pursuing a direct fitness strategy on foreign nests are expected to have developed ovaries (Sumner *et al.*, 2007; Blacher *et al.*, 2013). Here, the majority of drifters lacked developed ovaries, suggesting that direct fitness is not the main motivation for drifting for the majority of wasps. Instead, indirect fitness may motivate the majority of *P. satan* drifters, and genotyping is an important next step. In the previous chapter, I showed strong diminishing returns to cooperation in *P. canadensis*: likewise, a crucial next step will be addressing the scope for diminishing returns to cooperation in *P. satan*. However, contrary to previous findings in *P. canadensis* (Sumner *et al.*, 2007; this thesis, Chapter 5), ovary dissections showed that some drifters can and do up-regulate ovary development level in *P. satan*. This may be ‘opportunistic’ up-regulation (Birmingham *et al.*, 2004) following accidental drifting or a coherent strategy of deliberate drifting to maximise direct fitness (whether by egg-dumping or nest inheritance). The possibility of opportunistic drifter behaviour highlights that classifying individuals according to whether or not they actually drifted does not reflect an assumption that binary categories (‘drifter’ and ‘non-drifter’) exist: drifting may occur with a fixed probability in the lives of all wasps. Queen removal experiments on a large sample of nests should now be performed to establish whether drifters in *P. satan* attempt to secure foreign queen positions, and egg genotyping will be needed to assess whether drifters attempt egg-dumping. Preliminary data (see Question 2) suggest that drifters and non-drifters do not differ behaviourally (consistent with the results of Chapter 5 in *P. canadensis*): drifting is likely to be a behaviour occurring across the subordinate dominance hierarchy. Drifting may be a mixed direct and indirect fitness strategy: direct fitness maximisers may seek egg-laying opportunities on neighbour nests, but do so by entering dominance hierarchies on nests with related brood that will benefit from their helping effort.

How does drifting occur in *Polistes satan*? In principle, the presence of at least some ovary-developed non-nestmates in the nest poses a threat to the indirect fitness interests of the resident workers and the direct fitness interests of the resident queen and her likely successor. Is it possible that non-nestmates are indeed undesirable, but cannot be repelled due to an ineffective nestmate

discrimination system? In this chapter, I provide a rare test of nestmate recognition in a tropical *Polistes* species; although the polistine wasps evolved in the tropics (Carvalho *et al.*, 2015), previous tests of nestmate recognition have almost universally focused on temperate *Polistes* species (Gamboa *et al.*, 1986; Gamboa, 2004). The results allow us to exclude the possibility that drifting in *P. satan* occurs due to a lack of nestmate recognition: in forceps recognition trials, nestmates receive credibly less aggression than non-nestmates. Surprisingly, aggression scores to non-nestmates from far-away nests were not credibly different from aggression to residents (a pattern that did not hold for escalation score). Taken on its own, this pattern is seemingly consistent with a ‘nasty neighbour’ response (Christensen and Radford, 2018), which is expected if nest-members are more likely to encounter threats to inclusive fitness from closer neighbours. If drifting occurs locally over short ranges, this is likely to be case. Residents may be primed to detect the most frequently encountered foreign cuticular hydrocarbons: repeat exposure to a foreign hydrocarbon profile may establish a chemical ‘search image’ for intruders. Distant nests, whose drifters will rarely appear on the focal nest, would not contribute to the development of the search image.

Since nestmates and non-nestmates received differential treatment in recognition trials, resident wasps seem capable of categorising each type of arrival differently. Accordingly, I conclude that informational constraints do not impose a barrier to selection in favour of differential acceptance of nestmates over non-nestmates; widespread acceptance of non-nestmates on the nest can be interpreted as a ‘choice’ rather than a mistake due to uncertainty. Whilst forceps-based recognition trials showed differential treatment of non-nestmates, freely-interacting acceptance trials found that both nestmates and non-nestmates were typically accepted. There was no evidence of preferential acceptance of nestmates, and no evidence of preferential acceptance of known recent drifters over individuals without a history of recent drifting (over a six-day period). There was no preferential acceptance of foreigners carrying resources (honey), although it would be valuable to perform a similar assay with foreigners carrying large protein forage (a more natural situation) that is demonstrably of value. Together, these results imply that residents make a ‘knowing choice’ to tolerate individuals who they are capable of perceiving as foreign. Resolving whether this choice is made is because foreign wasps are, on average, beneficial for the nest – or, alternatively, whether the costs of escalating risky conflicts with intruders are too expensive – should now be the priority.

In principle, acceptance may be a two-step process: first, wasps arriving at the nest may be assessed for nest membership; second, any identified foreigners may be inspected for signs of reproductive activity (chemical cues of fertility). Screening of intruders according to detectable fertility has, for instance, been shown in *Bombus terrestris* (Blacher *et al.*, 2013). Such a two-step process may explain why wasps were generally accepted after a period of aggressive inspection: in general, most wasps may

have passed any hypothetical second-step inspection because they may have been detectably low-risk as direct fitness maximisers. It may be valuable to track the long-term process of drifter integration into host nests following first arrival. Indeed, since dominance status in *Polistes* is established through aggression (Jandt *et al.*, 2014), aggression directed towards newcomers to colonies may not always be an eviction mechanism but rather a process of assimilating and establishing the new group member's position in the nest.

Drifting in Neotropical *Polistes* wasps has posed a challenge to inclusive fitness theory since Hamilton (1964b) first identified the phenomenon in Brazil. The recognition test results in this chapter provide evidence that, whatever the (adaptive or accidental) drivers of drifting from the perspective of individual drifters, individuals on *P. satan* recipient nests possess a clear ability to distinguish nestmates from non-nestmates. Consequently, the subsequent acceptance of non-nestmates (acceptance test results) implies an adaptive choice in favour of integrating foreign arrivals, and suggests that *P. satan* drifting – at least from the perspective of host nest members – may be a strategic decision rather than a mistake.



A radio-tagged and colour-coded worker, French Guiana. Photograph: PK

Chapter 8

8 | General discussion

8.1 Chapter Summary

I began this thesis by asking two connected questions:

1. Does cooperation evolve differently in unpredictable environments?
2. What explains the evolution of drifting between paper wasp colonies in the Neotropics?

In this discussion, I address each of these questions in turn.

8.2 Question 1: Does cooperation evolve differently in unpredictable environments?

In Chapter 3, I addressed the link between altruism and bet-hedging by deriving an explicitly stochastic version of Hamilton's rule. This addressed speculation by Stevens *et al.* (2007), Rubenstein (2011), and Griesser *et al.* (2017), who have each proposed empirical situations in which altruism is favoured by reducing the exposure of recipients to a fluctuating environment at a cost to expected reproductive success. Specifically, Chapter 3 explored a neglected route to sociality in which altruists buffer relatives from unpredictable fluctuations in fitness despite failing to provide their relatives with a sufficiently large increase in expected reproductive success to justify cooperation alone ('altruistic bet-hedging'). This led to an answer to the first question of this thesis above: in unpredictable environments, there are cryptic benefits and costs that are omitted from Hamilton's rule as it is standardly used in empirical studies. Because these effects only arise in unpredictable environments, unpredictable environments provide a qualitatively different context for the evolution of cooperation.

The benefits of bet-hedging arise because bet-hedgers stabilise reproduction against a fluctuating background of competitors (Grafen, 1999; Starrfelt and Kokko, 2012). There are two questions arising from this statement: how 'fluctuating' is the background, and what exactly *is* the 'background'? In the stochastic version of Hamilton's rule derived in Chapter 3, I measured the extent of fluctuation in a single 'stochasticity coefficient' (v , the coefficient of variation in population average reproductive success). However, if a focal organism inhabits a large population that shows radical fluctuations locally but weak fluctuations globally, v would be high if measured locally but low if measured globally. In this case, the extent to which bet-hedging can evolve depends on how much the focal's individual's 'background of competitors' is comprised of other local individual versus other individuals from the

global population. Local fluctuations can only sustain bet-hedging if the focal organism's competitors are also drawn from the local area; otherwise, there is no fluctuating background against which bet-hedgers can stabilise their reproduction. I explored this principle in Chapter 4 by expanding the stochastic version of Hamilton's rule to include explicit terms for local and global fluctuation and local and global competition, which I consider as two key aspects of a population's 'demography'. The upshot of Chapter 4 elaborated the answer to the first question of this thesis: the form in which cooperation evolves in unpredictable environments depends crucially on demography. This also alerts us to the possibility that a population that appears completely stable (with $v \approx 0$ when measured at a global scale) may be an effective arena for the evolution of altruistic bet-hedging if fluctuation and competition both occur locally.

It is important to emphasise that altruistic effects on expected reproductive success (Bourke, 2014a) remain the primary forces in social evolution: volatility-suppressing effects require fluctuating populations, and can be overwhelmed by moderate costs to expected reproductive success when fluctuations are insufficiently strong. The strongest altruistic effects will arise when increases to the expected reproductive success of recipients ($b_\mu > 0$) occur together with decreases to recipients' reproductive volatilities ($b_\sigma > 0$). At a global scale, cooperative breeding is associated with unpredictable environments (Jetz and Rubenstein, 2011; Griesser *et al.*, 2017); a natural possibility is that b_σ effects provide an additional boost to altruism in these environments above b_μ , leading to a global correlation between unpredictability and cooperation (Cockburn and Russell, 2011).

There are several future directions that it may be useful to pursue, including the following:

1. **Are endogenous sources of stochasticity capable of driving altruistic bet-hedging?** I have focused on exogenous drivers of environmental stochasticity (*i.e.*, factors external to the population, such as famine, El Niño, parasite pressure, and drought). Could endogenous biotic fluctuations (*i.e.*, factors within the population, such as rock-paper-scissors dynamics, chaos, and limit cycles) have the same effect? Recently, Takeuchi *et al.* (2016) have outlined a hypothetical scenario during the origin of early cells comprising perpetually changing populations that appear superficially stable. In the Takeuchi scenario, lineages undergo independent internal fluctuations. The logic of Chapter 3 suggests that similar fluctuations may impose negative frequency-dependent selection on separate lineages.
2. **Could there be a link between altruistic bet-hedging and the subfertility hypothesis?** The 'subfertility hypothesis' (Craig, 1983) suggests that individuals with lower-than-average fertility are favoured by selection to become indirect fitness maximising helpers, as they have 'less to lose' from forgoing reproduction. Evidence of subfertility is lacking (Field and Foster, 1999; Rehan *et*

al., 2014). In principle, however, subfertility may be more likely to arise in periods of environmental stress. Simultaneously, altruistic bet-hedging predicts that helping in these periods is disproportionately valuable. Accordingly, future theoretical and empirical work might address the extent to which subfertility and bet-hedging might work synergistically to select for altruism. An extension of this idea is state-dependent parental manipulation for subfertility: in principle, a mother may withhold resources from her developing brood when environmental stress may be imminent, manipulating a proportion of her offspring into subfertility to ensure a supply of volatility-suppressing altruists.

3. **How does group size affect altruistic bet-hedging?** The strength of altruistic bet-hedging may be affected by threshold effects: small groups (below an optimum size) may be unable to suppress volatility effectively, whereas larger groups (above an optimum size) may be unable to secure further reductions in volatility. Are there diminishing returns to volatility suppression, in which each additional altruist has a less effective impact on the recipient's volatility?
4. **Could 'spiteful bet-hedging' exist?** In Chapter 4, I argued that very small demes with intense local competition can sustain altruistic bet-hedging in the absence of environmental fluctuations. For many biologists, the link between social behaviour and local competition is 'spite': harm inflicted on negatively related recipients ($r < 0$) at a cost to the actor (Hamilton, 1970; Gardner and West, 2004; Lehmann, Bargum, *et al.*, 2006). When competition is extremely local, an actor can reasonably interact with individuals who are negatively related, because the breeding value of an average competitor is shifted towards the actor's own breeding value. Accordingly, Gardner and West (2004) emphasise miniature demes (low N_d) with intense intra-demic competition (high a) as plausible contexts for the evolution of spite. This suggests a potential link between spite and bet-hedging (against *demographic* stochasticity): since both are favoured by increasing values of $\frac{a}{N_d}$ in metapopulations, spite and bet-hedging could potentially interact if $r < 0$, $b_{\sigma^2} < 0$ and $c_{\mu} < 0$. In this situation, the actor pays a cost to its expected fecundity to *increase* the recipient's reproductive volatility, spitefully exposing the non-relative to deleterious chance fluctuations in fitness. Equation 4.25 of Chapter 4 provides the conditions under which such 'spiteful bet-hedging' would evolve. However, ecological scenarios of spiteful bet-hedging are harder to imagine than realistic ecological scenarios of altruistic bet-hedging: I suggest it would be far rarer than altruistic bet-hedging. Nonetheless, it may be useful to explore whether opportunities to spitefully increase a recipient's volatility genuinely arise (potentially amongst deme-structured social microbes).
5. **Is altruistic bet-hedging more or less likely than non-social bet-hedging?** The 'monogamy hypothesis' (Boomsma, 2009) argues that strict lifetime monogamy effectively removes

relatedness (r) from Hamilton's rule: under strict lifetime monogamy, selection favours altruism whenever $B > C$. This is because the offspring of a monogamous mother are equally related to their own offspring and to siblings, so should be indifferent between reproducing or helping raise siblings. In support of the hypothesis, all transitions to eusociality are now widely thought to have arisen in the context of strict lifetime monogamy (Hughes *et al.*, 2008; Duffy and Macdonald, 2010; Smith *et al.*, 2018). By extension, strict lifetime monogamy means that altruistic bet-hedging ($B > C$ in monogamous species) and non-social bet-hedging ($-C > 0$) are equally powerful evolutionarily: in both cases, r vanishes from the stochastic version of Hamilton's rule, and variance reduction ($-c_\sigma$ or b_σ) must simply be larger than the loss of expected reproduction ($-c_\mu$ or b_μ).

Because altruistic bet-hedging depends on social behaviour, it may be easier for altruists to achieve volatility suppression than it is for non-social individuals to achieve volatility suppression. This is because cooperation by multiple individuals can generate non-additive benefits (Hauert *et al.*, 2006), in which individuals are 'more than the sum of their parts'. More concretely, a collaborative nest of sociable weavers might be buffered from the fluctuating environment disproportionately more effectively than a single solitary weaver's nest – or a small foundress association of *Polistes* or *Liostenogaster* might be buffered from the environment to a degree that would be impossible for a single foundress. I suggest, therefore, that – under conditions of lifetime monogamy – altruistic bet-hedging will be a more powerful driver of bet-hedging than non-social bet-hedging. This is a testable hypothesis, both theoretically and empirically: studies might, for instance, (a) assess effect size variation between contexts and (b) quantify the per-individual reduction in uncertainty for social versus non-social scenarios.

6. **What is the most realistic demography for the early evolution of eusociality?** In Chapter 4, I discussed demographic influences on altruistic bet-hedging. To test the viability of the altruistic bet-hedging hypothesis empirically, it will be crucial to identify plausible population structures in which sociality emerges. A first step, for instance, might be to quantify the extent of local density-dependent regulation (*Figure 8.1*) in facultatively social insects, for which long term data will be essential.
7. **Would a 'stationary Hamilton's rule' be more useful than a 'stochastic Hamilton's rule'?** Allen and Tarnita (2012) derive a 'stationary Price equation' for asexual populations without fluctuations in population size (the stationary distribution of a Markov chain is its unchanging probability distribution through time). The parameters of the 'stationary Price equation' are the parameters of the stationary distribution of the Markov chain representing the entire evolutionary process, rather than a single generation of change (the normal Price equation). Although Allen and Tarnita

(2012) express scepticism of both the value of Price-equation-style results and (elsewhere) inclusive fitness theory (Nowak et al., 2010; Allen et al., 2013), their approach of deriving expectations over the entire stationary distribution of the evolutionary process may be a productive route for formalising individual-level optimisation of inclusive fitness over the entire selective process. This step would require confirming that the ‘stationary Price equation’ generalises to fluctuating population sizes and sexual reproduction; indeed, Allen and Tarnita (2012) remark that generalising to fluctuations is an immediate priority. Like the normal Hamilton’s rule, the explicitly stochastic Hamilton’s rule in Chapters 3 and 4 focuses on the expectation over just a single generation of change. In contrast, if Allen and Tarnita’s (2012) stationary Price equation generalises beyond non-fluctuating asexual populations, it may be valuable to derive a ‘stationary Hamilton’s rule’ to capture the whole evolutionary process of social behaviour under stochasticity.

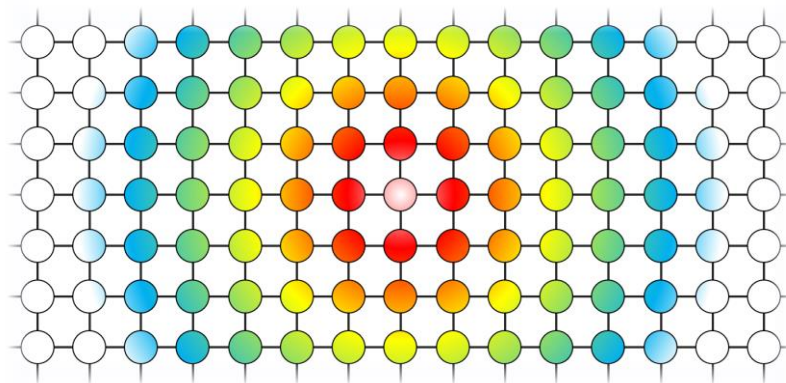


Figure 8.1 | Local density-dependent effects influence the absolute fitness of the focal individual (central node). In this scenario, the focal individual’s reproductive success is modulated in proportion to the average reproductive success in its competitive neighbourhood, which includes individuals (other nodes) at varying distances from the focal. Node colour reflects the extent to which individual neighbours feature in the focal’s competitive neighbourhood: offspring of warmer nodes are more directly in competition with offspring of the focal node.

8.3 Question 2: What explains the evolution of drifting between Neotropical paper wasp colonies?

Polistes populations in the Neotropics often form dense aggregations, nesting both on artificial substrates (Figure 8.2) and in natural habitats (Figure 8.3–Figure 8.4). Previous research on *P. canadensis* has shown that workers ‘drift’ between colonies within these aggregations (Sumner et al.,

2007; Lengronne, 2013), leading to a paradox: why would a worker divest from the most closely related recipient (the home queen) to aid less related recipients (neighbour queens)?

In Chapters 5–6, I explored drifting behaviour within *P. canadensis* aggregations in Panama and French Guiana, and in Chapter 7 I used RFID tagging to show for the first time high levels of drifting between post-emergence colonies in a second paper wasp species (*P. satan* in Brazil). Previous studies of drifting in *Polistes* have invoked indirect fitness (Sumner *et al.*, 2007; Lengronne, 2013); in contrast, one review has interpreted Sumner *et al.*'s (2007) results as workers simply 'accidentally shift[ing] between colonies' (Hughes, 2012). 54 years after Hamilton first highlighted drifting in *P. canadensis* as an 'anomaly' to inclusive fitness theory, can we answer the question: what drives drifting?

In this thesis, I have argued the following:

1. Drifters and non-drifters are behaviourally indistinguishable (Chapters 5 and 7);
2. Foreign drifters can obtain high dominance ranks in *P. canadensis* (Chapter 5);
3. The diversification bet-hedging hypothesis does not explain drifting in *P. canadensis* (Chapter 6);
4. The indirect reciprocity hypothesis does not explain drifting in *P. canadensis* (Chapter 6);
5. *P. canadensis* colonies show diminishing returns at a level that is sufficient to explain drifting (Chapter 6);
6. Contrary to point 5, there is currently no support for the prediction that drifters move from saturated to unsaturated colonies, but future tests of this will need to take account of parasitism and other drivers of nest quality (Chapter 6);
7. Drifting occurs at reasonably high levels (17.7% of wasps) in *Polistes satan* (Chapter 7);
8. Most drifters have undeveloped ovaries (Chapters 5 and 7); some drifters in *P. satan* have developed ovaries (Chapter 7);
9. Non-nestmates are accepted in *P. satan* despite being detectably foreign (Chapter 7);
10. Non-nestmate aggression in *P. satan* shows a pattern consistent with a 'nasty neighbour' response (Chapter 7).

8.3.1 How important are indirect fitness and direct fitness?

There are three published indirect fitness hypotheses for *Polistes* drifting: (1) diminishing returns (Hamilton, 1964b; Sumner *et al.*, 2007; Lengronne, 2013), (2) bet-hedging (Sumner *et al.*, 2007; Lengronne, 2013), and (3) indirect reciprocity (Nonacs, 2017). An extensive discussion of each is found in Chapter 6, which concluded that diminishing returns to cooperation (Hamilton, 1964b; Sumner *et al.*, 2007) provides the most plausible indirect fitness hypothesis for drifting. However, in Chapter 5, I

showed that a minority of drifting wasps do fight during the nest inheritance struggle on foreign nests, suggesting that drifting can plausibly lead to nest inheritance (direct fitness), even if limited to a small number of drifters.



Figure 8.2 | *P. canadensis* colonies are often found on anthropogenic structures. Here, one of the post-emergence colonies studied in Chapter 6 is built on the outside of a building in Panama. Photograph: PK.



Figure 8.3 | Dense aggregations of post-emergence colonies also occur naturally in *P. canadensis*. Here, an aggregation of large post-emergence colonies nests on a tree on Barro Colorado Island (Smithsonian Tropical

Research Institute, Panama). *Photograph*: Dr John Pickering (1976) © www.discoverlife.org. I show a similar tree-nesting aggregation in the Panamanian population studied in Chapter 6 (see *Figure 6.1*).



Figure 8.4 | A large nest aggregation on a cliff-face in Cuba, believed to be *Polistes cubensis*. A number of small active colonies occur amongst abandoned large colonies. Photographs by Thomas Spille © www.flickr.com.

The direct fitness payoff of successfully inheriting a foreign colony is undoubtedly vast (Monnin *et al.*, 2009; Leadbeater *et al.*, 2011). When the foreign nest is a post-emergence colony, the enormous payoff – inheriting a complete workforce, without a high-risk foundress period – may exert such a profound influence over selection that even extremely rare successes may justify high levels of drifting. In other words, even if the probability of success is vanishingly low for each individual drifter, it may be rational for a lineage to emit large numbers of wasps into the wider population to gain these occasional additional nests. The nest inheritance hypothesis may also explain why extreme drifting has been largely found in tropical *Polistes*. Although nest inheritance does occur in temperate *Polistes* (Monnin *et al.*, 2009), fixed nesting seasons in temperate populations (Leadbeater *et al.*, 2011) most likely make queenless post-emergence colonies rarer, and so temperate high-rankers may be less likely than tropical high-rankers to encounter queen struggles on foreign post-emergence colonies. Likewise, in the temperate zone but not in the tropics, there may not be enough time for a new queen’s brood to develop before the end of the season.

Problematic for the nest inheritance hypothesis, however, is the fact that most drifters perform standard worker tasks (Sumner *et al.*, 2007; Chapter 5). These are often high-risk activities (including foraging) typically associated with low dominance ranks and indirect fitness maximisation (Cant and Field, 2005). Even after queen removal, only a minority of wasps investing in multiple colonies entered the nest inheritance struggle (Chapter 5), and most drifters lacked active ovaries (Chapters 5 and 7). By implication, most drifters are not direct fitness maximisers.

A proponent of the nest inheritance hypothesis might make one the following claims in response to these objections:

1. **Multiple strategies:** High-ranking drifters may pursue nest inheritance whilst low-ranking drifters pursue indirect fitness. In this case, drifting is not a single strategy, but a behaviour employed by different classes of individual for different motives.
2. **Plasticity:** High plasticity may allow ovary-inactive workers to up-regulate ovary activation rapidly when exposed to queenlessness.
3. **Pay-to-stay:** Helping effort may be a 'pay to stay' mechanism tailored towards direct fitness, explaining why drifters perform cooperative tasks on foreign nests (Blacher *et al.*, 2013).
4. **Spandrels** (*sensu* Gould and Lewontin, 1979; see also Houston *et al.*, 2007): the non-reproductive majority of drifters may be dismissed as functionless by-products of selection on nest-inheriting drifters driven by rare nest inheritance events with huge payoffs. It may be optimal for the genotype to accept a degree of seemingly irrational behaviour by non-reproductive workers as the price of emitting reproductive drifters: allowing all individuals to diffuse from the natal nest at a fixed probability may be cheaper than a conditional decision rule ('*Drift only if you are an aggressive direct fitness maximiser; minimise navigational errors if you are an indirect fitness maximiser.*')

Testing each of these hypotheses should now be a priority.

8.3.2 Uncertainty, errors, and trade-offs

Each of the proposed adaptive hypotheses for drifting can be criticised as implausible (*Table 8.1*). It is tempting, therefore, to conclude that *Polistes* drifting is just a widespread mistake – or at least a tolerable navigation error (Free, 1956) arising from cognitive trade-offs (Kasuya, 1981). This 'error' hypothesis requires the following three statements to be true:

1. Wasps possess poor navigational abilities (Kasuya, 1981);
2. Wasps cannot always detect when they are on a foreign colony;
3. Wasps cannot always detect or reject foreigners arriving on the home colony.

Hamilton (1964b) discussed the possibility that *P. canadensis* drifters inappropriately invest in suboptimal nests, but that doing so is only mildly deleterious: relatedness to neighbour nests is sufficiently *high* that the loss of some work effort imposes little selective pressure on tighter navigation. Page *et al.* (1989) discussed a similar hypothesis for drifting in *P. fuscatus*, although here the proposed explanation is that relatedness is in general already *low* on the home colony (which is polygynous), so the loss of inclusive fitness is minimal. Although positively related neighbour nests may relax selection on navigation errors, this hypothesis would require the costs of improved navigation to be greater than

the squandered work effort produced by helping suboptimal recipients: *P. canadensis* drifters pay an approximately two-fold cost in relatedness to recipients (Sumner *et al.*, 2007), so this is not a negligible opportunity cost.

Table 8.1 | Proposed adaptive hypotheses and objections

Motive	Hypothesis	Objection
Direct fitness	Nest inheritance	All drifters have inactive ovaries in <i>P. canadensis</i> (Sumner <i>et al.</i> , 2007; Chapter 5); most drifters have inactive ovaries in <i>P. satan</i> (Chapter 7) Most drifters perform standard worker tasks (Sumner <i>et al.</i> , 2007; Chapter 5).
	Egg-dumping	All drifters have inactive ovaries in <i>P. canadensis</i> (Sumner <i>et al.</i> , 2007; Chapter 5); most drifters have inactive ovaries in <i>P. satan</i> (Chapter 7)
Indirect fitness	Diminishing returns	No evidence that wasps move from ‘diminished’ to ‘undiminished’ colonies (Chapter 6).
	Bet-hedging	Demographic stochasticity is unable to generate correlated fluctuations in general (Chapter 6).
	Indirect reciprocity	No mechanism for outcompeting non-reciprocators (Chapter 6).

An implication of the error hypothesis is that we may see *P. canadensis* and *P. satan* helping effort as a diffusible public good: cognitive trade-offs mean that it is too expensive to ensure that all helping effort is directed solely on the natal colony, so wasps target their helping effort on the natal nest as precisely as possible under constraints. Inevitably, some helping effort diffuses to neighbours. Help therefore has a spatial ‘diffusion rate’ (Allen, Gore, *et al.*, 2013) around each focal colony. The adaptive problem for the genotype is optimising the diffusion radius: too generous a radius squanders helping effort on distant relatives; too small a radius comes at the cost of cognitive and behavioural trade-offs.

In Chapter 7, I showed that *P. satan* nests can and do identify non-nestmates, which challenges *Point 3* of the error hypothesis. Nonetheless, nestmate discrimination will always involve a degree of uncertainty, and colonies are expected to optimise their acceptance thresholds under informational constraints to strike a balance between excessive acceptance and excessive rejection (Couvillon *et al.*, 2008). This is the central insight of signal-detection theory (Reeve, 1989; *Figure 8.5*): zealous rejection of all undesirable arrivals (here, exploitative drifters) may lead to collateral rejection of desirable arrivals (here, cooperative drifters and nestmates). In principle, the diffusion of unwittingly cooperative neighbour workers into the population may cause acceptance thresholds to relax, as a higher ratio of

cooperative to exploitative drifters will reduce the cost to benefit ratio of accepting non-nestmates. To summarise, drifting may involve two trade-offs by different parties:

1. **Drifter's perspective:** each individual drifting event would be an accident, tolerated by drifters as the unavoidable outcome of trading off navigational acuity against cognitive costs;
2. **Host colony residents' perspective:** the acceptance threshold is optimised to absorb accidentally incoming drifters (as useful workers) whilst minimising exposure to exploitation.

Social insect colonies can often modify their acceptance thresholds quickly in response to changing contexts (Couvillon *et al.*, 2008; Mora-Kepfer, 2013). Accordingly, a potential test of the role of acceptance trade-offs might ask whether experimentally changing the population-level frequency of ovary-active drifters (which pose a potential threat to host colonies) leads to a population-wide shift towards less tolerant acceptance thresholds. A similar experiment, focusing on helping effort rather than acceptance thresholds, has been performed by Grinsted and Field (2017) in pre-emergence *P. dominula* colonies. Experimental removal of all foundress nest combs, in the spirit of Grinsted and Field (2017), may force post-emergence colonies to raise their barriers to entry. Such experiments may be aided substantially by the imminent development of active RFID in insect monitoring (see Chapter 6 *Discussion*): anti-collision RFID antennae covering entry routes and the nest comb itself will allow the ratio of attempted entry to successful integration to be quantified precisely.

In Chapter 6, I argued that the diminishing returns hypothesis predicts that wasps should show a bias to drift from colonies with too many workers to colonies in need of workers. RFID data do not show such a bias (although additional variables, including parasitism rates and colony age, should be a focus of next steps). Wasps appeared to move near-randomly within aggregations. It is possible, however, that random diffusion does provide a mild diminishing returns benefit when averaged over all drifting events, because colonies with too many workers will tend to fall in size whilst colonies with too few workers will tend to rise in size by simple 'osmosis' (Figure 8.6). A next step might be modelling the extent to which random diffusion can provide a diminishing returns benefit, varying the cognitive costs of assessing the indirect fitness payoff rate on each nest. It will also be crucial to genotype further aggregations for drifter relatedness to brood on foreign nests, both in *P. canadensis* and *P. satan*.

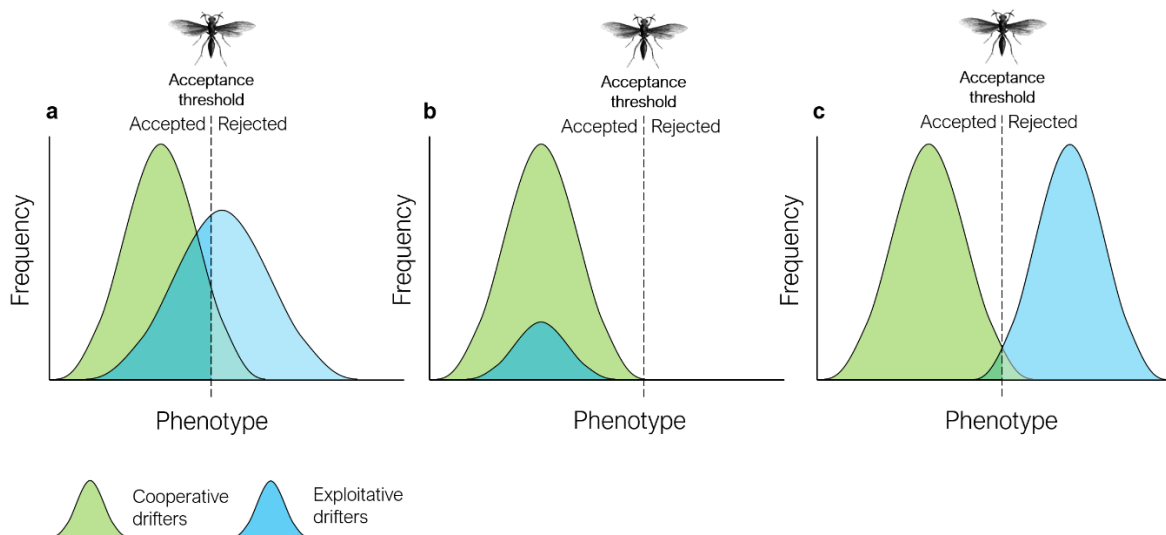


Figure 8.5 | The optimal acceptance threshold model (Reeve, 1989) predicts that the best acceptance threshold may involve admitting some undesirable partners if there is overlap in the phenotypic signal presented by desirables and undesirables. Diagram adapted from Figure 1 of Reeve (1989). Frequency of ‘desirable’ partners (cooperative drifters) is shown in green; frequency of ‘undesirable’ partners (exploitative drifters) is shown in blue. **(a)** If there is strong overlap, almost any chosen threshold will lead to false positives (rejecting cooperative drifters) and false negatives (accepting exploitative drifters). Only a threshold on the far left would exclude all exploitative drifters, but would admit very few cooperative drifters. **(b)** A scenario in which cooperative and exploitative drifters show identical signals, preventing discrimination. **(c)** A near-ideal scenario for resident wasps, in which exploitative drifters can be identified without incurring a high rate of false positive rejections.

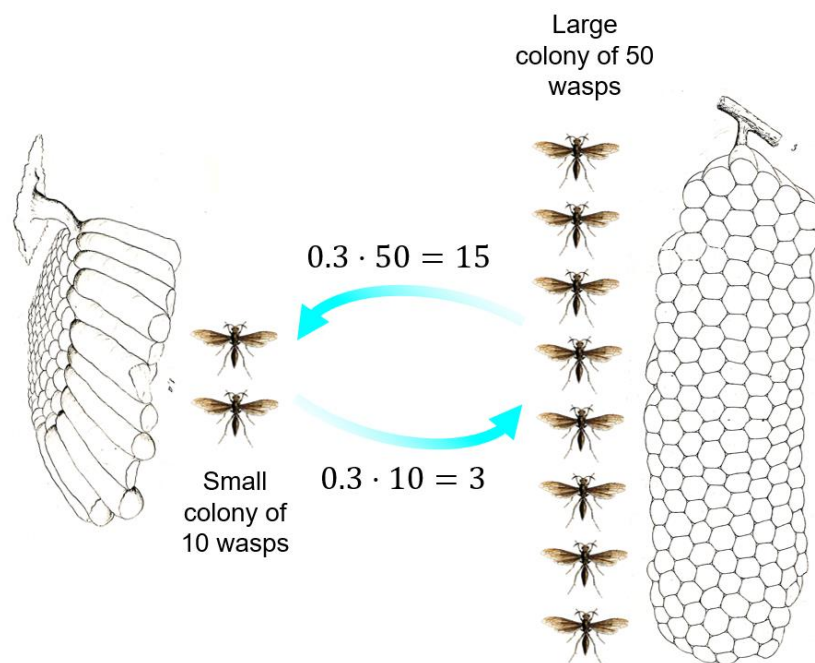


Figure 8.6 | Random movement of wasps between colonies will tend to equalise workforces across colonies. In small natural clusters involving only a limited number of large colonies, diffusion down the group size gradient will reallocate workers to colonies with fewer workers. *Colony and wasp illustrations from Saussure (1852).*

8.3.3 Caution in interpreting adaptation

The triumph of social evolution is largely due to its uncompromisingly adaptive perspective (Dawkins, 1976; Segerstråle, 2000; Abbot *et al.*, 2011; Welch, 2016). However, the convincing appearance of adaptation in social evolution can occasionally be explained as an artefact (Jamieson, 1989), at least in principle. A large part of our interpretation will be due to the prior probability we place on adaptive versus non-adaptive explanations. This is itself an ‘acceptance threshold’ problem (*Figure 8.5*): presuming adaptation will inevitably lead to the misinterpretation of a fraction of neutral traits as adaptive, and vice versa.

For instance, if we discover *Polistes* drifters favouring closely related nests (controlling for any confounding effects of distance), it would be natural to conclude that drifters favour relatives to maximise indirect fitness. Yet there is at least one neutral explanation: accidentally drifting wasps may be more likely to ‘stick’ to closer kin, because closer kin are harder to distinguish from one another than kin from non-kin (since hydrocarbon profiles are generally thought to be heritable; van Zweden *et al.*, 2009). As a result, drifters will accumulate accidentally at more closely related nests by survivorship bias (Wald, 1943). Conversely, seemingly clear evidence of non-adaptation is rarely decisive: even if wasps can be shown to drift entirely due to navigational errors, this does not necessarily imply that drifting is nonadaptive. An allele’s fitness interest may be best served by generating some degree of diffusion into the local population, for whichever indirect (or direct) fitness reason, and this might be achieved cheaply and directly by ‘fuzzy’ information use by individuals. Apparently irrational behaviour at the individual level may be rational for the genotype (*e.g.*, McNamara, 1995).

There are additional reasons for caution in interpreting adaptation. In Chapter 1, I described the central role of weak selection in evolutionary biology, including inclusive fitness theory. Weak selection is often invoked for convenience (Mullon and Lehmann, 2014), but the convenience is often justified by its apparent ubiquity in the real world (Lu and Wu, 2005; Birch, 2017). This means that adaptive pressures may often be extremely subtle, and nearly invisible to an observer: averaged across countless generations of (1) infinitesimal effects and (2) random fluctuations, selection may involve nothing stronger than a faint but persistent trend. This has been problematic since the origins of the study of evolutionary biology. Defending the power of selection, Weismann (1893) acknowledged that it is, for example, hard to imagine that ‘*any person succumbed in the struggle for existence because he had a less sensitive tongue-tip than others*’ (Weismann, 1893, p. 320). Yet bearers of less sensitive tongues must have succumbed, for today’s tongues are highly sensitive. The relevance here is that, for ambiguous traits like *Polistes* drifting, the effect sizes of adaptation may be subtle, and so fitness effects may be statistically undetectable in a necessarily limited sample. By analogy, an experimenter who

shaves the eyelashes of two hundred wildebeest may see no effect of the treatment on survival or reproduction; and yet, wildebeest presumably have their reasons for possessing long eyelashes.

8.4 Conclusion

In this thesis, I began by arguing that inclusive fitness theory and Hamilton's rule provide a powerful toolkit in social evolution (Chapter 1). I then explored links between this toolkit and bet-hedging, arguing that progress on understanding early eusociality and cooperative breeding may be made by a renewed empirical focus on variance components of fitness (Chapter 3) and demography (Chapter 4). In Chapter 2, I introduced drifting behaviour, and highlighted an enigma – the existence of cooperative drifting in Neotropical *Polistes* – that has been paradoxical since the origins of inclusive fitness theory (Hamilton, 1964b). Using a field manipulation of 1,450 RFID-tagged wasps in French Guiana, I found that drifters are behaviourally indistinguishable from non-drifters (Chapter 5), suggesting that drifting is not part of a specialist set of correlated behaviours but rather occurs across the subordinate dominance hierarchy. I then argued (Chapter 6) that drifting is unlikely to be explained by either indirect reciprocity (Nonacs, 2017) or bet-hedging (Sumner *et al.*, 2007), and that most drifters are not direct fitness maximisers (Chapter 5). In Chapter 6, I undertook a longitudinal study of developing *Polistes canadensis* brood in Panama. This suggested that *P. canadensis* workers face strong diminishing returns to cooperation, which may provide an adaptive context for the evolution of drifting – one that should be a focus of next steps. In Chapter 7, I showed drifting for the first time in the Neotropical wasp *Polistes satan* in Brazil, and used recognition tests to show that non-nestmates are accepted by colonies at high rates despite being detectably foreign. Last, in the general discussion, I have suggested caution in quickly inferring either adaptation or non-adaptation when faced with subtle social traits. In summary, I have argued that understanding the evolution of altruism may be advanced by exploring cryptic social effects – effects that may be easily overlooked and yet may exert profound influences on animal societies. Amongst these cryptic effects on social evolution, volatility-suppressing benefits (Chapters 3–4) and the behaviour of nestmates on foreign colonies (Chapters 5–7) may be valuable directions to pursue.

9 | References

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10 | Appendices

Appendices A–C are Supplementary Information for Chapter 3 (published as Supplementary Information to Kennedy *et al.*, 2018). Appendix D provides a short explanation of the multilevel Price equation as background for Chapter 4.

10.1 Appendix A: Derivation of results in Chapter 3

A1 | General stochastic Hamilton's rule

This Appendix provides a derivation of Inequality 3.1 in the main text. We start with the general condition for evolutionary change, the Price equation (Price, 1970). Note that the bet-hedging literature often makes use of the geometric mean approximation (which we derive from the stochastic Hamilton's rule in section A3 below); unless otherwise stated, when we use the unqualified term 'mean' we refer to the arithmetic mean.

The change in the mean value \bar{z} of a trait in a population is a function of the reproductive success w_x associated with the trait value z_x (across individuals $x \in N$) and the average reproductive success \bar{w} across the population:

$$\Delta\bar{z} = \mathbb{C}_x \left[z_x, \frac{w_x}{\bar{w}} \right] + \mathbb{E}_x \left[\left(\frac{w_x}{\bar{w}} \right) \Delta z_x \right] \quad (\text{A1})$$

$\mathbb{C}_x \left[z_x, \frac{w_x}{\bar{w}} \right]$ is the component of evolutionary change due to selection (the 'selection covariance'). The fraction $\frac{w_x}{\bar{w}}$ within this covariance is individual x 's relative fitness, which captures the intuition that natural selection favours the alleles that enable their bearer to outcompete conspecifics. $\mathbb{E}_x \left[\left(\frac{w_x}{\bar{w}} \right) \Delta z_x \right]$ deals with non-selective contributions to evolutionary change (such as biased transmission of alleles between parents and offspring). We are interested in the action of selection, so we will focus on the first term.

The Price equation in its form in Equation (A1) is retrospective: it looks back over the change that has happened and provides a convenient way of dividing it into its contributory components. A prospective (forward-looking) Price equation, on the other hand, would be an expectation of $\Delta\bar{z}$ over the possible states of nature into which the population may enter. $\Delta\bar{z}$ might be very different in a drought than in a year of plenty. Let the current environmental conditions be denoted π , of a set of possible environmental conditions Π into which the population may enter. Grafen (2000) and later Rice (2008)

have noted that the expectation over Π of the selection covariance provides the information required for the expectation of $\Delta\bar{z}$:

$$\mathbb{E}_\pi[\Delta\bar{z}] = C_x \left[z_x, \mathbb{E}_\pi \left[\frac{w_x}{\bar{w}} \right] \right] \quad (A2)$$

We are interested in the fate of genes in the population. The ‘trait’ we address is the organism’s genetic value, G_x , a quantity that captures the alleles that an individual carries (allele frequency within the individual). Accordingly, $z_x = G_x$. See *Extended Data Table E1* for a list of all parameters used in the model.

Both w_x and \bar{w} are random variables with their own probability distributions across environmental states. Equation (A2) states that the expected change in \bar{G} in the population will depend on how closely genetic values covary with the expectation of relative fitness. This fraction is the expectation of a ratio of random variables, which is not equal to the ratio of the expectations of each variable when w_x and \bar{w} are correlated:

$$\mathbb{E}_\pi \left[\frac{w_x}{\bar{w}} \right] \neq \frac{\mathbb{E}_\pi[w_x]}{\mathbb{E}_\pi[\bar{w}]} \quad (A3)$$

The expectation of a ratio of random variables can be expressed using the Taylor series (Rice, 2008; Starrfelt and Kokko, 2012), where the notation $\ll^k \bar{w} \gg$ denotes the k th central moment of \bar{w} across Π and $\ll w_x, {}^k \bar{w} \gg$ denotes the k th mixed moment of w_x and \bar{w} across Π (assuming $\bar{w} < 2\mathbb{E}_\pi[\bar{w}]$):

$$\mathbb{E}_\pi \left[\frac{w_x}{\bar{w}} \right] = \frac{\mathbb{E}_\pi[w_x]}{\mathbb{E}_\pi[\bar{w}]} + \sum_{k=1}^{\infty} (-1)^k \frac{\mathbb{E}_\pi[w_x] \ll^k \bar{w} \gg + \ll w_x, {}^k \bar{w} \gg}{\mathbb{E}_\pi[\bar{w}]^{k+1}} \quad (A4)$$

As Queller (1992a) does for relative fitness in a non-stochastic environment, we express the individual’s expected reproductive success (number of surviving offspring) in a stochastic environment, $\mathbb{E}_\pi[w_x]$, in the form of a multiple regression equation. Part of an individual’s reproductive success will be due to the genes it carries itself: thus, one partial regression slope must relate the individual’s genetic value G_x to its expected reproductive success ($\beta_{\mathbb{E}_\pi[w_x], G_x}$). Another part of its reproductive success will be due to the genetic value G_y of actors serving as social partners ($\beta_{\mathbb{E}_\pi[w_x], G_y}$). The expected reproductive success of individual x is:

$$\mathbb{E}_\pi[w_x] = \alpha_{\mathbb{E}_\pi[w_x]} + \beta_{\mathbb{E}_\pi[w_x], G_x} G_x + \beta_{\mathbb{E}_\pi[w_x], G_y} G_y + \epsilon_{\mathbb{E}_\pi[w_x]} \quad (A5)$$

The intercept of the regression slope ($\alpha_{\mathbb{E}_\pi[w_x]}$) is the ‘baseline’ expected reproductive success the organism expects before taking into account its own genotype and that of its social partners. $\epsilon_{\mathbb{E}_\pi[w_x]}$ captures noise around the regression line.

Equation (A4) contains the central moments characterising the probability distribution of the average reproductive success in the population (\bar{w}) across environmental states:

$$\langle\langle w \rangle\rangle^k = \mathbb{E}_\pi[(\bar{w} - \mathbb{E}_\pi[\bar{w}])^k] \quad (A6)$$

The shape of the distribution from which a focal individual samples its reproductive success appears in Equation (A4) within the mixed moments:

$$\langle\langle w_x, w \rangle\rangle^k = \mathbb{E}_\pi[(w_x - \mathbb{E}_\pi[w_x])(\bar{w} - \mathbb{E}_\pi[\bar{w}])^k] \quad (A7)$$

The most familiar of the mixed moments is the covariance, $\mathbb{C}_\pi[w_x, \bar{w}]$, which arises when $k = 1$. Higher mixed moments, such as the coskewness and cokurtosis, appear at higher values of k . Because each mixed moment can potentially be influenced by the organism's own genotype and its social partners, we can describe each one using linear regression equations:

$$\langle\langle w_x, w \rangle\rangle^k = \alpha_{\langle\langle w_x, w \rangle\rangle} + \beta_{\langle\langle w_x, w \rangle\rangle, G_x} G_x + \beta_{\langle\langle w_x, w \rangle\rangle, G_y} G_y + \epsilon_{\langle\langle w_x, w \rangle\rangle} \quad (A8)$$

We now substitute these regression slopes into selection covariance of the Price equation (Equation A2):

$$\begin{aligned} & \mathbb{E}_\pi[\Delta \bar{G}] \\ &= \mathbb{C}_x \left[G_x, \left(\frac{\alpha_{\mathbb{E}_\pi[w_x]} + \beta_{\mathbb{E}_\pi[w_x], G_x} G_x + \beta_{\mathbb{E}_\pi[w_x], G_y} G_y + \epsilon_{\mathbb{E}_\pi[w_x]}}{\mathbb{E}_\pi[\bar{w}]} \right) \right. \\ & \left. + \sum_{k=1}^{\infty} (-1)^k \frac{(\alpha_{\mathbb{E}_\pi[w_x]} + \beta_{\mathbb{E}_\pi[w_x], G_x} G_x + \beta_{\mathbb{E}_\pi[w_x], G_y} G_y + \epsilon_{\mathbb{E}_\pi[w_x]}) \langle\langle w \rangle\rangle^k + \alpha_{\langle\langle w_x, w \rangle\rangle} + \beta_{\langle\langle w_x, w \rangle\rangle, G_x} G_x + \beta_{\langle\langle w_x, w \rangle\rangle, G_y} G_y + \epsilon_{\langle\langle w_x, w \rangle\rangle}}{\mathbb{E}_\pi[\bar{w}]^{k+1}} \right] \end{aligned} \quad (A9)$$

The expected value of the population average reproductive success across states of nature is a constant (*i.e.*, for all individuals $x \in N$, it is identical). As a constant, it does not covary with the genetic values of individuals, so can be moved outside of the selection covariance (a covariance with a constant is by definition 0). By the linearity rule for covariances $\mathbb{C}[X, Y + Z] = \mathbb{C}[X, Y] + \mathbb{C}[X, Z]$, we also expand the selection covariance:

$$\begin{aligned}
\mathbb{E}_\pi[\Delta\bar{G}] = & \frac{1}{\mathbb{E}_\pi[\bar{w}]} \left(\mathbb{C}_x[G_x, \alpha_{\mathbb{E}_\pi[w_x]}] + \mathbb{C}_x[G_x, \beta_{\mathbb{E}_\pi[w_x], G_x} G_x] + \mathbb{C}_x[G_x, \beta_{\mathbb{E}_\pi[w_x], G_y} G_y] \right. \\
& + \mathbb{C}_x[G_x, \epsilon_{\mathbb{E}_\pi[w_x]}] \\
& + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(\mathbb{C}_x[G_x, \alpha_{\mathbb{E}_\pi[w_x]} \ll^k \bar{w} \gg] + \mathbb{C}_x[G_x, \beta_{\mathbb{E}_\pi[w_x], G_x} G_x \ll^k \bar{w} \gg] \right. \\
& + \mathbb{C}_x[G_x, \beta_{\mathbb{E}_\pi[w_x], G_y} G_y \ll^k \bar{w} \gg] + \mathbb{C}_x[G_x, \epsilon_{\mathbb{E}_\pi[w_x]} \ll^k \bar{w} \gg] + \mathbb{C}_x[G_x, \alpha_{\ll w_x, k\bar{w} \gg}] \\
& \left. \left. + \mathbb{C}_x[G_x, \beta_{\ll w_x, k\bar{w} \gg, G_x} G_x] + \mathbb{C}_x[G_x, \beta_{\ll w_x, k\bar{w} \gg, G_y} G_y] + \mathbb{C}_x[G_x, \epsilon_{\ll w_x, k\bar{w} \gg}] \right) \right)
\end{aligned} \tag{A10}$$

$\mathbb{C}_x[G_x, \alpha_{\mathbb{E}_\pi[w_x]}]$, $\mathbb{C}_x[G_x, \alpha_{\mathbb{E}_\pi[w_x]} \ll^k \bar{w} \gg]$ and $\mathbb{C}_x[G_x, \alpha_{\ll w_x, k\bar{w} \gg}]$ can all be dropped from the equation, because they involve the covariances of the variable G_x with a constant. Similarly, we follow Queller (1992a) and Birch and Marshall (2014) in assuming that there is no covariance between individual genetic value and (in our case) the three residual error terms: $\mathbb{C}_x[G_x, \epsilon_{\mathbb{E}_\pi[w_x]}] = \mathbb{C}_x[G_x, \epsilon_{\mathbb{E}_\pi[w_x]} \ll^k \bar{w} \gg] = \mathbb{C}_x[G_x, \epsilon_{\ll w_x, k\bar{w} \gg}] = 0$.

The partial regression slopes are constants so can be moved outside of their respective covariances with G_x . We can now express the condition for an expected increase in \bar{G} (*i.e.*, $\mathbb{E}_\pi[\Delta\bar{G}] > 0$) as follows:

$$\begin{aligned}
& \frac{1}{\mathbb{E}_\pi[\bar{w}]} \left(\beta_{\mathbb{E}_\pi[w_x], G_x} \mathbb{C}_x[G_x, G_x] + \beta_{\mathbb{E}_\pi[w_x], G_y} \mathbb{C}_x[G_x, G_y] \right. \\
& \left. + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(\ll^k \bar{w} \gg \beta_{\mathbb{E}_\pi[w_x], G_x} \mathbb{C}_x[G_x, G_x] + \ll^k \bar{w} \gg \beta_{\mathbb{E}_\pi[w_x], G_y} \mathbb{C}_x[G_x, G_y] \right) \right) \\
& > 0
\end{aligned} \tag{A11}$$

Dividing both sides of Inequality (A11) by the variance in genetic value across individuals, $\mathbb{V}_x[G_x]$, obtains relatedness(Queller, 1992a; Rousset, 2015) $\left(r \equiv \frac{\mathbb{C}_x[G_y, G_x]}{\mathbb{V}_x[G_x]} \right)$:

$$\frac{1}{\mathbb{E}_\pi[\bar{w}]} \left(\beta_{\mathbb{E}_\pi[w_x], G_x} + r \beta_{\mathbb{E}_\pi[w_x], G_y} + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(\ll^k \bar{w} \gg \left(\beta_{\mathbb{E}_\pi[w_x], G_x} + r \beta_{\mathbb{E}_\pi[w_x], G_y} \right) \right) \right) > 0 \tag{A12}$$

We multiply both sides of this inequality by $\mathbb{E}_\pi[\bar{w}]$. Grouping the coefficients of r gives:

$$\begin{aligned}
& r \left(\beta_{\mathbb{E}_\pi[w_x], G_y} + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(\llcorner^k \bar{w} \gg \beta_{\mathbb{E}_\pi[w_x], G_y} + \beta_{\llcorner w_x, k \bar{w} \gg, G_y} \right) \right) \\
& > -\beta_{\mathbb{E}_\pi[w_x], G_x} + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(-\llcorner^k \bar{w} \gg \beta_{\mathbb{E}_\pi[w_x], G_x} - \beta_{\llcorner w_x, k \bar{w} \gg, G_x} \right)
\end{aligned} \tag{A13}$$

For clarity, we denote the regression slopes of the individual's genetic value G_x and the genetic value of its social partner G_y on the different parameters of the individual's probability distribution for reproductive success as follows:

$$b_\mu \equiv \beta_{\mathbb{E}_\pi[w_x], G_y} = \beta_{\mathbb{E}_\pi[w_y], G_x} \tag{A14a}$$

$$b_k \equiv \beta_{\llcorner w_x, k \bar{w} \gg, G_y} = \beta_{\llcorner w_y, k \bar{w} \gg, G_x} \tag{A14b}$$

$$c_\mu \equiv -\beta_{\mathbb{E}_\pi[w_x], G_x} \tag{A14c}$$

$$c_k \equiv -\beta_{\llcorner w_x, k \bar{w} \gg, G_x} \tag{A14d}$$

The general expression for a stochastic Hamilton's rule is then:

$$r \left(b_\mu + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(\llcorner^k \bar{w} \gg b_\mu + b_k \right) \right) > c_\mu + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} \left(\llcorner^k \bar{w} \gg c_\mu + c_k \right) \tag{A15}$$

which is Inequality 3.1 in the main text.

A2 | Approximation for the first two moments

A bet-hedging genotype reduces the variance in fitness at the expense of reducing arithmetic mean fitness. We obtain the stochastic approximation of Hamilton's rule suitable for bet-hedging effects by ignoring $k > 1$ in Equation (A4) (e.g. skew) to focus only on the arithmetic mean and variance effects. This allows us to approximate the selection covariance of the Price equation as follows:

$$\mathbb{E}_\pi[\Delta \bar{G}] \approx \mathbb{C}_x \left[G_x, \left(\frac{\mathbb{E}_\pi[w_x]}{\mathbb{E}_\pi[\bar{w}]} - \frac{\mathbb{C}_\pi[w_x, \bar{w}]}{\mathbb{E}_\pi[\bar{w}]^2} \right) \right] \tag{A16}$$

The covariance between individual fitness w_x and population average fitness \bar{w} in Equation (A16) can be alternatively expressed as:

$$\mathbb{C}_\pi[w_x, \bar{w}] = \rho_x \sigma_\pi[w_x] \sigma_\pi[\bar{w}] \tag{A17}$$

where $\sigma_\pi[w_x]$ is the standard deviation of the individual's reproductive success, $\sigma_\pi[\bar{w}]$ is the standard deviation of the population's average reproductive success over Π , and ρ_x is the product-moment correlation coefficient for w_x and \bar{w} as they fluctuate over Π . Substituting these terms into the approximation of the selection covariance (Equation (A16)) obtains:

$$\mathbb{E}_\pi[\Delta\bar{G}] \approx \frac{1}{\mathbb{E}_\pi[\bar{w}]} \mathbb{C}_x[G_x, (\mathbb{E}_\pi[w_x] - \nu\rho_x\sigma_\pi[w_x])] \quad (\text{A18})$$

where ν denotes the coefficient of variation of the population's average reproductive success:

$$\nu = \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]} \quad (\text{A19})$$

ν is independent of the organism's decisions, and quantifies the degree to which the environment is stochastic.

The condition for expected increase in \bar{G} ($\mathbb{E}_\pi[\Delta\bar{G}] > 0$) is then:

$$\mathbb{C}_x[G_x, (\mathbb{E}_\pi[w_x] - \nu\rho_x\sigma_\pi[w_x])] > 0 \quad (\text{A20})$$

Above (Equation (A5)), we have already defined $\mathbb{E}_\pi[w_x]$ using multiple linear regression. We follow a similar approach with standard deviation, weighted by the degree to which it correlates (ρ_x) with the fluctuating average reproductive success \bar{w} in the population:

$$\rho_x\sigma_\pi[w_x] = \alpha_{\rho_x\sigma_\pi[w_x]} + \beta_{\rho_x\sigma_\pi[w_x],G_x}G_x + \beta_{\rho_x\sigma_\pi[w_x],G_y}G_y + \epsilon_{\rho_x\sigma_\pi[w_x]} \quad (\text{A21})$$

Substituting Equation (A5) and Equation (A21) into the condition for selection (Inequality (A20)), we obtain:

$$\begin{aligned} \mathbb{C}_x \left[G_x, \left(\alpha_{\mathbb{E}_\pi[w_x]} + \beta_{\mathbb{E}_\pi[w_x],G_x}G_x + \beta_{\mathbb{E}_\pi[w_x],G_y}G_y + \epsilon_{\mathbb{E}_\pi[w_x]} \right. \right. \\ \left. \left. - \nu \left(\alpha_{\rho_x\sigma_\pi[w_x]} + \beta_{\rho_x\sigma_\pi[w_x],G_x}G_x + \beta_{\rho_x\sigma_\pi[w_x],G_y}G_y + \epsilon_{\rho_x\sigma_\pi[w_x]} \right) \right) \right] > 0 \end{aligned} \quad (\text{A22})$$

As before, the covariances of G_x with the constants equal 0 (*i.e.*, $\mathbb{C}_x[G_x, \alpha_{\mathbb{E}_\pi[w_x]}] = \mathbb{C}_x[G_x, \nu\alpha_{\rho_x\sigma_\pi[w_x]}] = 0$), and the covariances with the error terms are assumed to be zero (*i.e.*, $\mathbb{C}_x[G_x, \epsilon_{\mathbb{E}_\pi[w_x]}] = \mathbb{C}_x[G_x, \nu\epsilon_{\rho_x\sigma_\pi[w_x]}] = 0$). For clarity, we denote the effects on the correlated variation of the recipient's reproductive success as follows:

$$b_\sigma \equiv -\beta_{\rho_x\sigma_\pi[w_x],G_y} = -\beta_{\rho_x\sigma_\pi[w_y],G_x} \quad (\text{A23a})$$

$$c_\sigma \equiv \beta_{\rho_x\sigma_\pi[w_x],G_x} \quad (\text{A23b})$$

Substituting Equations (A23a) and (A23b) into (A22) gives:

$$b_\mu \mathbb{C}_x[G_x, G_y] - c_\mu \mathbb{C}_x[G_x, G_x] - v(c_\sigma \mathbb{C}_x[G_x, G_x] - b_\sigma \mathbb{C}_x[G_x, G_y]) > 0 \quad (\text{A24})$$

Dividing both sides of Inequality (A24) by $\mathbb{V}_x[G_x]$ to obtain relatedness ($r \equiv \frac{\mathbb{C}_x[G_y, G_x]}{\mathbb{V}_x[G_x]}$), we can rewrite the condition for selection as follows:

$$r(b_\mu + vb_\sigma) > c_\mu + vc_\sigma \quad (\text{A25})$$

which is Inequality 3.2 in the main text.

Note that a positive benefit b_σ (beneficial for the recipient) will be a *negative* regression slope, since it will be *reducing* the volatility of the recipient's reproduction. Likewise, a positive cost c_σ (deleterious for the actor) will be a *positive* regression slope, since it will be *increasing* the volatility of the actor's reproduction. If the actor can succeed in reducing its own reproductive volatility, c_σ will be negative (*i.e.*, a 'negative cost').

Accordingly, the benefit term B to expected relative fitness is:

$$B \approx b_\mu + vb_\sigma \quad (\text{A26})$$

The cost term C to expected relative fitness is:

$$C \approx c_\mu + vc_\sigma \quad (\text{A27})$$

These are approximations of the exact benefit and cost terms captured in the general expression for Hamilton's rule (Inequality 3.1 in the main text), showing that selection can favour paying a cost to expected reproductive success ($c_\mu > 0, c_\sigma = 0$) to reduce the \bar{w} -correlated variation of a relative's reproductive success ($b_\sigma > 0$) even in the absence of any effect on the expected reproductive success of the recipient ($b_\mu = 0$). In this situation:

$$\mathbb{E}_\pi[\Delta\bar{G}] > 0 \iff r > \frac{c_\mu}{vb_\sigma} \quad (\text{A28})$$

The relative importance of mean effects (b_μ and c_μ) versus volatility effects (b_σ and c_σ) is determined by v . If we denote the importance of mean effects (*i.e.*, their power to determine the outcome of selection) with the weight a_μ and the importance of volatility effects with the weight a_σ , such that Inequality (A25) can be written as $r(a_\mu b_\mu + a_\sigma b_\sigma) > a_\mu c_\mu + a_\sigma c_\sigma$, these weights are the numerator and denominator of v (*i.e.*, $a_\mu = \mathbb{E}_\pi[\bar{w}]$ and $a_\sigma = \sigma_\pi[\bar{w}]$). In short, we emphasise that the true benefits and costs in social evolution should be measured using the expectation of relative fitness (Gardner *et*

al., 2011), which we decompose here into mean fecundity and volatility effects, rather than mean fecundity effects alone.

Under the definition of ‘bet-hedging’, a behaviour must incur a cost to arithmetic mean number of offspring whilst deriving a benefit by reducing the variance associated with the number of offspring (Starrfelt and Kokko, 2012). The role of fitness variation reduction in social evolution has long attracted verbal speculation (Reed and Walters, 1996; Soucy *et al.*, 2003; Stevens *et al.*, 2007; Rehan *et al.*, 2011; Rubenstein, 2011; Gonzalez *et al.*, 2013; Koenig and Walters, 2015), but has evaded formalisation. We define ‘altruistic bet-hedging’ as occurring when the cost (a reduction in arithmetic mean number of offspring) is paid by the actor whilst a recipient derives the benefit (a reduction in the variance associated with the number of offspring). It is, of course, possible that the recipient may also experience either an increase or a decrease in arithmetic mean number of offspring (a b_μ effect). For clarity, we include such cases as ‘altruistic bet-hedging’ only if the b_μ effect is insufficient to overcome the costs paid by the actor without the additional b_σ effect. A behaviour is altruistic bet-hedging if it (i) involves a cost c_μ paid by the actor and (ii) would not evolve without a socially mediated reduction in the variation of a recipient’s reproductive success (a b_σ effect).

In short, each state has a mean fitness \bar{w} , and a distribution of realised fitnesses for every individual. Unlike environmental stochasticity, within-genotype demographic stochasticity (inter-individual variation in fitness within the same environmental state) is shown by Inequality 3.2 (main text) not to matter to the outcome of selection in large populations, because the regression slopes cut through this variation to obtain the relationship between alleles and fitness visible to natural selection. The one condition in which inter-individual variation in fitness within the same environment state does matter is when population sizes (the scale of the competitive population) are tiny, a well-known result in the bet-hedging literature that we generalise for social interactions in section A5 below (Inequality 3.3 in the main text).

Note that when the ‘natural’ distribution for reproductive success is sufficiently skewed (*i.e.*, either good years or bad years are rare), Hamilton’s rule will need to be approximated to higher moments (e.g. $k = 2$), using Inequality 3.1 in the main text, to capture effects on the asymmetry of the probability distributions from which the social partners are sampling their reproductive success (although under such conditions, organisms will tend to be specialised to the common environmental state).

A3 | Non-social bet-hedging and Hamilton’s rule

In this section, we show how the stochastic Hamilton's rule (Inequality (A25)) captures familiar forms of bet-hedging as special cases. In the absence of social interaction ($rB = 0$), the rule is simply:

$$c_\mu + vc_\sigma < 0 \quad (\text{A29})$$

Note that $c_\mu = -\beta_{\mathbb{E}_\pi[w_x], G_x}$ (Equation (A14c)), so a reduction in the reproductive success of the actor ($\beta_{\mathbb{E}_\pi[w_x], G_x} < 0$) represents a positive cost c_μ . In terms of regression effects, therefore, the stochastic Hamilton's rule shows the condition for non-social bet-hedging to be as follows, where $\beta_{\mathbb{E}_\pi[w_x], G_x} < 0$ and $\beta_{\rho_x \sigma_\pi[w_x], G_x} < 0$:

$$\beta_{\mathbb{E}_\pi[w_x], G_x} > v\beta_{\rho_x \sigma_\pi[w_x], G_x} \quad (\text{A30})$$

To see how these results recover previous results in the non-social bet-hedging literature, consider a non-social haploid population consisting of two rival alleles, denoted A_1 and A_2 . To identify whether selection is expected to favour the A_1 allele ($\mathbb{E}_\pi[\Delta\bar{G}] > 0$), we ask whether there will be a change in genetic value for A_1 (individuals with the allele of interest A_1 have a genetic value $G_x = 1$, whilst those lacking it have a genetic value of $G_x = 0$).

Each individual x has an expected number of offspring μ_x and a standard deviation in number of offspring σ_x . Following Frank & Slatkin (1990) and Starrfelt & Kokko (2012), set μ_x equal to the value μ_1 for all carriers of allele 1 (and equal to μ_2 for all carriers of allele 2) and σ_x equal to the value σ_1 for all carriers of allele 1 (and equal to σ_2 for all carriers of allele 2). In other words, members of a genotype sample their fitness w_x from a probability distribution shared by all members of the genotype, but they may in principle do so in an uncorrelated fashion with other members of the genotype. The degree to which an individual's fitness w_x correlates with fluctuations in population average reproductive success \bar{w} is given by $\rho_{w_x, \bar{w}}$.

To obtain the exact expected change in gene frequency, Hamilton's rule can be expressed in the following format:

$$\mathbb{E}_\pi[\Delta\bar{G}] = \frac{r(b_\mu + vb_\sigma) - c_\mu - vc_\sigma}{\mathbb{E}_\pi[\bar{w}]} \cdot \mathbb{V}_x[G_x] \quad (\text{A31})$$

In Equation (A31), we derive Hamilton's rule without dividing by the variance $\mathbb{V}_x[G_x]$ in genetic value; see Equation (2.3) in Okasha & Martens (2016).

We now set b_μ and b_σ in Equation (A31) to zero to focus on non-social cases. Fitting the stochastic Hamilton's rule (Inequality (A25)) obtains the following non-social components c_μ and c_σ :

$$c_\mu = \mu_2 - \mu_1 \quad (\text{A32a})$$

$$c_\sigma = \rho_{1,\bar{w}}\sigma_1 - \rho_{2,\bar{w}}\sigma_2 \quad (\text{A32b})$$

In other words, there are two horizontal positions (0 and 1) on a graph of μ against genetic value G_x ; the two vertical positions are μ_1 and μ_2 . The slope $\beta_{\mathbb{E}_\pi[w_x],G_x}$ of μ against G_x is then simply $\mu_1 - \mu_2$. The cost term c_μ is $-\beta_{\mathbb{E}_\pi[w_x],G_x}$, i.e., $\mu_2 - \mu_1$. Likewise, on the graph of \bar{w} -correlated volatility against genetic value G_x , there are two vertical positions $\rho_{1,\bar{w}}\sigma_1$ and $\rho_{2,\bar{w}}\sigma_2$, so the slope $\beta_{\rho_x\sigma_\pi[w_x],G_x}$ of \bar{w} -correlated volatility against G_x is $\rho_{1,\bar{w}}\sigma_1 - \rho_{2,\bar{w}}\sigma_2$. The coefficient c_σ is equal to $\beta_{\rho_x\sigma_\pi[w_x],G_x}$ (Equation (A23b)).

Recall that v is the coefficient of variation in population average reproductive success $\left(\frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}\right)$, Equation (A19)). The variance in breeding value, $\mathbb{V}_x[G_x]$, is equal to q_1q_2 , as it represents a two-point distribution (i.e., $\mathbb{V}_x[G_x] = q_1q_2(1 - 0)^2 = q_1q_2$). Equation (A31) can now be written:

$$\mathbb{E}_\pi[\Delta\bar{G}] = \frac{\mu_1 - \mu_2 - \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}(\rho_{1,\bar{w}}\sigma_1 - \rho_{2,\bar{w}}\sigma_2)}{\mathbb{E}_\pi[\bar{w}]} q_1q_2 \quad (\text{A33})$$

As there are only two genetic values in a haploid world (0 and 1), $\rho_{1,\bar{w}}\sigma_1$ and $\rho_{2,\bar{w}}\sigma_2$ are the expected values of $\rho_{w_x,\bar{w}}\sigma_x$ for members of each genotype, obtained as a predicted value in a least-squares regression (Inequality (A25)). We denote individuals with the index i :

$$\rho_{1,\bar{w}}\sigma_1 = \sigma_1 \cdot \frac{1}{q_1N} \sum_{i=1}^{q_1N} \rho_{w_i,\bar{w}} \quad (\text{A34a})$$

$$\rho_{2,\bar{w}}\sigma_2 = \sigma_2 \cdot \frac{1}{q_2N} \sum_{i=1}^{q_2N} \rho_{i,\bar{w}} \quad (\text{A34b})$$

The summation term in Equation (A34a) contains the correlation between individual i 's reproductive success w_i and the average reproductive success \bar{w} in the population. Since a correlation can be expressed in the form $\rho_{Z,Y} = \frac{\mathbb{C}[Z,Y]}{\sigma[Z]\sigma[Y]}$, we express this summation term as follows:

$$\frac{1}{q_1N} \sum_{i=1}^{q_1N} \rho_{w_i,\bar{w}} = \frac{1}{q_1N} \sum_{i=1}^{q_1N} \frac{\mathbb{C}_\pi[w_i, \bar{w}]}{\sigma_1\sigma_\pi[\bar{w}]} \quad (\text{A35})$$

We then carry the summation inside the covariance:

$$\frac{1}{q_1N} \sum_{i=1}^{q_1N} \rho_{w_i,\bar{w}} = \frac{\mathbb{C}_\pi \left[\frac{1}{q_1N} \sum_{i=1}^{q_1N} w_i, \bar{w} \right]}{\sigma_1\sigma_\pi[\bar{w}]} \quad (\text{A36})$$

The term $\frac{1}{q_1 N} \sum_{i=1}^{q_1 N} w_i$ is the average reproductive success for carriers of allele A_1 . To match notation in Starrfelt & Kokko (2012), we call this R_1 :

$$R_1 = \frac{1}{q_1 N} \sum_{i=1}^{q_1 N} w_i \quad (\text{A37})$$

Equation (A37) can now be expressed more simply as:

$$\frac{1}{q_1 N} \sum_{i=1}^{q_1 N} \rho_{w_i, \bar{w}} = \frac{\mathbb{C}_\pi[R_1, \bar{w}]}{\sigma_1 \sigma_\pi[\bar{w}]} \quad (\text{A38})$$

Likewise, since $\bar{w} = q_1 R_1 + q_2 R_2$, we substitute this formula for \bar{w} into Equation (A38) and expand the covariance (since $\mathbb{C}[X + Z, Y] = \mathbb{C}[X, Y] + \mathbb{C}[Z, Y]$):

$$\frac{1}{q_1 N} \sum_{i=1}^{q_1 N} \rho_{w_i, \bar{w}} = \frac{q_1 \sigma_\pi[R_1]^2 + q_2 \mathbb{C}_\pi[R_1, R_2]}{\sigma_1 \sigma_\pi[\bar{w}]} \quad (\text{A39})$$

As Starrfelt and Kokko (2012) note in their Equations (7–9), $\mathbb{C}_\pi[R_1, R_2] = \rho_{12} \sigma_1 \sigma_2$, and $\sigma_\pi[R_1]^2 = \rho_1 \sigma_1^2$, letting σ_1 denote the standard deviation in reproductive success of an individual carrying allele 1 and ρ_1 denote the correlation in reproductive success between individuals carrying allele 1. Therefore:

$$\frac{1}{q_1 N} \sum_{i=1}^{q_1 N} \rho_{w_i, \bar{w}} = \frac{q_1 \rho_1 \sigma_1^2 + q_2 \rho_{12} \sigma_1 \sigma_2}{\sigma_1 \sigma_\pi[\bar{w}]} \quad (\text{A40})$$

We can perform the same series of rearrangements for carriers of allele A_2 :

$$\frac{1}{q_2 N} \sum_{i=1}^{q_2 N} \rho_{w_i, \bar{w}} = \frac{q_2 \rho_2 \sigma_2^2 + q_1 \rho_{12} \sigma_1 \sigma_2}{\sigma_2 \sigma_\pi[\bar{w}]} \quad (\text{A41})$$

Substituted into Hamilton's rule (Equation (A33)), this obtains:

$$\mathbb{E}_\pi[\Delta \bar{G}] = \frac{\mu_1 - \mu_2 + \frac{1}{\mathbb{E}_\pi[\bar{w}]} (q_2 \rho_2 \sigma_2^2 - q_1 \rho_1 \sigma_1^2 + (q_1 - q_2) \rho_{12} \sigma_1 \sigma_2)}{\mathbb{E}_\pi[\bar{w}]} q_1 q_2 \quad (\text{A42})$$

If the population is neither rising nor falling in size, $\mathbb{E}_\pi[\bar{w}] = 1$:

$$\mathbb{E}_\pi[\Delta \bar{G}] = q_1 q_2 \left(\mu_1 - \mu_2 + (q_2 \rho_2 \sigma_2^2 - q_1 \rho_1 \sigma_1^2 + (q_1 - q_2) \rho_{12} \sigma_1 \sigma_2) \right) \quad (\text{A43})$$

Equation (A43) recovers Frank and Slatkin's (1990) Equation (7) and Starrfelt and Kokko's (2012) Equation (10) for the canonical bet-hedging model familiarly used in the literature (*i.e.*, two alleles in a fixed-size population at a haploid locus in a fluctuating environment of two or more states).

From Equation (A43), we can recover the geometric mean heuristic (which provides a prediction of which allele will fixate) by assuming (Frank and Slatkin, 1990) that there is no correlation between genotypes ($\rho_{12} = 0$) and setting the population to equal frequencies (Frank and Slatkin, 1990) of each allele ($q_1 = q_2 = \frac{1}{2}$). These conditions provide the well-known geometric-mean approximation (Equation (12) in Frank and Slatkin (1990); note that, as heuristic approximations, there are at least five different estimates for the geometric mean, all of which perform roughly equally well (Young and Trent, 1969)):

$$\mu_1 - \frac{\rho_1 \sigma_1^2}{2} > \mu_2 - \frac{\rho_2 \sigma_2^2}{2}$$

A4 | Uncertain relatedness

The potential effects of stochasticity on relatedness have been raised by Goodnight (1992) and Lehmann & Balloux (2007). In this section, we explore how uncertainty over relatedness influences the outcome of selection. We show that the mean relatedness of recipients is sufficient to predict the outcome of selection when there is no strong correlation (across environmental states) between the relatedness r of social partners and the average reproductive success in the population (\bar{w}). We denote this correlation as $\rho_{r, \bar{w}}$. However, if the relatedness of interactants and average reproductive success are negatively correlated ($\rho_{r, \bar{w}} < 0$), investments in social partners become more valuable as environmental stochasticity increases (*i.e.*, at high values of v). Conversely, investments in social partners become less valuable in a stochastic environment if this correlation is positive ($\rho_{r, \bar{w}} > 0$).

To illustrate this result, we denote the reproductive success of individual x in state π as $w_{x(\pi)}$, and express this quantity as a function of its own genetic value G_x and the genetic value G_y of its social partner:

$$w_{x(\pi)} = \alpha_{w_{x(\pi)}} + \beta_{w_{x(\pi)}, G_x} G_x + \beta_{w_{x(\pi)}, G_y} G_y + \epsilon_{w_{x(\pi)}} \quad (A44)$$

We substitute this regression formula into the Price equation (Equation (A2)) to express the condition for selection ($\mathbb{E}_\pi[\Delta \bar{G}] > 0$) as:

$$\mathbb{E}_\pi \left[\mathbb{C}_x \left[G_x, \frac{\alpha_{w_x} + \beta_{w_x, G_x} G_x + \beta_{w_x, G_y} G_y + \epsilon_{w_x}}{\bar{w}} \right] \right] > 0 \quad (A45)$$

For a given environmental state π , \bar{w} is a constant with respect to G_x , so we move it outside the covariance, which is defined only for the environmental state π . By the linearity of covariances ($\mathbb{C}[X + Y, Z] = \mathbb{C}[X, Z] + \mathbb{C}[Y, Z]$), this is equal to:

$$\mathbb{E}_\pi \left[\frac{\left(\mathbb{C}_x[G_x, \alpha_{w_x}] + \mathbb{C}_x[G_x, \beta_{w_x, G_x} G_x] + \mathbb{C}_x[G_x, \beta_{w_x, G_y} G_y] + \mathbb{C}_x[G_x, \epsilon_{w_x}] \right)}{\bar{w}} \right] > 0 \quad (\text{A46})$$

$\mathbb{C}_x[G_x, \alpha_{w_x}] = 0$ (since α_{w_x} is a constant) and we assume $\mathbb{C}_x[G_x, \epsilon_{w_x}] = 0$. Then:

$$\mathbb{E}_\pi \left[\frac{\left(\beta_{w_x, G_x} \mathbb{C}_x[G_x, G_x] + \beta_{w_x, G_y} \mathbb{C}_x[G_x, G_y] \right)}{\bar{w}} \right] > 0 \quad (\text{A47})$$

We now divide both sides of Inequality (A47) by the variance in genetic value ($\mathbb{V}_x[G_x]$) to obtain state-specific relatedness $r_\pi = \frac{\mathbb{C}_x[G_x, G_y]}{\mathbb{V}_x[G_x]}$:

$$\mathbb{E}_\pi \left[\frac{\beta_{w_x, G_x} + \beta_{w_x, G_y} r}{\bar{w}} \right] > 0 \quad (\text{A48})$$

Retaining the first two terms of the Taylor series expansion of Inequality (A48) gives:

$$\frac{\mathbb{E}_\pi[\beta_{w_x, G_x}] + \mathbb{E}_\pi[\beta_{w_x, G_y} r]}{\mathbb{E}_\pi[\bar{w}]} - \frac{\mathbb{C}_\pi[\beta_{w_x, G_x}, \bar{w}] + \mathbb{C}_\pi[\beta_{w_x, G_y} r, \bar{w}]}{\mathbb{E}_\pi[\bar{w}]^2} > 0 \quad (\text{A49})$$

We now consider the case in which the benefit conferred on a recipient and the cost paid by the actor are the same in all environmental states ($\beta_{w_x, G_y} = b$ and $\beta_{w_x, G_x} = -c$ for all π). However, we allow relatedness to the recipient to vary among states π . This captures the possibility that actors associate with either closer or more distant relatives when the conditions change. The covariance of cost and population average fitness is zero, because cost is now a constant across states ($\mathbb{C}_\pi[\beta_{w_x, G_x}, \bar{w}] = \mathbb{C}_\pi[c, \bar{w}] = 0$). Multiplying both sides by $\mathbb{E}_\pi[\bar{w}]$, Inequality (A49) can be simplified to:

$$b \cdot \mathbb{E}_\pi[r] - b \cdot \frac{\mathbb{C}_\pi[r, \bar{w}]}{\mathbb{E}_\pi[\bar{w}]} - c > 0 \quad (\text{A50})$$

We now rearrange Inequality (A50) by expanding the covariance. The covariance between relatedness and population average fitness ($\mathbb{C}_\pi[r, \bar{w}]$) can be written as $\rho_{r, \bar{w}} \sigma_\pi[r] \sigma_\pi[\bar{w}]$, where ρ denotes correlation and σ_π denotes standard deviation across environmental states. We introduce v as the stochasticity coefficient (the coefficient of variation in population average reproductive success, $v = \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}$, which we introduced earlier in Equation (A19)). We also use the following notation for clarity: we denote the expectation of relatedness across environmental states as r_μ , and we denote the standard deviation of relatedness across environmental states as r_σ :

$$r_\mu = \mathbb{E}_\pi[r] \quad (\text{A51a})$$

$$r_\sigma = \sigma_\pi[r] \quad (\text{A51b})$$

Accordingly, Inequality (A50) can be expressed as:

$$(r_{\mu} - \rho_{r, \bar{w}} v r_{\sigma}) b > c \quad (\text{A52})$$

Inequality (A52) shows that uncertainty over relatedness (r_{σ}) only influences selection if relatedness fluctuates strongly in either a positively or negatively correlated fashion with population average reproductive success. A negative correlation, across environmental states, between relatedness and average reproductive success ($\rho_{r, \bar{w}} < 0$) results in an actor's most valuable investments being focused on closer relatives. These investments are the 'most valuable' because an increase in recipient fecundity of a given size b is more valuable when competitors are underperforming (low \bar{w}): the recipient will enjoy a proportionally greater market share of reproduction than if the increase had occurred when competitors were overperforming (high \bar{w}). Mean relatedness r_{μ} is sufficient to capture the outcome of selection when population mean reproductive success does not fluctuate ($v \approx 0$), even if actors face high levels of uncertainty r_{σ} about the kinship of recipients.

A5 | Demographic stochasticity

We now consider the role of risk in a 'static' environment, for which the environment does not fluctuate between states (the influence of the environment is identical across the set Π). In a population of size N in which organisms sample their reproductive success independently ($\mathbb{C}_{\pi}[w_x, w_{j \neq x}] = 0$), the covariance (defined across possible fitness outcomes) between the focal individual's reproductive success (w_x) and the average reproductive success in the population (\bar{w}) is:

$$\begin{aligned} \mathbb{C}_{\pi}[w_x, \bar{w}] &= \mathbb{C}_{\pi} \left[w_x, \frac{1}{N} \sum_j w_j \right] = \frac{1}{N} \sum_j \mathbb{C}_{\pi}[w_x, w_j] = \frac{1}{N} \left(\mathbb{C}_{\pi}[w_x, w_x] + \sum_{j \neq x} \mathbb{C}_{\pi}[w_x, w_j] \right) = \frac{\mathbb{V}_{\pi}[w_x]}{N} \\ &= \frac{\sigma_{\pi}[w_x]^2}{N} \end{aligned} \quad (\text{A53})$$

We substitute this into the selection covariance of the Price equation (and multiply out $\mathbb{E}_{\pi}[\bar{w}]$):

$$\mathbb{C}_x \left[G_x, \left(\mathbb{E}_{\pi}[w_x] - \frac{\sigma_{\pi}[w_x]^2}{N \mathbb{E}_{\pi}[\bar{w}]} \right) \right] > 0 \quad (\text{A54})$$

Applying Queller's (1992a) regression method (as in Appendix A2) to this equation, we obtain Inequality (3) in the main text (where b_{σ^2} is the effect of the partner's genotype on the organism's

within-generation variance in reproductive success ($-\beta_{V_{\pi}[w_x], G_y}$), and c_{σ^2} is the effect of the organism's genotype on its own variance in reproductive success ($\beta_{V_{\pi}[w_x], G_x}$):

$$r\left(b_{\mu} + \frac{b_{\sigma^2}}{N\mathbb{E}_{\pi}[\bar{w}]}\right) > c_{\mu} + \frac{c_{\sigma^2}}{N\mathbb{E}_{\pi}[\bar{w}]} \quad (A55)$$

10.2 Appendix B: Deriving regression effects

Here, we describe how the benefit and cost terms are obtained in a specific model (implemented as a simulation in *MATLAB*, for which code is given in *Appendix D* of Kennedy *et al.*, 2018).

B1 | Discrete environment states

Let a haploid asexual population consist of two genotypes, with genetic values **0** and **1**, at a single locus. Genotype **0** is non-cooperative, whilst genotype **1** pays a cost c to reduce the volatility of its recipients' reproductive success to a proportion η of its natural level. The frequency of genotype **1** in the population is p (and so the frequency of genotype **0** is $1 - p$). The environment fluctuates between two states ('good' and 'bad').

Following the assortment rules in the first model in Gardner *et al.* (2011, p. 1030), we assume that individuals preferentially pair with same type (cooperators or noncooperators) with the probabilities in Table B1.

Without cooperation, individuals have a fecundity of z_1 in a good year and z_2 in a bad year. Good years occur with probability d and bad years with probability $1 - d$. The standard deviation of a genotype **0** individual with a genotype **0** social partner is then:

$$\sigma_{00} = \sqrt{(1 - d)d(z_1 - z_2)^2} \quad (B1)$$

Supplementary Table B1 | Mean and variation of reproductive success as a function of social partners in a world fluctuating unpredictably between two states

Genotypes		Probability of interaction	Mean reproductive success (μ_{xy})	Volatility of reproductive success (σ_{xy})	ρ if $\eta \neq 0$
Focal (x)	Partner (y)				
1	1	$p^2 + \alpha p(1 - p)$	$d(z_1 - c) + (1 - d)(z_2 - c)$	$\eta\sqrt{d(1 - d)((z_1 - c) - (z_2 - c))^2}$	1

1	0	$(1 - \alpha)p(1 - p)$	$d(z_1 - c) + (1 - d)(z_2 - c)$	$\sqrt{d(1 - d)((z_1 - c) - (z_2 - c))^2}$	1
0	1	$(1 - \alpha)p(1 - p)$	$dz_1 + (1 - d)z_2$	$\eta\sqrt{d(1 - d)(z_1 - z_2)^2}$	1
0	0	$(1 - p)^2 + \alpha p(1 - p)$	$dz_1 + (1 - d)z_2$	$\sqrt{d(1 - d)(z_1 - z_2)^2}$	1

Assortment rules follow the first model in Gardner *et al.* (2011), leading to $r = \alpha$.

A focal individual encountering a genotype 1 social partner experiences a reduction in its fecundity variation by the coefficient η .

From Inequality (A25), Hamilton's rule (approximated to the first two central moments) is:

$$r(b_\mu + vb_\sigma) > c_\mu + vc_\sigma \quad (B2)$$

To find the four partial regression slopes ($b_\mu, b_\sigma, c_\mu, c_\sigma$), we fit the following equations to Supplementary Table B1:

$$\mathbb{E}_\pi[w_x] = \alpha_{\mathbb{E}_\pi[w_x]} + \beta_{\mathbb{E}_\pi[w_x], G_x} G_x + \beta_{\mathbb{E}_\pi[w_x], G_y} G_y + \epsilon_{\mathbb{E}_\pi[w_x]} \quad (B3)$$

$$\rho_x \sigma_\pi[w_x] = \alpha_{\rho_x \sigma_\pi[w_x]} + \beta_{\rho_x \sigma_\pi[w_x], G_x} G_x + \beta_{\rho_x \sigma_\pi[w_x], G_y} G_y + \epsilon_{\rho_x \sigma_\pi[w_x]} \quad (B4)$$

Thus, we solve two linear regression equations: one for expected reproductive success ($\mathbb{E}_\pi[w_x]$) and one for the correlated variation of reproductive success ($\rho_x \sigma_\pi[w_x]$). The partial regression slopes m_1 and m_2 in a multiple regression with two predictors h_1 and h_2 of l can be found by solving the following simultaneous equations (Gardner *et al.*, 2011):

$$m_1 = \frac{\mathbb{C}[l, h_1]}{\mathbb{V}[h_1]} - m_2 \frac{\mathbb{C}[h_1, h_2]}{\mathbb{V}[h_1]} \quad (B5)$$

$$m_2 = \frac{\mathbb{C}[l, h_2]}{\mathbb{V}[h_2]} - m_1 \frac{\mathbb{C}[h_1, h_2]}{\mathbb{V}[h_2]} \quad (B6)$$

To find b_μ and c_μ , we simultaneously solve:

$$m_1 = \frac{\mathbb{C}[\mathbb{E}_\pi[w_x], G_x]}{\mathbb{V}[G_x]} - m_2 \frac{\mathbb{C}[G_x, G_y]}{\mathbb{V}[G_x]} \quad (B7)$$

$$m_2 = \frac{\mathbb{C}[\mathbb{E}_\pi[w_x], G_y]}{\mathbb{V}[G_y]} - m_1 \frac{\mathbb{C}[G_x, G_y]}{\mathbb{V}[G_y]} \quad (B8)$$

The components of Equations (B7) and (B8) fitted to Table B1 are:

$$\frac{\mathbb{C}[\mathbb{E}_\pi[w_x], G_x]}{\mathbb{V}[G_x]} = -c \quad (C9)$$

$$\frac{\mathbb{C}[G_x, G_y]}{\mathbb{V}[G_x]} = \alpha \quad (\text{B10})$$

$$\frac{\mathbb{C}[\mathbb{E}_\pi[w_x], G_y]}{\mathbb{V}[G_y]} = -c\alpha \quad (\text{B11})$$

$$\frac{\mathbb{C}[G_x, G_y]}{\mathbb{V}[G_y]} = \alpha \quad (\text{B12})$$

We therefore simultaneously solve:

$$m_1 = -c - m_2\alpha \quad (\text{B13})$$

$$m_2 = -(m_1 + c)\alpha \quad (\text{B14})$$

This obtains $m_1 = -c$ and $m_2 = 0$, which are the partial regression slopes $\beta_{\mathbb{E}_\pi[w_x], G_x}$ and $\beta_{\mathbb{E}_\pi[w_x], G_y}$, respectively. Since the components c_μ and b_μ in Inequality (A25) are $c_\mu = -\beta_{\mathbb{E}_\pi[w_x], G_x}$ and $b_\mu = \beta_{\mathbb{E}_\pi[w_x], G_y}$, these components are therefore:

$$c_\mu = c \quad (\text{B15})$$

$$b_\mu = 0 \quad (\text{B16})$$

We solve an equivalent pair of simultaneous equations to find b_σ and c_σ :

$$m_3 = \frac{\mathbb{C}[\sigma_\pi[w_x], G_x]}{\mathbb{V}[G_x]} - m_4 \frac{\mathbb{C}[G_x, G_y]}{\mathbb{V}[G_x]} \quad (\text{B17})$$

$$m_4 = \frac{\mathbb{C}[\sigma_\pi[w_x], G_y]}{\mathbb{V}[G_y]} - m_3 \frac{\mathbb{C}[G_x, G_y]}{\mathbb{V}[G_y]} \quad (\text{B18})$$

Simultaneously solving Equations (B17) and (B18) obtains:

$$m_3 = 0 \quad (\text{B19})$$

$$m_4 = (\eta - 1)\sigma_{00} \quad (\text{B20})$$

m_3 is the partial regression slope $\beta_{\rho_x \sigma_\pi[w_x], G_x}$, which provides the component c_σ in Inequality (A25). m_4 is the partial regression slope $\beta_{\rho_x \sigma_\pi[w_x], G_y}$. The component b_σ in Inequality (A25) is equal to $-\beta_{\rho_x \sigma_\pi[w_x], G_y}$. Accordingly, these two components are:

$$c_\sigma = 0 \quad (\text{B21})$$

$$b_\sigma = (1 - \eta)\sigma_{00} \quad (\text{B22})$$

v is a simple function of allele frequency p :

$$v \equiv \frac{\sigma_{\pi}[\bar{w}]}{\mathbb{E}_{\pi}[\bar{w}]} = \frac{(p\eta + (1-p))\sigma_{00}}{\mu_{00} - pc} \quad (B23)$$

This is an intuitive measure of stochasticity in this environment fluctuating unpredictably between two states: the numerator is the standard deviation of two completely correlated random variables (*i.e.*, the sum of $\eta\sigma_{00}$ and σ_{00} , weighted by the frequency of each allele), whilst the denominator is the average number of offspring across states (again, weighted by allele frequency).

Since p appears in the equation for v , v is frequency-dependent. Differentiating stochasticity (v) with respect to the frequency of altruistic bet-hedgers (p), v decreases with rising p when:

$$1 - \eta > \frac{c}{\mu_{00}} \quad (B24)$$

Accordingly, stochasticity v falls as frequency p rises (*Figure 3.4*) if the effect of variation reduction ($1 - \eta$) is greater than the relative size of mean-fecundity reduction ($\frac{c}{\mu_{00}}$).

When this condition (Inequality (B24)) is met, as the frequency p rises the bet-hedgers begin to render the environment effectively stable. At high frequency, the value of volatility-reducing altruism b_{σ} therefore falls, because v is low. The result is that the population can be reinvaded by familiar mean-fecundity-maximisers, much as a ‘conspiracy of doves’ in the well-known hawk–dove game is vulnerable to invasion by hawks (Dawkins, 1976). (At low costs (c), intermediate levels of variation reduction η are less constrained from reaching fixation.) Connections between coexistence and bet-hedging have been analysed in non-social settings (Seger and Brockmann, 1987), although not interpreted in terms of frequency-dependent effects on whole-population stochasticity.

B2 | Frequency at which expected change due to selection is zero

We now have all the components of Hamilton’s rule ($r = \alpha$, $c_{\mu} = c$, $b_{\mu} = 0$, $c_{\sigma} = 0$, $b_{\sigma} = -(\eta - 1)\sigma_{00}$, $v = \frac{(p\eta + (1-p))\sigma_{00}}{\mu_{00} - pc}$). Putting these components together, we solve for the frequency p^* at which there is no expected change due to selection ($\mathbb{E}_{\pi}[\Delta\bar{G}] = 0$):

$$p^* = \frac{\alpha(\eta - 1)\sigma_{00}^2 + c\mu_{00}}{c^2 - (\eta - 1)^2\sigma_{00}^2\alpha} \quad (B25)$$

When $0 < p^* < 1$, the expected frequency of the social bet-hedgers is intermediate. If $rB > C$ for all p , then the population is expected to tend to $p^* = 1$. Likewise, if $rB < C$ for all p , the population is expected to tend to $p^* = 0$.

B3 | Individual-based simulation

To ensure that gene frequency makes incremental changes through generations in numerical simulation for the system in Table B1, we let offspring production across the population be driven by social interactions, and then sample a random 1% of the adult population for replacement in proportion to the balance of genotypes amongst the offspring (*i.e.*, each environmental state, 1% of the breeding spots become available for offspring produced that generation).

p^* is the gene frequency at which $rB - C = 0$ (Figure 3.3). The equilibrium frequency around which the population is expected to fluctuate over the long run, p' , is equal to p^* when the changes in gene frequency that occur each generation are small and the sign changes from $rB > C$ below p^* to $rB < C$ above p^* (Figure 3.3c). The first condition reduces displacement from equilibrium: when the population takes extreme leaps in gene frequency each generation, gene frequencies can enter random cycles for which p^* is not the midpoint ($p^* \neq p'$), as gene frequency moves between extremely different values at which the slope of selection differs. Under a regime of weak selection, $p^* = p'$.

B4 | Effects of chance and autocorrelation in the fluctuating environment

Even if both states are equally probable, the environment may by chance have a run of several good or several bad states. At the predicted equilibrium p^* , the change $\Delta\bar{G}$ from a good state is exactly opposite to the change from a bad state, so the expected change in average genetic value is zero ($\mathbb{E}_\pi[\Delta\bar{G}] = 0$). However, the magnitude of the effect is important. If the two types of change $\Delta\bar{G}$ have a very large effect, the frequency of altruists may alter rapidly due to a chance sequence of many of the same states: a chance run of five bad years, for instance, might cause one genotype to crash completely. Sustained runs of the same environmental state are more probable when the environment fluctuates in a temporally autocorrelated fashion.

A stochastic population is predicted to occupy its polymorphic position p^* when $\mathbb{V}_\pi[\Delta\bar{G}] \approx 0$ (*i.e.*, $\mathbb{V}_\pi\left[\mathbb{C}_x\left[G_x, \frac{w_x}{w}\right]\right] \approx 0$) and p^* is convergence-stable (*i.e.*, the frequency-dependent stochasticity coefficient v favours altruists at frequencies p_t below p^* but selects against it above). Since selection favours altruists when $v(b_\sigma - c_\sigma) > c_\mu - rb_\mu$, as long as $(b_\sigma - c_\sigma) > 0$ we can divide by $(b_\sigma - c_\sigma)$ without changing the sign of the inequality to find the conditions for a globally convergence-stable population in terms of the magnitude of the stochasticity coefficient v at a given frequency p_t (denoted

v_{p_t}):

$$\begin{aligned} p_t < p^* &\Rightarrow v_{p_t} > \frac{c_\mu - rb_\mu}{rb_\sigma - c_\sigma} \\ p_t > p^* &\Rightarrow v_{p_t} < \frac{c_\mu - rb_\mu}{rb_\sigma - c_\sigma} \end{aligned} \tag{B26}$$

In the individual-based simulation, we focus on weak selection, where only 1% of the population's genotype frequencies are available to change each generation. Under weak selection, even high levels of temporal autocorrelation (leading to frequent runs of the same environmental states across years) do not necessarily deter the population from its convergence point. In general, we emphasise that the Price equation – and its derivation, Hamilton's rule – focuses on generational changes: accordingly, both the non-stochastic version familiarly used in the literature and the stochastic version presented here can predict the frequency at which there is no change or no expected change (respectively) due to selection. Under appropriate conditions, including low-amplitude fluctuations in allele frequency between generations, this frequency will be realised as an equilibrium state for the population; outside these conditions, the frequency at which there is no expected change due to selection need not represent an equilibrium state.

B5 | Inducible altruism

An actor in a fluctuating environment does not necessarily need to produce a 'constitutive' strategy (e.g. help in all states or defect in all states). If the actor possesses information about the current state π , it may be able to tailor its response to produce an optimal strategy for the given state. In principle, this form of phenotypic plasticity may produce 'inducible' altruism in a stochastic world: help relatives if you know that a drought is imminent, for instance. In this section, we show how the reliability of information in a stochastic world determines whether cooperation should be constitutive or inducible.

We introduce to the population a plastic allele I , such that there are three alleles in competition:

S : 'Selfish': carriers never cooperate

C : 'Constitutive cooperator': carriers cooperate in all states

I : 'Inducible cooperator': carriers cooperate only when they believe they are in the 'bad' state

These alleles have frequencies p_S , p_C , and p_I respectively (*i.e.*, $p_S + p_C + p_I = 1$).

Let an act of cooperation incur a cost c to the actor's fecundity. In 'bad' states (such as drought), receiving cooperation increases an individual's fecundity by δ_+ . In 'good' states, we allow the presence of a cooperator to be detrimental to the recipient's fecundity: the cooperator reduces recipient

fecundity by δ_- (note that δ_- can equal zero, or even be negative if the co-operator always benefits the recipient).

Let the plastic allele I pay an additional cost ($c_{plastic}$) as the ‘cost of plasticity’, determined by both the costs of information gathering and utilisation and the costs of maintaining behavioural flexibility. The quality of the information available to carriers of the plastic allele is determined by its accuracy A : the environmental state π is what the actor thinks it is with probability A .

The frequency of each type of pairing is as follows (Supplementary Table B2):

Supplementary Table B2 | Frequencies of interactions

Genotype of focal individual x (allele carried)	Genotype of partner individual y (allele carried)	Frequency (F_{xy})
I	I	$p_I^2 + \alpha p_I(1 - p_I)$
I	S	$(1 - \alpha)p_I p_S$
I	C	$(1 - \alpha)p_I p_C$
S	I	$(1 - \alpha)p_S p_I$
S	S	$p_S^2 + \alpha p_S(1 - p_S)$
S	C	$(1 - \alpha)p_S p_C$
C	I	$(1 - \alpha)p_C p_I$
C	S	$(1 - \alpha)p_C p_S$
C	C	$p_C^2 + \alpha p_C(1 - p_C)$

We can define the fecundity of each of the types of focal individual described in Supplementary Table B2 as follows (Supplementary Table B3):

Supplementary Table B3 | Fecundities of types of focal individual

Focal individual x	Partner y	Fecundity in good years ($Good_{xy}$)	Fecundity in bad years (Bad_{xy})
I	I	$Az_1 + (1 - A)(z_1 - c - \delta_-) - c_{plastic}$	$A(z_2 - c + \delta_+) + (1 - A)z_2 - c_{plastic}$
I	S	$Az_1 + (1 - A)(z_1 - c) - c_{plastic}$	$A(z_2 - c) + (1 - A)z_2 - c_{plastic}$
I	C	$A(z_1 - \delta_-) + (1 - A)(z_1 - c - \delta_-) - c_{plastic}$	$A(z_2 + \delta_+ - c) + (1 - A)(z_2 + \delta_+) - c_{plastic}$
S	I	$Az_1 + (1 - A)(z_1 - \delta_-)$	$A(z_2 + \delta_+) + (1 - A)z_2$
S	S	z_1	z_2

S	C	$z_1 - \delta_-$	$z_2 + \delta_+$
C	I	$A(z_1 - c) + (1 - A)(z_1 - c - \delta_-)$	$A(z_2 + \delta_+ - c) + (1 - A)(z_2 - c)$
C	S	$z_1 - c$	$z_2 - c$
C	C	$z_1 - c - \delta_-$	$z_2 - c + \delta_+$

In *Figure 3.7* of the main text, we plot the expected direction of change in allele frequency under selection for this population. Note that the stochastic Hamilton's rule identifies the points in frequency space $\{p_S, p_C, p_I\}$ at which each allele is expected to increase in frequency under selection.

An instructive empirical example is found in the temperate paper wasp *Polistes annularis*: field data (Queller and Strassmann, 1988) for foundresses suggest that inclusive fitness is positive in a 'bad' state (characterised by drought) but negative in a 'good' state (when drought is absent). The existence of cooperative foundress groups in the 'good' state, when cooperation is predicted to be deleterious, implies that foundresses do not take up the theoretically-plausible option of being socially-plastic 'bad-year specialists'. In general, constitutive cooperation (cooperation in all states) can outcompete plastic cooperation ('bad-year specialists') when information is insufficiently reliable or the costs of plasticity are too high.

10.3 Appendix C: Feasibility of $b_\sigma > 0$

Hamilton's rule is predictive in the sense that it provides a falsifiable criterion to be applied to any specific hypothesis: a proposed combination of measured fitness effects must conform to the rule if they are to explain a given adaptation. In this section, we explore the potential for b_σ effects in social evolution.

In the main text and *Appendix A*, we highlight that the magnitude of v depends on the extent to which environmental fluctuations are correlated across patches in a matrix or metapopulation, and the extent to which temporal fluctuations within the organism's reproductive lifespan are correlated. Our intention here is to highlight the feasibility of b_σ -driven sociality, in principle, in the real world; at present, empirical data on the direct links between stochasticity and sociality are sparse. Direct empirical tests of the principle should aim to quantify the factors influencing v .

C1 | Elimination of parasite pressure

Recently, Rehan *et al.* (2014) have found that observed mean fecundity effects ($rb_\mu - c$) are unable to explain the evolution of cooperation between sisters ($r = 0.75$) in a facultatively social bee (*Ceratina*

australensis). This species inhabits a fluctuating environment, and Rehan *et al.* (2011) have previously suggested that bet-hedging could drive the evolution of cooperation: parasite numbers rise and fall between generations, generating ‘periods of extreme parasite pressure’ (Rehan *et al.*, 2011), but social nests are better able to evade brood loss to parasites. Bees may be effectively blind to environmental state (ambient level of brood loss to parasitism), since parasitoid activity (Rehan *et al.*, 2011) occurs only once larvae and pupae are available for ovipositing. Whether pupae have been parasitized may be essentially unknowable, as they are sealed within the stem nest.

In this section, we model the evolution of sister-to-sister cooperation in a fluctuating world. Although we necessarily remain agnostic about the drivers of cooperation in the particular species *C. australensis*, we show that, in principle, highly stochastic environments (high v) can be more hospitable than static environments for sister–sister cooperation in such species when sociality buffers parasite pressure.

We obtain matching results through an individual-based haplodiploid simulation and an application of Inequality (A25) to the life-history parameters of Supplementary Table C1. To simplify the interpretation, we first consider a single diallelic haploid locus, with assortment following Gardner *et al.* (2011): individuals are matched with a social partner identical at the focal locus with probability α and a random partner with probability $1 - \alpha$. This obtains $r = \alpha$, which allows us to set $\alpha = 0.75$ to recover assortment levels between haplodiploid sisters. We let the environment fluctuate between high and low parasite states; a solitary individual has z_G offspring in a ‘good year’ (low parasite pressure) and z_B offspring in a ‘bad year’ (high parasite pressure, $z_B < z_G$). We let the presence of social partners buffer the breeder from parasite pressure, so that breeders with helpers attain z_G offspring regardless of environmental state.

Supplementary Table C1 | Life history

G_x	G_y	Power	Result	Frequency in the population of this focal individual	Mean fecundity (across environmental states) of focal individual	Standard deviation (across environmental states) of focal individual’s fecundity
1	1	Dominant	Queen	$\frac{1}{2}(p^2 + \alpha p(1-p))$	z_G	0
1	1	Subordinate	Worker	$\frac{1}{2}(p^2 + \alpha p(1-p))$	0	0
1	0	Dominant	Solitary	$\frac{1}{2}(1-\alpha)p(1-p)$	$dz_G + (1-d)z_B$	$\sqrt{d(1-d)(z_G - z_B)^2}$
1	0	Subordinate	Worker	$\frac{1}{2}(1-\alpha)p(1-p)$	0	0
0	1	Dominant	Queen	$\frac{1}{2}(1-\alpha)p(1-p)$	z_G	0
0	1	Subordinate	Solitary	$\frac{1}{2}(1-\alpha)p(1-p)$	$dz_G + (1-d)z_B$	$\sqrt{d(1-d)(z_G - z_B)^2}$
0	0	Dominant	Solitary	$\frac{1}{2}((1-p)^2 + \alpha p(1-p))$	$dz_G + (1-d)z_B$	$\sqrt{d(1-d)(z_G - z_B)^2}$
0	0	Subordinate	Solitary	$\frac{1}{2}((1-p)^2 + \alpha p(1-p))$	$dz_G + (1-d)z_B$	$\sqrt{d(1-d)(z_G - z_B)^2}$

The frequencies are the sum of (1) direct pairings with genetically-identical individuals (occurring with probability α) and (2) random assortment with random members of the population (occurring with probability $1 - \alpha$), who may or may not be genetically identical. Thus, a $G_x = 1$ and $G_y = 1$ pairing occurs directly with probability α (representing αp of the total pairings in the population, since the frequency of $G = 1$ is p ; equivalently, of the α proportion of pairings that are directly with identical individuals, p of them will be between $G = 1$ individuals) and via random assortment with probability $(1 - \alpha)p^2$. Accordingly, the pairing frequency is $\alpha p + (1 - \alpha)p^2$, or, equivalently, $p^2 + \alpha p(1 - p)$. In half of these pairings, the focal individual is the dominant, and so the frequency of the dominant type in such a pairing is $\frac{1}{2}(p^2 + \alpha p(1 - p))$.

Solving for the coefficients in Inequality (2) of the main text obtains the following, where μ_\bullet and σ_\bullet are the average and standard deviation respectively (across the two states) of a solitary individual's number of offspring. Detail about obtaining regression coefficients for social effects is provided in *Appendix B*.

$$b_\mu = \frac{(1 - d)(z_G - z_B)}{2} \quad (C1a)$$

$$c_\mu = \frac{\mu_\bullet}{2} \quad (C1b)$$

$$b_\sigma = \frac{\sigma_\bullet}{2} \quad (C1c)$$

$$c_\sigma = -\frac{\sigma_\bullet}{2} \quad (C1d)$$

The means-based Hamilton's rule implies that cooperation will not evolve by mean fecundity effects alone for this system. The condition for the evolution of altruism by mean fecundity effects is:

$$r(1 - d)(z_G - z_B) > \mu_\bullet \quad (C2)$$

When high-parasite and low-parasite years occur with equal frequency ($d = 0.5$), the critical ratio of $z_G : z_B$ ($= \frac{(1-d)(1+r)}{(1-d)r-d}$) is negative: even with helpers conferring substantial gains in fecundity on breeders in high-parasite years (Table B1), cooperation cannot evolve by mean fecundity effects. When low-parasite states occur in 40% of years ($d = 0.4$), cooperation only evolves due to mean fecundity effects if individuals have at least 21 times more offspring without parasites than with parasites.

However, incorporating volatility effects increases the scope for cooperation when the environment is stochastic (high v):

$$r((1 - d)(z_G - z_B) + v \cdot \sigma_\bullet) > \mu_\bullet - v \cdot \sigma_\bullet \quad (C3)$$

In *Figure 3.6* of the main text, we illustrate this increased scope for the evolution of cooperation, both in terms of Inequality (A25) and individual-based simulation. For instance, whilst equal frequencies of high- and low-parasite years are unable to sustain cooperation by mean fecundity effects at any level

of z_G and z_B , *Figure 3.6a* reveals a high-stochasticity region in which cooperation invades a solitary population due to volatility effects. The 21-fold difference in fecundity between high-parasite and low-parasite states required for the evolution of cooperation by mean fecundity effects when low-parasite states occur in 40% of years shrinks to a 3-fold difference with the addition of volatility effects. Volatility effects can, accordingly, extend the region of the adaptive landscape in which social traits evolve, and in principle reduce the gap between B and C in paradoxical cases where Hamilton's rule appears to fail. Not all social species evolve from solitary ancestors inhabiting a highly stochastic world, but those that do may in principle obtain hidden b_σ and c_σ effects that increase the payoff from cooperation. Note that when high-parasite states are very frequent, b_μ effects rise in power: when parasites constantly threaten the population, and helpers eliminate parasite pressure, mean fecundity is increased; in this situation, the environment is no longer stochastic (low ν). Incorporating volatility effects means that cooperation can still evolve when high-parasite states are not extremely frequent.

C2 | Galapagos mockingbirds

Empirical data are sorely lacking for testing the effects of b_σ . One encouraging dataset, however, comes from the cooperatively breeding Galapagos mockingbird (*Mimus parvulus*). Curry and Grant (1989) recorded demographic information over an 11-year period on Isla Genovesa (Ecuador). Helping is polymorphic in *M. parvulus* (occurring at 34% of nests), allowing a comparison of cooperative and non-cooperative nesting attempts.

Using the relevant summary statistics in Curry and Grant (1989) (based on 153 helper-present nests and 297 helper-absent nests), we estimate partial regressions of expected recipient fecundity against actor phenotype (helper or non-helper). We play the 'phenotypic gambit', and adopt a phenotypic (as opposed to genotype) variant of the stochastic Hamilton's rule. We therefore regress fitness components against the focal individual's phenotype P_x and the phenotype of a social partner P_y , and we assign the phenotypic values 0 and 1 for non-helping and helping respectively:

$$b_\mu = \beta_{E_\pi[w_x], P_y} = 0.3 \quad (C6)$$

Sample size varies considerably between years (from two helper-attended nests in 1984 to 33 in 1987). We cannot calculate b_σ directly from the data, therefore, as we cannot distinguish 'true' population variance from sampling variance. Instead, our approach is to ask whether a b_σ component can significantly change the estimated benefits of cooperation.

Galapagos mockingbirds inhabit a stochastic environment: Curry and Grant (1989) report a coefficient of variation in fledgling production of 0.92 across years, a proxy for the coefficient of variation in

average reproductive success ($v = \frac{\sigma_{\pi}[\bar{w}]}{\mathbb{E}_{\pi}[\bar{w}]}$) across states of nature. We assume that helping has no effect on the volatility of the helper's own reproductive success ($c_{\sigma} = 0$), and we consider the payoff for a sibling helper-at-the-nest ($r = 0.5$):

$$0.5(0.3 + 0.92b_{\sigma}) > c_{\mu} \quad (C7)$$

$$b_{\sigma} > 2.2c_{\mu} - 0.33 \quad (C8)$$

The cost of cooperation remains to be quantified in *M. parvulus*. If helpers suffer a loss of expected reproductive success exactly equal to the amount they increase the reproductive success of their recipients (*i.e.*, $c_{\mu} = b_{\mu} = 0.3$), then:

$$b_{\sigma} > 0.33 \quad (C9)$$

The regression of recipient fecundity volatility against actor phenotype ($\beta_{\rho_x \sigma_{\pi}[\bar{w}_x], P_y}$) must have a slope of at least -0.33 to justify altruism if $b_{\mu} - c_{\mu} = 0$. The upshot is that, in principle, b_{σ} can provide missing components of B in a sufficiently stochastic environment. Conclusively demonstrating altruistic bet-hedging in Galapagos mockingbirds will require (as with any empirical test of such models) elucidating how mockingbird-specific demography and population structure determines the relation between phenotype and the separate components of fitness.

Risk plays an important role in behavioural ecology. A stochastic approach is useful even if risk-management strategies affect the mean reproductive successes (Frank and Slatkin, 1990) of actors or their social partners (c_{μ} and b_{μ} respectively) without affecting the reproductive variation of either individual. In the social insects, for instance, the so-called 'Wenzel-Pickering effect' proposes that larger groups are able to reduce the variation in the supply of food for the brood, preventing shortfalls in which brood would otherwise die (Wenzel and Pickering, 1991; Poethke and Liebig, 2008). Whether the Wenzel-Pickering effect in real organisms derives its benefit from a consequent reduction in the variation of the production of offspring (Stevens *et al.*, 2007) ($b_{\sigma} > 0$), an increase in mean offspring production (Poethke and Liebig, 2008) ($b_{\mu} > 0$), or a combination of both ($b_{\mu} > 0$ and $b_{\sigma} > 0$) remains unknown. Similarly, in the mockingbirds, nesting attempts may be more 'risky' in a given state π : this risk may mean that only a proportion of nests will succeed. This more proximate form of 'risk' differing between years influences the payoffs from social behaviour in each type of year, and therefore can affect both expected fecundity and the volatility of fecundity across states. Classifying benefits accruing to different statistical parameters in the stochastic Hamilton's rule offers a framework for diagnosing these diverse forms of risk-management benefits and costs.

10.4 Appendix D: Multilevel Price equation

The multilevel Price equation (Price, 1972) is normally derived from the familiar Price equation by the following few lines (Okasha, 2004; Frank, 2012; Gardner, 2015c), which I provide here as background for Chapter 4. The familiar Price equation (Price, 1970) is as follows (see Chapter 1 Equation 1.2):

$$\Delta \bar{G} = \mathbb{C}_x \left(\frac{w_x}{\bar{w}}, G_x \right) + \mathbb{E}_x \left[\left(\frac{w_x}{\bar{w}} \right) \Delta G_x \right]$$

ΔG_x can be expanded in its own Price equation. Thus, if the entity x is composed of sub-entities j :

$$\Delta \bar{G} = \mathbb{C}_x \left(\frac{w_x}{\bar{w}}, G_x \right) + \mathbb{E}_x \left[\left(\frac{w_x}{\bar{w}} \right) \left(\mathbb{C}_j \left(\frac{w_j}{\bar{w}_j}, G_j \right) + \mathbb{E}_j \left[\left(\frac{w_j}{\bar{w}_j} \right) \Delta G_j \right] \right) \right]$$

Although we could continue generating new layers of the Price equation (*i.e.*, doing the same for ΔG_j , and so on), we can stop here by assuming the term $\mathbb{E}_j \left[\left(\frac{w_j}{\bar{w}_j} \right) \Delta G_j \right]$ to be approximately zero. The result is the normal way in which the multilevel Price equation is written. Given that $w_x = \bar{w}_j$ and $\bar{w} = \bar{w}_x$ we end up with a partition into selection between groups (here, x) and selection within groups (here, amongst the within-group entities j):

$$\Delta \bar{G} = \mathbb{C}_x \left(\frac{w_x}{\bar{w}}, G_x \right) + \mathbb{E}_x \left[\mathbb{C}_j \left(\frac{w_j}{\bar{w}}, G_j \right) \right]$$

In Chapter 4, the higher-level groups x I consider are demes (denoted d) and the lower level groups j are individuals (denoted i).

“Natural selection is a mechanism for generating an exceedingly high degree of improbability.”

R. A. Fisher, quoted in Edwards (2000)

“Mundane events acquired the raiment of symbolism, and this is what I concluded from them: ...that it is possible to spend a lifetime in a magellanic voyage around the trunk of a single tree. ...Humanity is exalted not because we are so far above other living creatures, but because knowing them well elevates the very concept of life.”

E. O. Wilson (1984)