

## REVIEW

## A conceptual model for the origin of worker behaviour and adaptation of eusociality

J. H. HUNT

Departments of Biology and Entomology, W. M. Keck Center for Behavioral Biology, North Carolina State University, Raleigh, NC, USA

### Keywords:

altruism;  
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 conceptual model;  
 exaptation;  
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*Polistes*.

### Abstract

In a model based on the wasp family Vespidae, the origin of worker behaviour, which constitutes the eusociality threshold, is not based on relatedness, therefore the origin of eusociality does not depend on inclusive fitness, and workers at the eusociality threshold are not altruistic. Instead, incipient workers and queens behave selfishly and are subject to direct natural selection. Beyond the eusociality threshold, relatedness enables 'soft inheritance' as the framework for initial adaptations of eusociality. At the threshold of irreversibility, queen and worker castes become fixed in advanced eusociality. Transitions from solitary to facultative, facultative to primitive, and primitive to advanced eusociality occur via exaptation, phenotypic accommodation and genetic assimilation. Multilevel selection characterizes the solitary to highly eusocial transition, but components of multilevel selection vary across levels of eusociality. Roles of behavioural flexibility and developmental plasticity in the evolutionary process equal or exceed those of genotype.

...one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory....

[I]t can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection. But I must pass over this preliminary difficulty. The great difficulty lies in the working ants differing from both the males and the fertile females in structure, as in the thorax, and in being destitute of wings and sometimes of eyes, and in instinct.....

I can see no great difficulty in any character becoming correlated with the sterile condition of certain members of insect-communities: the difficulty lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection.

This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end....Charles Darwin (1859)

Correspondence: James H. Hunt, Department of Entomology, North Carolina State University, Campus Box 7613, Raleigh, NC 27695, USA. Tel.: +1 919 513 2721; fax: +1 919 515 7746; e-mail: jim\_hunt@ncsu.edu

### Introduction

To learn and understand the evolution of animal sociality is a challenge that is Darwinian in heritage, daunting in complexity and subtlety, and a gateway to understanding fundamental biological processes. The challenge is particularly daunting in instances of eusociality, an advanced state of sociality found primarily in insects and characterized by reduced reproduction in workers that care for offspring other than their own (Wilson, 1971). For more than 40 years, eusociality has been studied and interpreted primarily within the paradigm of inclusive fitness (Hamilton, 1964a) and kin selection (Maynard Smith, 1964; West-Eberhard, 1975; Queller & Strassmann, 1998; Foster *et al.*, 2006; Hughes *et al.*, 2008) in which relatedness between worker altruist and reproductive beneficiaries is central to the origin of worker behaviour (Hamilton, 1964b). Recently, however, kin selection and inclusive fitness perspectives have been challenged as obscuring rather than clarifying an understanding of the worker/reproductive dichotomy (Wilson, 2005, 2008; Fletcher *et al.*, 2006; Wilson & Wilson, 2007; Nowak *et al.*, 2010). Prominently among these, Nowak *et al.* (2010) argue that 'standard natural selection theory' is adequate to address eusocial evolution and

that kin selection models are a subset of the more general natural selection model. This proposition by Nowak *et al.*, their strongly worded negative assessment of kin selection, and the socio-politics of high-profile publication that framed the paper's publication have drawn strong rebuttals (Wild *et al.*, 2010; Abbot *et al.*, 2011; Boomsma *et al.*, 2011; Gardner *et al.*, 2011; Herre & Wcislo, 2011; Regis Ferriere & Michod, 2011; Rousset & Lion, 2011; Strassmann *et al.*, 2011). The Nowak *et al.* publication, consisting of a main text and extensive supplementary material, is divisible into several parts: the harsh critique of kin selection and inclusive fitness theory, a mathematical model showing that kin selection models perform no better than and often not as well as general models for natural selection, a game-theoretic model for the origin of worker behaviour, and a five-stage conceptual model for the origin and adaptive evolution of animal societies. Published criticism of the Nowak *et al.* paper is directed at aspects of the paper other than the conceptual model.

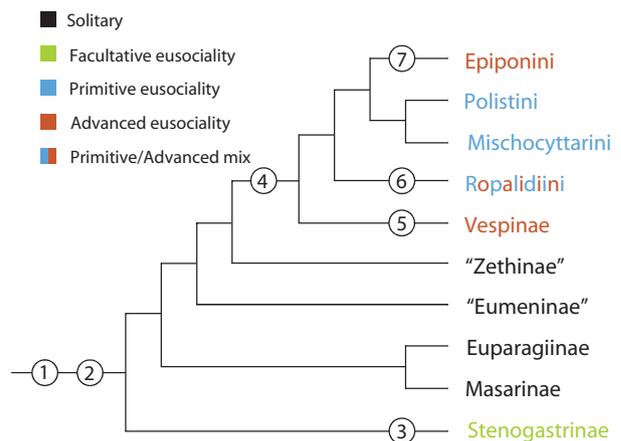
Conceptual models have played significant roles in evolutionary biology, with natural selection the *ne plus ultra*. Inclusive fitness is a conceptual model with its *modus operandi*, kin selection, captured in the famous inequality known as Hamilton's rule. Other conceptual models in social evolution include parent-offspring conflict (Trivers, 1974), reciprocal altruism (Trivers, 1971) and the prisoner's dilemma (Axelrod & Hamilton, 1981). All of these have served as contexts for modelling and empirical studies.

This paper presents a conceptual model for the origin of worker behaviour and adaptation of eusociality as exemplified by the wasp family Vespidae. The model partitions the solitary to advanced eusocial transition into incremental steps, with each step framed by a mode of evolution: exaptation, phenotypic accommodation, and genetic assimilation. Implications for broader evolutionary questions are discussed. Importantly, it will be argued that the origin of worker behaviour and the adaptation of eusociality are discrete phenomena wherein the origin of worker behaviour is not based on relatedness between workers and the beneficiaries of their work, whereas adaptations of eusociality require it. Failure to distinguish the origin of worker behaviour from subsequent adaptation of eusociality underlies much of the contentiousness that currently characterizes evolutionary studies of eusociality.

## Background

### Phylogeny and trait mapping

A well-supported four-gene molecular phylogeny (Hines *et al.*, 2007) gives the distribution of solitary, facultatively eusocial, primitively eusocial and advanced eusocial taxa in the family Vespidae (Fig. 1). Numbers on branches mark the first appearance of morphological, behavioural and life history traits of relevance to eusociality. Trait



**Fig. 1** Subfamilies and tribes of Vespidae from a four-gene molecular phylogeny. 'Eumeninae' and 'Zethinae' taken together have traditionally been considered to comprise the subfamily Eumeninae. Subfamily Polistinae here is subdivided into its four tribes. Traits salient to sociality are placed on numbered branches where they first appear. 1: (Suborder Aculeata) Emergence from pupation with undeveloped ovaries, constraint by the narrow wasp waist to obtain nourishment for ovarian development and oogenesis from liquid and slurry sources, ova large and yolky, ova produced sequentially, larvae ingest intact prey, haplodiploidy, monandry? 2: (Family Vespidae) Nest construction, nest cells constructed and provisioned sequentially, one offspring per nest cell, larvae mass provisioned with intact prey, monandry? 3: Nests of multiple cells constructed sequentially or simultaneously, nest cells often arranged irregularly, multiple larvae provisioned simultaneously, larvae progressively provisioned with minced or lightly kneaded prey items, provisioning indirect (not mouth to mouth), adults lap a clear liquid from the ventral surface of large larvae. 4: Nests of multiple cells constructed simultaneously in a honeycomb-like single plane, multiple larvae provisioned simultaneously, provisioning direct (mouth to mouth) with thoroughly kneaded prey, adults drink haemolymph from prey items and nutrient-rich saliva directly from the mouths of large larvae. 5: Discrete worker and queen behavioural and physiological castes, life cycle includes single-foundress solitary phase. 6: Some as at branch 4. Some with discrete worker and queen behavioural, physiological and morphological castes, perennial life cycle, new colonies founded by swarming. 7: Discrete worker and queen behavioural and physiological castes often accompanied by morphological difference, perennial life cycle, new colonies founded by swarming.

group 1 contains traits of the order Hymenoptera and its suborder Aculeata, which is comprised of all stinging Hymenoptera. Trait group 2 contains traits common to all Vespidae. Higher numbers denote traits that are more narrowly distributed and found only in the eusocial taxa they subtend. The salience of particular traits to eusociality corresponds to descending numerical order. Higher numbers on each branch denote traits of high salience, and lower numbered traits are of lower salience, with traits at numbers 1 and 2 having the lowest salience to sociality (Hunt, 1999). The following discussion and analysis apply only to female wasps, as only females construct nests, provision larvae and have worker and reproductive castes.

### Grades of sociality

The majority of species in Vespidae are solitary. There are three grades of eusociality: facultative, primitive and advanced. These categories are well established in entomological literature (Batra, 1966; Michener, 1974; Crespi & Yanega, 1995), but all species, of course, have successful life history strategies. No grade of social organization is an imperfect manifestation of another. However, these grades of social organization serve to conceptually envision how life history strategies at one grade could have evolved from ancestry at the earlier grade. Each of the four grades is characterized by particular features.

### Solitary

The majority of adult female solitary wasps have no inter-individual contact outside the context of mating. Most nest alone; some nest in aggregations in suitable habitats; a very few species are communal and raise offspring independently in a shared nest at which inter-female interactions occur. Solitary vespids construct one nest cell at a time, fill the cell with prey insects, close the cell and proceed to construct the next cell. Some leave the cell open and introduce prey items progressively. Some of these crush or knead the prey items before placing them in the cell. Solitary vespids in aseasonal tropics can have year-round reproduction (Fig. 2a). Those in seasonal environments typically have one generation annually (Fig. 2b). Some have bivoltine life cycles in which there are two generations per favourable season. The first generation passes the entire life cycle in a single season, and the second generation completes larval development but then passes the unfavourable season as a last-instar larva in developmental diapause prior to completing metamorphosis, emerging from pupation, and reproducing in the ensuing favourable season (Fig. 2c). Some solitary Vespidae are partially bivoltine, a life history pattern in which adults of the first generation have lifetimes sufficiently long to contribute offspring to both generations of a single season (Fig. 2d). Solitary species produce from few to a modest number of offspring. For life history details on solitary Vespidae, see Cowan (1991), O'Neill (2001) and Hunt (2007).

### Facultative eusociality

The distinguishing feature of facultative eusociality is absence of clear delineation between reproductives and nonreproductives. All females are morphologically similar and have the capacity to produce their own offspring, and many do so. Some individuals live their lifetimes as nonreproducing workers, but this is believed to reflect death before reproduction rather than inability to reproduce (Field *et al.*, 1999; Shreeves & Field, 2002). There are diverse possibilities for direct reproduction: to found a

new nest, usurp an existing nest, or join an alien colony (Turillazzi, 1991). A female may also remain at her natal nest and ascend to the alpha rank in a dominance hierarchy (Hansell *et al.*, 1982). Colonies can have low intra-colony relatedness due to high usurpation rates (Strassmann *et al.*, 1994; Field *et al.*, 2000) or queen turnover (Landi *et al.*, 2003). New nests begin with a single foundress or small group of foundresses, a mode called independent founding.

Worker behaviour at the natal nest is often a transient phase (Field *et al.*, 1999) prior to producing a modest number of offspring, even with the aid of workers. Most species have small colonies; some species have nesting aggregations in suitable habitats. Adults interact on the nest. Larvae are progressively provisioned using minced prey items that are placed near a larva's mouthparts. Adults lap a clear liquid from the ventral surface of larger larvae. There is no mouth-to-mouth interaction between adults and larvae.

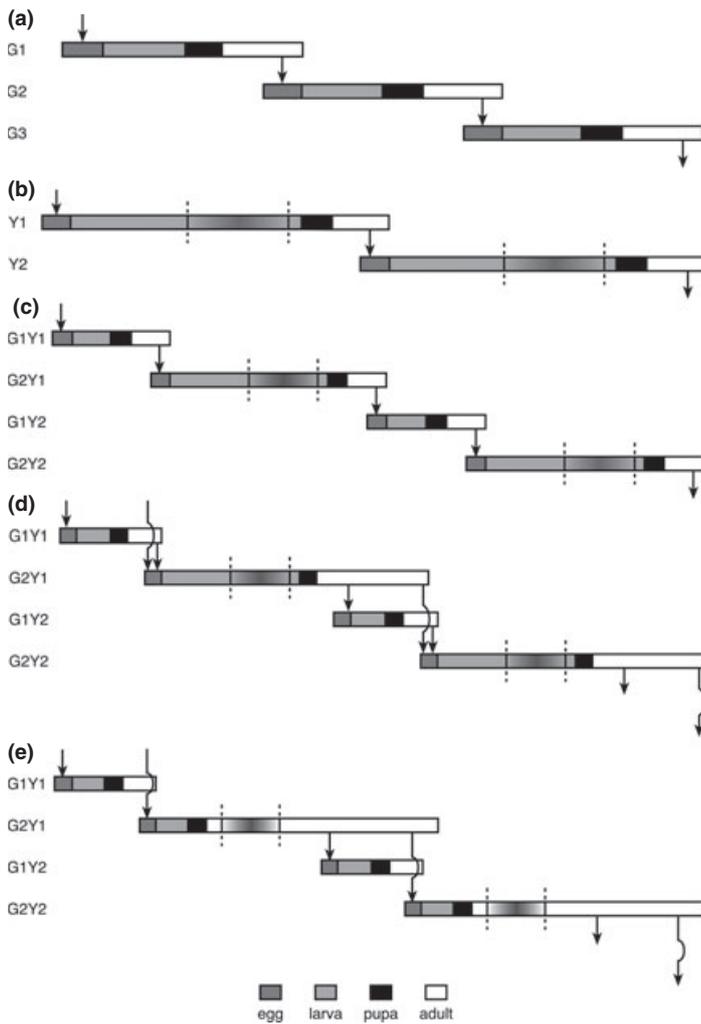
Facultatively eusocial Vespidae occur only in the subfamily Stenogastrinae. For life history details and introductions to literature on Stenogastrinae, see Turillazzi (1991, 1996) and Hunt (2007).

### Primitive eusociality

Primitive eusociality is characterized by reproductive queens and nonreproductive workers that are morphologically similar and whose reproductive status is typically lifelong, although some workers may become colony queens via queen replacement (Strassmann & Meyer, 1983) or independent nesting (Tibbetts, 2007), and sub-dominants of queen co-foundress associations may become workers (Pardi, 1948; West, 1967; West Eberhard, 1969). All primitively eusocial vespids are independent founding wasps.

Primitively eusocial vespids in aseasonal tropics can found nests at any time of the year (Yamane, 1996). Those in seasonal environments have annual colony cycles with fundamental similarities to those of partially bivoltine solitary wasps but with important differences (Hunt & Amdam, 2005). Offspring that correspond to the first generation of bivoltine solitary wasps work at their natal nest, die at the end of their natal season and do not reproduce. Offspring that correspond to the second generation of bivoltine solitary wasps become adults in their natal season, do not work at the natal nest and then pass the unfavourable season in quiescence. In the following favourable season, these wasps emerge from quiescence, feed at flowers and activate their ovaries, found nests to initiate the next generation and become queens that lay eggs for both generations of that reproductive season (Fig. 2e).

Primitively eusocial vespids have a high level of inter-individual interactions at the nest. Adults feed thoroughly kneaded prey items directly to larvae, and they drink saliva produced by larvae. Adults form dominance hierarchies



**Fig. 2** Life cycles of solitary and primitively eusocial Vespidae. Each horizontal bar represents life spans of cohorts. Each life span is divided sequentially into egg, larva, pupa and adult. Vertical arrows denote oviposition. G = generation, Y = year, thus G1Y2 = first generation of year two. Shaded regions between vertical dotted bars signify unfavourable periods in a seasonal environment. (a) Solitary wasps in aseasonal environments with uninterrupted sequential broods. (b) Solitary wasps in a seasonal environment and one generation per year. (c) Bivoltine solitary wasps with two discrete generations per year. (d) Partially bivoltine solitary wasps with oviposition by the first generation continuing into the second generation. (e) Primitively eusocial wasps. In primitively eusocial wasps, metamorphosis is passed prior to the unfavourable season; wasps with phenotypes of first-generation solitary wasps do not oviposit, and they die prior to the unfavourable season. Wasps with phenotypes of the second generation of solitary wasps pass the unfavourable season as adults and then lay eggs of both generations in the following favourable season.

and transfer food among individuals. Larval feeding, drinking saliva, and inter-adult food transfers involve direct mouth-to-mouth contact. Primitively eusocial vespids can produce moderate numbers of offspring, reaching hundreds in the most successful colonies.

An extensive literature exists on primitively eusocial wasps, especially the one on the genus *Polistes*. Reviews and compendia of the literature include Gadagkar (1991), Reeve (1991), Turillazzi & West-Eberhard (1996), O'Donnell (1998) and Hunt (2007).

### Advanced eusociality

Advanced eusociality is characterized by discrete non-reproducing worker and reproducing queen castes, often accompanied by morphological difference. Advanced eusociality occurs in two forms (thereby illustrating limitations and confusions caused by the currently used classification scheme for insect sociality). Independent founding with morphologically different worker and

queen castes occurs in one species of Polistinae (Wenzel, 1992) and three of four genera of Vespinae. Three lineages of Polistinae have swarm founding in which swarms that contain multiple egg-laying queens and a larger number of workers move in concert to found a new nest. The vespine genus *Provespa* founds new colonies when a swarm of workers moves with a single queen to establish a new nest. Inter-individual trophic interactions in advanced eusocial forms are the same as for primitively eusocial forms. Numbers of offspring in advanced eusocial species with multiple queens can reach into the thousands or hundreds of thousands or even millions (Zucchi *et al.*, 1995), although reproductive success for swarm-founding species would be measured by number of daughter colonies rather than number of reproductive offspring.

Vespinae have been treated extensively in the literature (Edwards, 1980; Matsuura & Yamane, 1990; Greene, 1991; Matsuura, 1991). Introductions to the literature on swarm-founding polistines can be found in Jeanne (1991) and Hunt (2007).

### Key commonalities and differences

All adult aculeate (stinging) Hymenoptera can feed only on liquids or slurries (Hunt, 2007), and all emerge from pupation with undeveloped ovaries (Fig. 1, trait group 1). Therefore, females of all Vespidae must feed in order to develop their ovaries, and nourishment must be proteinaceous in addition to being a source of energy. Solitary vespids emerge from pupation and feed on amino-acid rich flower nectar (Baker & Baker 1973) prior to ovary development and nesting. Some facultatively eusocial females do the same, but many linger at their natal nest prior to reproducing. Primitively eusocial wasps follow one of three pathways. A few proceed directly to nest founding and reproduction (Strassmann, 1981; Page *et al.*, 1989), but most do not. Some remain and work at the natal nest, and these do not reproduce. In seasonal environments, at least, others, called gynes, do not work or reproduce in their natal season but instead initiate ovary development and reproduction as nest foundresses in the ensuing favourable season. Gynes of independent founding Vespinae follow the same path as gynes of Polistinae. The time lag between emergence and ovarian activity for the multiple queens of polistine swarm founders is unknown, but newly emerged pre-queens could enter directly into ovary activation and reproduction in a pattern of changing queen numbers called cyclical oligogyny (Gastreich *et al.*, 1993).

Single foundresses of facultatively and primitively eusocial polistines and of independent founding vespines are *de facto* solitary wasps, but unlike solitary vespids they add open cells to their nest and care simultaneously for an increasing number of larvae. Offspring emerge into contexts where at least the foundress is present or, more often, where multiple nestmates are present. In particular, wasps emerge onto a nest containing multiple larvae that are being provisioned by the foundress and/or workers using thoroughly kneaded prey items from which the provisioning adult extracts proteinaceous haemolymph for its own nourishment (Hunt, 1984). Adults of primitively eusocial and advanced eusocial species also drink a nutritious saliva from their larvae (Hunt *et al.*, 1982, 1987). Swarm founders have the same trophic interactions as primitively eusocial wasps, and the colony cycle never includes a solitary phase.

### The model

Based on the preceding natural history information, Fig. 3 presents a conceptual model for the origin of worker behaviour and the evolution of eusociality in Vespidae. The model contains four grades of social organization, three modes of evolutionary change, two thresholds, and a gradient of selection. Maternal behaviours lie to the right of the vertical dotted line. Allomaternal behaviours, that is, those directed to offspring not the caregiver's own, lie to the left of the

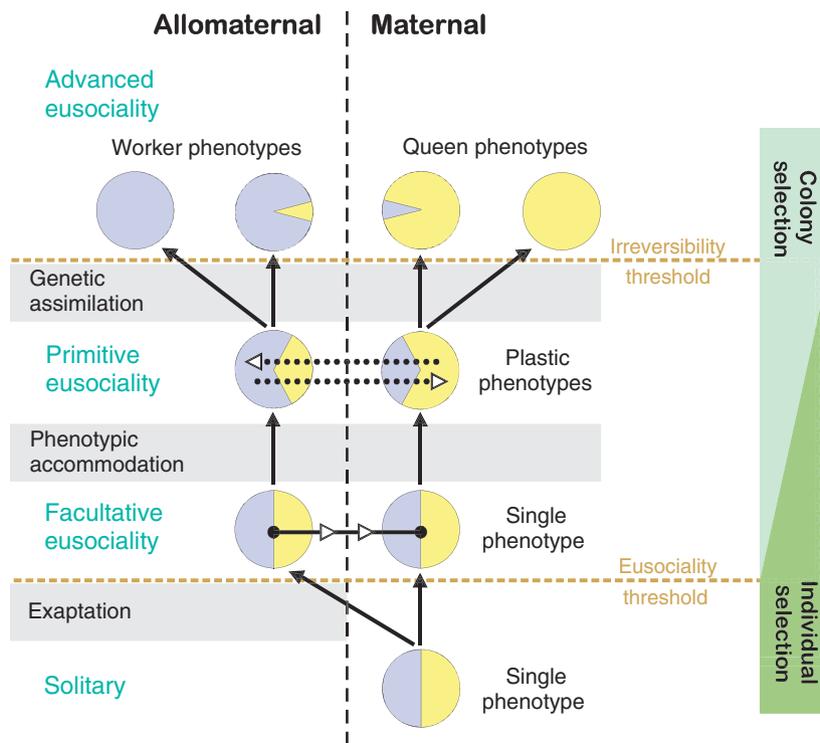
dotted line. Solitary females and queens of eusocial species have maternal status. Workers of eusocial species have allomaternal status. Each circle denotes an adult phenotype. For each phenotype, reproductive activities are divided into two parts. The darker colour represents nonovarian activities such as nest building, foraging and nest defence; the lighter colour represents ovary activation and oviposition. Vertical arrows denote evolutionary phenotype transitions rather than reproductive descent.

Solitary wasps have a single reproductive phenotype and exhibit all aspects of maternal behaviour. Facultatively eusocial wasps have a single reproductive phenotype that is sometimes expressed maternally after emergence, but in other instances maternal behaviour is expressed following a period of allomaternal care on the natal nest (Fig. 3 horizontal solid arrow). All primitively eusocial wasps can express maternal behaviours, and maternal and allomaternal phenotypes can transition from one to the other (Fig. 3 dotted arrows), although in most instances the phenotypes are constant throughout a wasp's lifetime. Advanced eusocial wasps have fixed maternal and allomaternal phenotypes.

In the transition from facultative to primitive eusociality, maternal and allomaternal roles become more constant, and the working/ovarian aspects of the ancestral maternal phenotype are expressed at different frequencies. However, because transition between maternal and allomaternal phenotypes is possible, newly emerged allomaternal caregivers have finite, nonzero capacity for direct reproduction. In the transition from primitive to advanced eusociality, the working/ovarian aspects of maternal and allomaternal phenotypes are discrete or nearly so and become fixed phenotypes. Workers of independent Vespinae, although morphologically distinct from queens, retain some reproductive capacity in that they can produce male offspring if their queen should die. Workers and queens of advanced eusocial polistines have discrete phenotypes.

The scenario is marked by two thresholds, indicated by the horizontal dashed lines. The appearance of allomaternal care is synonymous with the appearance of worker behaviour, which is the threshold of eusociality. The appearance of discrete queen and worker castes is a threshold of irreversibility, a 'point of no return' (Wilson & Hölldobler, 2005) at which change from the highly eusocial state is no longer possible. At and beyond the threshold of irreversibility, specialized queens and workers are divergent but not dissociable, and neither form can reproduce on its own (West-Eberhard, 1992).

The nature of selection is a gradient shown by the vertical bar at right. In solitary wasps, natural selection acts on individuals. Species with fixed castes can respond only to selection at the colony level. Between those poles, selection would be a mix of individual and colony selection, constituting multilevel selection (Sober & Wilson, 1998; Okasha, 2006; Wilson & Wilson, 2007,



**Fig. 3** Model for the origin of worker behaviour and evolution of eusociality in paper wasps. Allomaternal (left) and maternal (right) females are divided by the vertical dotted line. Circles encompass maternal behaviour divided into two components. The dark colour represents foraging, larval care and nest construction. The light colour represents ovary activity and oviposition. All solitary females (bottom) have a single morphology and exhibit the full spectrum of maternal behaviours. Facultatively eusocial females have a single morphology, but some exhibit allomaternal behaviour as a transient phase prior to becoming maternal (horizontal solid arrow). Primitively eusocial females have a single morphology, and most have lifelong maternal or allomaternal status, although transitions between adult castes can occur (horizontal dotted arrows). Among advanced eusocial species, queens of Vespinae work as solitary wasps prior to worker emergence, and workers retain the ability to lay unfertilized eggs if the queen should die (inner circles). In polistine wasps with morphologically distinct queen/worker castes and in swarm-founding wasps, the capacity for expressing alternate reproductive phenotypes has been lost and queen/worker castes are fixed (outer circles). Transitions between grades of sociality are shown as horizontal shaded bars. The transition from solitary to facultatively eusociality occurs via exaptation; that from facultative to primitive eusociality via phenotypic accommodation; that from primitively to advanced eusociality via genetic assimilation. The vertical bar at right illustrates the pattern of selection. Prior to and at the eusociality threshold, selection would act on individuals. At and after the irreversibility threshold, selection would act primarily on colonies. Between the thresholds selection would be a mix of individual, kin-group and colony selection.

2008; Wade *et al.*, 2010), although the mix need not be linear as shown.

There are three modes of evolutionary transition between grades of social organization. The solitary to facultatively eusocial transition occurs via exaptation in which there is no change in maternal phenotype, only the expression of maternal behaviour in the novel context of allomaternal care. The facultatively to primitively eusocial transition occurs via phenotypic accommodation (West-Eberhard, 2003) in which the consistent repetition of caste-like behaviours across generations enables selection to act in a context of nongenetic mechanisms (Bonduriansky & Day, 2009). The constancy of phenotypic accommodation provides context for fixation of regulatory mechanisms or novel alleles via genetic assimilation (Waddington, 1953, 1961;

West-Eberhard, 2003), ultimately marking the transition from primitive to advanced eusociality.

### Three questions

Three questions arise with regard to worker behaviour: (1) What causes newly emerged wasps to remain at their natal nest rather than depart? (2) What induces them to undertake allomaternal larval care? (3) What constrains them from independent reproduction?

**1** Polistini in seasonal environments and Vespinae have annual life cycles that include a solitary phase in which future reproductives, the gynes, are reared in one nesting season and pass the unfavourable season in behavioural quiescence prior to founding nests in the following season. The hypothesis that gynes of *Polistes*

*metricus* emerge from pupation in reproductive diapause before winter quiescence (Hunt & Amdam, 2005) is supported by developmental and physiological data from adults (O'Donnell, 1998; Toth *et al.*, 2009) and larvae (Hunt *et al.*, 2007) and differential expression of diapause related genes and peptides/proteins in larvae (Hunt *et al.*, 2010). Because diapause is a binary state, non-gynes must have active reproductive physiology. Indeed, worker *Polistes* wasps can develop their ovaries and lay eggs in nature (Tibbetts, 2007) and when experimentally given an opportunity to do so (Bohm, 1972; Mead *et al.*, 1995; Tibbetts *et al.*, 2011). This active reproductive physiology in newly emerged non-gynes leads them to seek proteinaceous nourishment for ovarian development. In eusocial Vespidae, the natal nest is a locus of protein-rich nourishment in the form of saliva produced by larvae and incompletely kneaded prey items brought to the nest by the foundress or nestmate workers. These nourishment sources entice newly emerged wasps to remain at their natal nest (Roubaud, 1916). Thus, the answer to question 1 is that newly emerged facultatively eusocial wasps and primitively eusocial wasps corresponding to the first generation of bivoltine solitary wasps require proteinaceous nourishment for ovary development. The nest with its larvae and foraging adults has rich resources, and the newly emerged wasps remain at their natal nest to obtain them.

- 2 Maternal behaviour occurs only in a context of active reproductive physiology. Newly emerged wasps with active reproductive physiology that remain at their natal nest to obtain nourishment would encounter cues from growing larvae and from partially completed nest cells that are the releaser cues to which maternal wasps primed by active reproductive physiology respond with brood care and nest construction behaviours. However, because the nest and larvae are not their own, behaviours are expressed in identical form to maternal behaviours but directed allomaternally to a nest and larvae not their own. Thus, the answer to question 2 is that because maternal behaviour is a tightly coordinated suite of physiology and stimulus-response behaviours, wasps primed by active reproductive physiology will respond to releaser cues by performing maternal behaviour even if the nest and larvae are not their own.
- 3 Foundresses (the previous year's gynes) of the temperate zone paper wasp *P. metricus* have enlarged ovaries by the time they found nests, but their ovary size diminishes when they undertake larval care (Haggard & Gamboa, 1980). Nests begin with a single cell containing an egg, and nest cells and eggs are added serially until nest size remains at a plateau prior to emergence of the first offspring (Figure 3 in Hunt & Dove, 2002). This plateau coincides with the foundress' diminished ovary size, which can reasonably be attributed to the energetic costs of solitary brood care for the colony that

contains increasing numbers of large larvae with correspondingly increasing food demands. As the first newly emerged wasps enter into allomaternal behaviour in the context of seeking their own proteinaceous nourishment, they would immediately encounter a level of nourishment demand from the number and size of larvae in the nest that had been sufficiently large to diminish the foundress' ovaries. Energy demand transferred from the foundress to newly emerged reproductively ready wasps with undeveloped ovaries would be sufficient to constrain their ovarian development (Marchal, 1897). This transfer of larval care would enable ovary reactivation by the foundress, now queen, whose ovaries reach a level of development greater than when she was a foundress. Nest size and the number of larvae begin to increase rapidly (Figure 3 in Hunt & Dove, 2002), causing the energy demand on working, nutrient-seeking wasps to remain high and continue to constrain their ovarian development.

#### Exaptation, behavioural flexibility, phenotypic accommodation and genetic assimilation

Environmentally induced changes in behaviour and development provide foundations for adaptive evolution throughout the plant and animal kingdoms (West-Eberhard, 1989, 2003; Schlichting & Pigliucci, 1998; Bonduriansky & Day, 2009; Pigliucci, 2010). Nonetheless, the evolutionary significance of environmentally induced adaptive evolution has for decades been rejected by most evolutionary biologists (West-Eberhard, 2003; Pigliucci *et al.*, 2006) and has been characterized as tinged with Lamarckianism (Bonduriansky & Day, 2009) or a 'source of nuisance, not of significant micro- and macro-evolutionary change' (Pigliucci & Müller, 2010a). Recently, however, the evolutionary role of environmentally induced phenotypic variation is gaining increasing recognition (Bell & Robinson, 2011) and study (Moczek, 2008, 2010; Fusco & Minelli, 2010; Minelli & Fusco, 2010; Beldade *et al.*, 2011).

Facultatively eusocial Stenogastrinae achieve maternal status via behavioural flexibility – their ability as individuals to adaptively respond to a variety of reproductive opportunities. The reproductive/worker dichotomy of primitively eusocial Polistinae encompasses two phenomena. The assortment of co-foundresses into reproductive and worker roles via dominance interactions reflects flexibility of the behavioural phenotype. Developmental divergence onto pathways leading to worker and future foundress phenotypes (generations 1 and 2 of Fig. 2e; Hunt & Amdam, 2005) occurs via phenotypic accommodation – 'adaptive mutual adjustment among variable parts [of an individual] during development without genetic change' (West-Eberhard, 2003:51). '[W]ithout genetic change' implies without change in genotype, because quantitative differences in gene expression of single genotypes during larval develop-

ment contribute significantly to the two adult phenotypes (Hunt *et al.*, 2007, 2010). Dichotomous expression of reproductive and worker castes in advanced eusociality is achieved via genetic assimilation (Waddington, 1953, 1961; West-Eberhard, 2003; Pigliucci *et al.*, 2006) in which regulatory pathways, and perhaps novel alleles, become fixed in a population such that caste phenotypes are expressed in the absence of the environmental cues that affect phenotype outcomes of primitive eusociality.

It should be highlighted that the initiation of eusociality in the model is marked by invariance in maternal behaviour. Any deviation in performance would be subject to strong negative selection. At the origin of allomaternal care, that is, at the eusociality threshold, there is no change in maternal behaviour, only a novel context in which maternal behaviours are performed. In that context, if allomaternal care is directed to larvae related to the allomother, then the allomaternal care would be adaptive even though it was not itself an adaptation that resulted from natural selection (Rosenberg & McShea, 2008). Thus, allomaternal care at the threshold of eusociality meets the concept of an exaptation (Gould & Vrba, 1982) that plays a novel 'causal role function' prior to any 'selected effects aetiology' (Rosenberg & McShea, 2008). Exaptation is a widespread enabler of evolutionary change (Dennett, 1996). The more familiar term 'pre-adaptation' can be substituted for exaptation without changing the conceptual content of the model presented here; however, pre-adaptation is less precise in describing the phenomenon and has a tinge of teleology.

Colony life with maternal and allomaternal caregivers enables relaxed selection on correlated performance frequency of the two components of maternal care illustrated in Fig. 3. Increased foraging, brood care and nest construction by allomaternal wasps can dovetail with decreased performance of those behaviours by maternal wasps. Thus, although maternal behaviour is a tightly correlated and strongly selected suite of traits in solitary wasps, context-dependent exposure of underlying potential for behavioural flexibility and developmental pathway divergence enables novel expression frequencies of those traits in contexts of synchronous allomaternal and maternal care. This sets the stage for 'soft inheritance' (Mayr, 1982) in which new variations that result from environmental effects (in this instance the behavioural environment) are transmitted to the next generation (Mayr, 1982; Jablonka & Lamb, 2010). Soft inheritance of different expression frequencies of the components of maternal care sets the stage for quantitative differences in gene expression. Adaptive quantitative changes of gene expression characterize genetic accommodation – 'gene-frequency (evolutionary) change due to selection on variation in the regulation, form, or side effects of the novel trait in the subpopulation of individuals that express the trait' (West-Eberhard, 2003:140). Genetic accommodation is a process

that may pervade organic evolution (West-Eberhard, 2003; Moczek, 2008). The concept of genetic accommodation contains within it West-Eberhard's more focused concept of phenotypic accommodation. Phenotypic accommodation closely captures the behavioural flexibility and developmental divergence that characterize primitive eusociality in the model presented here.

Environmentally induced quantitative variants of regulatory pathways could respond to selection via genetic accommodation and increase in frequency in the population even if initially rare. Another possibility is exposure via phenotypic accommodation of 'deep homology' (Shubin *et al.*, 2009), a 'conserved core process' (Kirschner & Gerhart, 2010), in the insect groundplan of physiological and developmental pathways that could lead to the morphologically and physiologically different castes of highly eusocial hymenopterans (Wheeler, 1986; Hoffman & Goodisman, 2007). For example, in the highly eusocial Oriental hornet, *Vespa orientalis*, experimental transfer of larvae between worker and queen nest cells has shown that developmental pathways are labile in early development but fixed onto either worker or queen pathways following the moult from third to fourth instar (Ishay, 1975). This developmental divergence is analogous to the developmental divergence leading to worker and queen honey bees (Linksvayer *et al.*, 2011), and in both the hornet and honey bee, the caste divergence could reflect context-dependent expression of homologous regulatory pathways in the ground plan of ancestral taxa. The final step of the evolutionary scenario is fixed expression of caste phenotype differences. In addition to population-wide fixation of gene expression pathways, it is possible that novel alleles that might underlie or enhance caste phenotype differences could respond to selection and be incorporated into the gene pool, although no alleles 'for' eusociality (Kaplan & Pigliucci, 2001) have yet been discovered.

The scenario as a whole exemplifies the Baldwin (1896, 1902) effect (Waddington, 1942; West-Eberhard, 2003), in which organic selection precedes evolutionary change (Dennett, 1996; West-Eberhard, 2003). Every step in the scenario, from the initial exaptation to highly eusocial, would occur by incremental steps in which small variations in simple algorithms would respond to selection to yield new phenotypes (Dennett, 1996).

### The origin of castes

Differential gene expression and protein abundance between workers and gynes of the temperate zone primitively eusocial *P. metricus* (Toth *et al.*, 2007, 2010) and corresponding differences between worker-destined and gyne-destined larvae (Hunt *et al.*, 2003, 2007) show that divergence of a single genotype into reproductive and nonreproductive phenotypes could initially have been based on quantitative changes of gene expression and protein abundance (Hunt *et al.*, 2010). These studies

have shown significant differences in genes and peptides/proteins associated with insulin signalling pathways and storage proteins, which is evidence that caste differences in *P. metricus* are affected by nutritional inequities. These findings are concordant with the hypothesis that workers and gynes of *P. metricus* reflect the underlying physiology of the two generations of a bivoltine solitary wasp, with the second generation – the gynes in *P. metricus* – in ovarian diapause (Hunt & Amdam, 2005; Hunt *et al.*, 2007). Diapause is widespread in Insecta and is probably a deep homology in the insect groundplan (Hahn & Denlinger, 2011).

Indicators of ovarian diapause are not apparent in the tropical, primitively eusocial *Polistes canadensis* (Sumner *et al.*, 2006; cf. Giray *et al.*, 2005), which lives in relatively constant environments. For *Polistes* in seasonal environments, including tropical wet-dry seasonality, gynes in ovarian diapause that pass the unfavourable season are analogous to seeds in a seed bank that are available to start the next generation of an annual plant species (Schaal & Leverich, 1981; Hunt, 2007). Thus, maximization of gyne production would confer high fitness, and traits of individuals and colonies that favour it would be selectively advantageous. Given that nesting behaviour is a requisite of eusocial evolution (West-Eberhard & Hanson, 1995; Hansell, 1996), possibilities for response to selection include changes in nest architecture (Karsai & Penzes, 1993, 1998, 2000) leading to the context for simultaneous brood provisioning that in turn provides the context for allomaternal care, enhancement of the volume and nutrient content of larval saliva (Hunt, 1988), and protogyny of the only sex that engages in brood care (Alexander, 1974; Hunt, 1999).

Characteristics of larval saliva and its larva to adult exchange exemplify a possible evolutionary history for one component of the overall scenario. The saliva may at first have been a lubricant for the relatively dry provision mass that remains after the provisioning female has extracted haemolymph of a prey item during the thorough kneading that characterizes primitively eusocial and advanced eusocial wasps (Hunt, 1984). (Male *Polistes* sometimes extract haemolymph for self-nourishment via extended kneading of a prey item brought to the nest by a forager female [Hunt & Noonan, 1979].) At the same time, however, *Polistes* wasps are well known to cannibalize larvae both early in the colony cycle (Hunt, 1991) and at its end (Deleurance, 1955). Any resemblance of larval saliva to amino acid-containing floral nectar (Baker & Baker, 1973), however scant, could have led adults to intentionally seek it as liquid nourishment (Hunt, 2007), and it could also have led the larva to secrete it to forestall cannibalism (Hunt, 1988). Selection favouring nutrient-rich saliva could place a cost on larval development, leading to adult females that subsequently emerge to have characteristics of the first generation of a bivoltine solitary wasp (Hunt & Amdam, 2005; Hunt *et al.*, 2007,

2010). When these females engage in allomaternal care, subsequent larvae become better nourished and may secrete less or less-rich saliva prior to emerging with traits of the diapause generation of a bivoltine solitary wasp. A further refinement of the interaction could be enhancement of the volume of saliva, which is accomplished by adults foraging for nectar that they then feed to larvae. The scenario thus progresses from individual selection favouring traits specific to either larvae or adults to selection favouring traits reflecting their interdependence in colony contexts in which an allomaternal caste is present.

### Relatedness at the eusociality threshold

Allomaternal care in Vespidae is directed to nonrelatives in cases of nest usurpation (Klahn, 1988; Nonacs & Reeve, 1995), nest inheritance (Leadbeater *et al.*, 2011), conspecific adoption of abandoned nests (Nonacs & Reeve, 1993, 1995), interspecific adoption of abandoned nests (Hunt, 2009), nest switching (Nonacs & Reeve, 1995), social parasitism (Cervo & Dani, 1996), unrelated conspecific co-foundress associations (Queller *et al.*, 2000; Leadbeater *et al.*, 2011), and interspecific co-foundress associations (Hunt & Gamboa, 1978; O'Donnell & Jeanne, 1991). It is identical in all these cases to allomaternal care directed to relatives by wasps at their natal nest. Therefore, even though allomaternal care is most commonly directed to related larvae at a worker's natal nest and establishes the context for the adaptation of eusociality, relatedness *qua* relatedness plays no role in the expression of allomaternal care. By direct inference, relatedness *qua* relatedness could have played no role in the initial expression of allomaternal care at the origin of eusociality. In the initial, transitory expression of maternal behaviour in an allomaternal way as envisioned in the model presented here, workers would have benefited directly by obtaining nourishment with which to depart their natal nest and initiate independent reproduction, whereas the mother of larvae being cared for would have benefited during their presence at the nest by receiving their aid in rearing her larvae. In neither case is relatedness between the two required in order for each to receive benefit.

In an independent line of thought, it has been proposed that close relatedness arises after eusociality originates in groups that share an allele for helping behaviour that is not correlated with overall relatedness among group members (Wilson & Hölldobler, 2005; Wilson & Wilson, 2007, 2008; Nowak *et al.*, 2010). As argued here, however, available evidence strongly indicates that although the origin of worker behaviour does not depend on relatedness between allomother(s) and the larvae that they care for, any subsequent adaptation of eusociality requires it. The proposition that relatedness arises following the evolution of eusociality is untenable.

### Monogyny at the eusociality threshold

Eusocial adaptations always evolve in a mother–daughter context. Even co-foundress associations of facultatively and primitively eusocial wasps are considered to be eusocial because of the presence of worker offspring of the queen rather than the presence of same-generation working subordinates. Questions have existed in the past, however, as to whether eusociality originated in single-female or multiple-female nesting situations. The model presented here is based on single-foundress colonies consisting of a mother and offspring – a family structure called subsocial (Michener, 1974) that has long been proposed to be the fundamental framework for eusocial evolution in Hymenoptera (Wheeler, 1928; Evans, 1958; Alexander, 1974; Alexander *et al.*, 1991). Colonies of nest-sharing same-generation adult females with behavioural castes are called semisocial (Michener, 1974), and a semisocial route to eusociality in Vespidae has been most strongly advocated by West-Eberhard (West, 1967; West-Eberhard, 1975, 1978, 1987b). The model, called the ‘polygynous family hypothesis’ (West-Eberhard, 1978), presumes groups of simultaneously ovipositing females in a dominant/subdominant framework among which subdominants orphan their own larvae and assume a worker role whereas dominants adopt abandoned larvae and assume a queen role. The proposed basis of the polygynous family hypothesis is the ‘ovarian ground plan hypothesis’ (West-Eberhard, 1987b), which posits a cycle marked by phases of active reproductive physiology around the time of oviposition and diminished reproductive physiology during periods of nest construction between ovipositions. Although the ovarian ground plan hypothesis captures the partitioning of reproductive and labour components of maternal behaviour analogously to the model presented here, whether the envisioned ovarian cycle is truly cyclical has not been tested by experimental studies. In the model presented here and in widely held opinion, eusociality arose and became adaptive in a subsocial rather than semisocial context. The proposition that eusociality originated in Vespidae via partitioning of same-generation co-foundresses into worker and reproductive castes is untenable. In the context of the model presented here, however, inter-adult dominance interactions (West-Eberhard, 2003:146–147) could come into play following an initial divergence of maternal and allomaternal behavioural phenotypes if the dominance interactions mediate the transition from mutual exploitation at the origin of eusociality to mutual interdependence at later stages.

### Monogamy at the irreversibility threshold

The monogamy hypothesis (Boomsma, 2007, 2009) posits that lifetime sterility that characterizes permanent workers at and beyond the irreversibility threshold of Fig. 3 has evolved only in taxa with lifetime monogamy.

Published discussions in the 1990s and again in 2005 addressed definitions and interpretations of eusociality (Gadagkar, 1994; Crespi & Yanega, 1995; Sherman *et al.*, 1995; Costa & Fitzgerald, 1996, 2005; Wcislo, 1997, 2005; Lacey & Sherman, 2005). Among these, Crespi & Yanega (1995) argued that ‘eusocial’ should be reserved exclusively for those social species that have fully discrete queen and worker castes and in which workers have lost all possibility of direct reproduction. The monogamy hypothesis rests on this strict definition of the term and thereby bypasses the fundamental question raised by Hamilton (1964b): How did workers arise in the first place? This leads to the question of monogamy in facultatively and primitively eusocial hymenopteran taxa. Boomsma (2009) uses a quotation from E. O. Wilson as an epigram: ‘monogamy and especially monogamy outside the breeding season, is the rare exception’. This broad brush assertion has no bearing on any particular taxon, and the ‘likely ranges of relatedness’ in Figure 1 of Boomsma (2009) are sheer speculation with regard to Hymenoptera. However, because the ancestors of eusocial Hymenoptera were solitary, they were, by definition, monogynous. Questions of monogamy therefore depend on monandry. Hughes *et al.* (2008) present phylogenetic analysis of relatedness data from species in every lineage of eusocial (*sensu lato*) Hymenoptera except the bee tribe Allodapini. The analysis shows monandrous ancestry for each lineage. It is generally agreed that hymenopteran females mate only in a narrow time window following emergence, and a spermathecum (sperm storage organ) in a symphytan (Naumann, 1991) at the base of the Hymenoptera phylogeny is evidence of sperm storage as an early and likely universal trait of Hymenoptera. Therefore, to assert that ‘the data do not allow us to determine whether monandry was already present in the solitary ancestors or whether monandry and eusociality evolved concurrently, but they are clearly linked’ (Hughes *et al.*, 2008) constitutes an appeal to ignorance (Walton, 1999). The phylogenetic reconstruction in Hughes *et al.* shows monandry to be present at every internal node of the tree containing eusocial Hymenoptera – a tree that, if complete for suborder Apocrita, would contain many times more solitary taxa than social taxa. Therefore, the proposition that currently available data ‘strongly indicate that kin selection and high relatedness have played a decisive role in the evolution of eusociality’ (Hughes *et al.*, 2008) is untenable. Monogamy could be a trait of order Hymenoptera that has salience to eusociality equally as low as another much-discussed trait of the order – haplodiploidy (Hunt, 1999).

Beyond the irreversibility threshold, polygamy is now known from an increasing number of highly eusocial insects (Boomsma *et al.*, 2009). The numerous independent origins of polygamy in highly eusocial forms lend credence to a simulation exercise by Nonacs (2011), showing that polygamy, rather than monogamy, favours

the spread of an allele for cooperation. Although such alleles have not yet been identified, their existence in already-eusocial forms is concordant with the model presented here.

### Role of haplodiploidy

Haplodiploidy gives all Hymenoptera control over production of female or male offspring. In eusocial Vespidae, haplodiploid-enabled sex determination has responded to selection to yield life histories in which females of social forms, the only offspring that engage in allomaternal care, are the first to emerge. Numerous proposals have been put forward to suggest how haplodiploidy might play a role in eusociality, including homozygosity as a constraint on morphological and behavioural diversity in males (Flanders, 1946; Lin & Michener, 1972; Michener, 1974), exposure of deleterious alleles in homozygous males (Snell, 1932; Smith & Shaw, 1980; Saito, 1994), antagonistic pleiotropy in maternal effect genes (Wade, 2001) and Hamilton's 'haplodiploid hypothesis' (West-Eberhard, 1975). Among these and other suggested roles, reviewed by Linksvayer & Wade (2005), sex determination that enables protogyny – production early in the colony cycle of the only sex that engages in brood care – is the only unambiguous role played by haplodiploidy in hymenopteran eusocial adaptation (Hunt, 2007).

### Discussion

In the epigraph to this paper, Darwin posed two questions with regard to the evolution of insect sociality. Although he did not directly address the origin of sterility *per se*, he proposed that if some individuals of a social species should be capable of work but incapable of procreation, this would not be a major challenge to the theory of natural selection. Thus, he called the origin of worker behaviour a 'preliminary difficulty' and found no difficulty for sterile workers in a social context evolving as a product of natural selection if their work 'had been profitable to the community'. The more subtle and intellectually challenging question was the evolution of adaptations expressed only in sterile individuals. This was his 'one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory [of natural selection]'. Among writers on insect social evolution, Linksvayer & Wade (2005), Hunt (2007) and Ratnieks *et al.* (2011) draw attention to and discuss the two different questions. Previously, however, the distinction between Darwin's two questions was submerged from view by Wilson (1971, 1975) when he combined Darwin's two questions into a single question, the evolution of eusociality. That question has dominated the discipline ever since, as illustrated by passages from the Nowak *et al.* controversy. Nowak *et al.* (2010) titled their paper 'The evolution of eusociality'. Some rebuttals

use the same phrase: 'explaining the evolution of eusociality' (Abbot *et al.*, 2011), 'departures from high relatedness would almost certainly have prevented the evolution of eusociality' (Boomsma *et al.*, 2011), 'inclusive fitness, kin selection and Hamilton's rule have been extraordinarily productive for understanding the evolution of sociality' (Strassmann *et al.*, 2011). A minority of writings (e.g. West-Eberhard, 1978, 1987a; Linksvayer & Wade, 2005; Hunt, 2007; Wilson, 2008; Boomsma, 2009; Nowak *et al.*, 2010) focus explicitly on the origin of eusociality. The majority of writings on eusociality, however, address adaptation of already-social forms, and many of these extrapolate current adaptation to explain the origin of eusociality. Such extrapolations can quickly lead to pitfalls due to the 'well known fact that many causal paths may lead to very similar phenotypic outcomes, and the latter cannot be used to go back to the former, no matter how clever and sophisticated the statistical tools' (Pigliucci *et al.*, 2006). Because Wilson's single question commingles and confounds Darwin's two questions, failure to distinguish the origin of worker behaviour from the adaptation of eusociality lies at the heart of much of the Nowak *et al.* controversy.

Individual, kin-group, and multilevel selection were addressed by Darwin, although not in current terminology. In individual selection – natural selection – factors of the abiotic and biotic environment differentially affect individuals' survival and reproduction. Darwin's ascribing the action of selection at the level of the family in his explanation of morphological divergence in worker and queen ants is a statement of kin-group selection (Wilson, 2010). The concept of multilevel selection was inherent in Darwin's discussion (1871) of how selection could favour individually disadvantageous behaviours in human individuals yet favour spread of those traits through the population (Wilson, 2010). All three modes of selection play roles in the scenario presented here. At the threshold of eusociality, natural selection would operate exclusively at the individual level. Offspring that emerge into a colony environment in which they can obtain nourishment prior to departure for independent reproduction would have selective advantage over newly emerged wasps that leave the nest to seek nourishment. This advantage would occur whether or not allomaternal behaviour is expressed towards relatives. At the same time, an egg layer that receives transitory assistance in brood rearing would derive individual benefit, and this would occur whether or not the assistance is received from relatives. Thus, at the threshold of eusociality, both mother and allomother behave selfishly in a pattern of reciprocal exploitation and are subject to individual selection. The proposition that eusociality evolved via maternal manipulation of offspring (Alexander, 1974) captures one axis of this mutual exploitation scenario. At the threshold of irreversibility, swarm-founding advanced eusocial species live in permanent colonies, thus individual selection never occurs. Intra-colony

reproductive competition can occur among individuals and kin-groups in both primitively and advanced eusocial colonies (Queller *et al.*, 1993), but a high level of internecine contests could have negative impact on production of gynes or daughter colonies. Colonies with fewer or no internecine contests could have higher reproductive success. If this is the case, then mutualism (Lin & Michener, 1972; Michener, 1974) could be an important component of the evolutionary process as an emergent property of already-eusocial colonies. From the perspective of the model presented here, therefore, adaptation between the thresholds of eusociality and irreversibility would be a changing balance of individual, kin-group, and colony selection, with relative roles of contributing selective factors changing in a multilevel context over the course of eusocial adaptation. Factors that could modulate multilevel selection include gene expression (Sumner *et al.*, 2006; Hunt *et al.*, 2007, 2010; Toth *et al.*, 2007, 2010), novel alleles (Ross & Keller, 1998), indirect genetic effects (Moore *et al.*, 1997; Wolf *et al.*, 1998, 1999; Wolf, 2003; Linksvayer & Wade, 2005; Bijma & Wade, 2008), social physiology (Grassé, 1946; Seeley, 1995; Johnson & Linksvayer, 2010) and ecology (Strassmann & Queller, 1989; Yamane, 1996). The importance of relatedness between workers and reproductives relative to these and other factors need not be equal for each factor nor linear across evolutionary time.

A shared feature of kin selection models, group selection models, the heterochrony model of Linksvayer and Wade, and the game-theoretic model of Nowak *et al.* is that all of these invoke allelic foundations. Kin selection models rely on inclusive fitness and hypothesize alleles for helper behaviour; the group selection scenarios of Wilson & Hölldobler (2005) and Wilson & Wilson (2008) envision assemblages of nonrelatives that share a particular allele for altruism; Linksvayer and Wade envision a heterochrony gene for early expression of maternal care; Nowak *et al.* hypothesize a mutant allele for remaining at the natal nest. Thus, a shared feature of these models is that they hypothesize allelic differences as the foundation for eusociality. In the model presented here, heterochronic allomaternal expression of maternal care behaviours is based on context-dependent foreshortening of maternal development in wasps that emerge with active reproductive physiology, and any alleles that might enhance the partitioning of castes and the programming of caste-specific phenotypes come to be exposed to selection only after the origin of caste-like behavioural phenotypes themselves. Thus, the model presented here exemplifies 'genes as followers' (West-Eberhard, 2003, 2005), 'phenotype precedes genotype' (Palmer, 2005) and 'plasticity first' (Pigliucci, 2010).

The transition from solitary to highly eusocial is a major transition in evolution (Maynard Smith & Szathmáry, 1995; cf. Queller & Strassmann, 2009). The model presented here addresses that transition, and it

does so not only by phylogenetic reconstruction combined with trait mapping (Brooks & McLennan, 1991) but also by means of natural history and empirical studies. Worker and reproductive phenotypes are characterized by sets of physiological and behavioural variables. Above and beyond description and documentation, these can be experimentally manipulated. Experimental outcomes indicate that underlying differences in caste-like phenotypes are affected by factors in real time at both individual (Dew & Michener, 1981; Strassmann *et al.*, 1984; Rossi & Hunt, 1988; Solís & Strassman, 1990; Mead & Gabouriaut, 1993; Mead *et al.*, 1995; Karsai & Hunt, 2002; Tibbetts *et al.*, 2011) and colony levels (Hunt & Dove, 2002; Mead & Pratte, 2002; Seal & Hunt, 2004). It is noteworthy that all of the factors can be linked to differential nourishment either among larvae or among adults or both.

Little of the eusociality literature is placed in a phylogenetic context, although a complete view of the origin of worker behaviour and subsequent evolution of eusociality in any particular taxon is rendered difficult unless relevant traits are placed in a phylogenetic context. The proposition that ancestral monogamy is key to understanding 'the evolution of eusociality' (Hughes *et al.*, 2008) could be either supported or undermined by data on the many solitary taxa not included in that analysis. An exemplary phylogenetic analysis of eusociality shows that sweat bees had three independent evolutions of eusociality, reversals to solitary life, and re-reversals to eusociality (Wcislo & Danforth, 1997; Danforth, 2002; Danforth *et al.*, 2003).

Phenotypes have been at the periphery of evolutionary research and theory for more than a half century (West-Eberhard, 2003). As part of the main flow of evolutionary research and theory, the evolution of eusociality, taken broadly, has generally been assessed in the context of the Modern Synthesis (Huxley, 1963), which frames current models that posit alleles as the gateway to eusociality. Within this context, analytical tools of population genetics can model and measure the spread of an allele through a population (Falconer & Mackay, 1996). However, there is increasing recognition of the need to merge phenotypic plasticity in its diverse expressions and concomitant definitions together with the Modern Synthesis into a postmodern extended synthesis (Hunt, 2007; Pigliucci & Müller, 2010b) in which phenotypic plasticity plays a major, central role. The starting point for the model presented here is constancy in performance of maternal care. As components of maternal care come to be divided in frequency among mothers and allomothers, underlying capacity for developmental divergence is revealed. Behavioural flexibility and developmental divergence provide the substrates needed for nongenetic inheritance of traits leading to queen/worker phenotypes, which then provide the context for developmental fixation of regulatory pathways or novel alleles for developmental determination of worker and queen

castes. Any model for the adaptation of eusociality that does not incorporate development will be inescapably incomplete.

## Future directions

### Theory

In an accessible and important review of nongenetic inheritance, Bonduriansky & Day (2009) present an algebraic model that incorporates nongenetic inheritance into the commonly used model of evolutionary change in which phenotype and underlying genotype are essentially completely coupled. The Bonduriansky and Day model incorporates an inherited nongenetic component that partially decouples phenotype and genotype, and they then incorporate the maternal effects model of Kirkpatrick & Lande (1989) into a model that explicitly decomposes the evolutionary process into changes that occur due to underlying genotype and nongenetic inheritance. Two challenges are thereby raised for theoreticians of eusociality. The first will be to develop models of this kind that decouple underlying genotype and nongenetic inheritance and that also incorporate maternal effects, allomaternal effects, and any indirect genetic effects of gynes and males in a social context. A second challenge for theoreticians of eusociality will be to capture the dynamics at the origin of allomaternal care in which both allomother and mother initially derive benefit – the  $b$  of Hamilton's rule – but also in which cost in terms of direct reproduction by allomothers – the  $c$  of Hamilton's rule – segues into a context of mutual benefit between allomothers and mothers. Hamilton's rule hypothesized  $b > c$  as the basis for worker 'altruism' when benefits accrue to reproductives and workers incur costs. Simultaneous cost/benefit analyses for reproductives as well as for workers were not part of Hamilton's rule. In the conceptual model presented here, there is no worker altruism. Instead, mutual exploitation is the gateway to mutual benefit. The overarching challenge, then, will be to develop models that focus simultaneously on allomothers and mothers and that dynamically capture the fitness costs and benefits to both.

### Empiricism

Because *Polistes* wasps live in unenclosed nests that enable open access to larvae, they are particularly suitable for experimentation on potential selective factors such as quantity and nutritional quality of adult and larval nourishment, allomother/larva ratio, numbers or ratio of early- vs. late-instar larvae (only late-instar larvae produce copious saliva), and presence at the nest of resource-consuming nonworking males and gynes. The honey bee *Apis mellifera* was the first social insect to have its genome sequenced (Honey Bee Genome Sequencing Consortium, 2006), and additional genomes of social insects are on the

near horizon. These can support empirical studies that could shed considerable light on the evolutionary processes of eusociality. Sequences for genes of known or proposed functions can be used for quantitative differential expression studies. Underlying mechanisms regulating gene expression can be pursued via the action and inheritance of epigenetic effects, which can include methylation patterns and interference RNAs (Bossdorf *et al.*, 2008; Jablonka & Raz, 2008). Proposed roles of particular proteins and biosynthetic pathways can be explored using RNA interference to knockdown expression of candidate genes (e.g. Zhou *et al.*, 2006, 2008; Hunt *et al.*, 2011; Mutti *et al.*, 2011). In addition, because *Polistes* larvae are fed nectar, dsRNA can be administered directly to larvae in sucrose solution (Hunt *et al.*, 2011), making *Polistes* perhaps an ideal model system for RNA interference studies in natural environments.

### Focus

Most literature on the evolution of eusociality, in the sense of that phrase as it is widely used, is couched in a context of Hamilton's rule. Of the three variables, relatedness,  $r$ , is the only variable that is easily quantified, whereas benefit to the beneficiary,  $b$ , and cost to the performer,  $c$ , generally defy measurement. In the conceptual model presented here, relatedness *qua* relatedness is not needed for the origin of worker behaviour, and intra-colony relatedness diversity in some species beyond the point of no return is evidence that high relatedness is not needed to sustain the highly eusocial state. From a kin selection perspective, West-Eberhard (1987a) observed that kin selection is not needed to explain the origin of eusocial workers, but kin selection can instead play a role in the maintenance and regulation of worker behaviour. Unquestionably, eusociality as an adaptation beyond the eusociality threshold incorporates relatedness between workers and reproductives and therefore brings kin selection into the broader framework of multilevel selection, but the  $r$  in Hamilton's rule is only one of three of its variables. One of the few measurements of  $b$  and  $c$  as well as  $r$  was carried out on the primitively eusocial wasp *Ropalidia marginata* by Gadagkar (2001), who concluded, 'the benefit and cost terms in Hamilton's rule deserve more attention than the relatedness term'.

### Perspective

Not long after introducing kin selection as an explanation for the origin of worker behaviour, Hamilton (1966:108) said, 'the real difficulty is explaining why the juveniles develop the altruistic trait'. This perspective is the foundation of decades of difficulty in understanding the origin of eusociality (Hunt, 2007). Putting aside the misapplication to insects of altruism, a consciously chosen behaviour that requires cognitive thinking at a high

level, the conceptual flaw in the question is that it asks 'why?' rather than 'how?' In research framed exclusively by the Modern Synthesis, including research framed by Hamilton's rule, the roles of plasticity, environmental factors and specific mechanisms responsible for major changes of organismal form were largely sidelined. However, these aspects of evolutionary biology are increasingly coming to the fore (Pigliucci, 2010). Pigliucci argues that a hugely expanded and rapidly increasing knowledge base consisting of large data sets in genetics, development, plasticity, inheritance, and other empirical domains is now throwing open the black box that contained mechanisms as they existed in the context of the Modern Synthesis. It thus has become possible to address evolutionary phenomena using 'how?' questions rather than 'why?', a perspective emphasized by Hunt (2007). Pigliucci (2010:12) captures this conceptual and methodological transition and its importance: 'this shift of emphasis from statistical correlation to mechanistic causation arguably represents the most critical change in evolutionary theory today'. The model presented in this paper derives from and is contained wholly within a perspective of mechanistic causation.

## Conclusions

Studies of phylogeny, natural history, behaviour, physiology, and development in the wasp family Vespidae lead to a 'plasticity first, genes as followers' conceptual model from which it can be reasoned that existing allele-based models may be insufficient for fully understanding the origin and adaptation of eusociality. Specific inferences that can be drawn from the model are that the origin of allomaternal worker behaviour was not necessarily based on relatedness *qua* relatedness and that at the eusociality threshold both care-giving allomothers and assistance-receiving mothers were acting selfishly in their own interest. In this view, the origin of allomaternal behaviour at the eusociality threshold did not require inclusive fitness, kin selection played no role, and the first workers were not altruists. However, between-generation relatedness that underpins soft inheritance was required for eusociality to evolve as an adaptation beyond the eusociality threshold. Transitions from solitary to facultatively eusocial, to primitively eusocial and thence to advanced eusocial took place via exaptation, phenotypic accommodation, and genetic assimilation. Across that sequence, the gradient of selection would have been from individual selection at the eusociality threshold to primarily colony selection at the threshold of irreversibility, with a mix of the factors that constitute multilevel selection acting between the thresholds. These conclusions derive from a careful distinction that can and should be drawn between the origin of allomaternal worker behaviour and the adaptation of eusociality after workers are present. This distinction will be informative when applied to other eusocial taxa.

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