Animal Behaviour 106 (2015) 37–42

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Review

Developmental plasticity and social specialization in cooperative societies

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ARTICLE INFO

Article history:
Received 20 January 2015
Initial acceptance 26 February 2015
Final acceptance 24 April 2015
Published online
MS. number: 15-00046R

Keywords:
alternative phenotypes
behavioural specialization
cooperative breeding
developmental plasticity
early life conditions
inclusive fitness
information

Cooperative breeding systems showcase the diversity of social trajectories within and among species, ranging from the extremes of eusocial insects where individuals become irreversibly specialized as fecund queens or sterile workers, to vertebrate systems where individuals maintain the flexibility to breed throughout life. Between these extremes lies a continuum with individuals exhibiting varying degrees of specialization in their behaviour. Most research on cooperative breeders, particularly on vertebrate systems, has focused on why helping has evolved, rather than addressing this diversity. Here, we present a framework to explain variation in the timing, extent and flexibility of phenotypic divergence across vertebrate and invertebrate cooperative systems. We base our framework on recent theory about how individuals integrate information about the environment from different sources (genes, parents and direct experiences) when establishing their developmental trajectory. We discuss how the timing and degree of divergence and specialization are influenced by the availability and reliability of information about later fitness options and by the extent to which individuals have control over their development. Throughout, we use this developmental perspective to draw broad comparisons across vertebrate and invertebrate systems, which are often considered separately.

Cooperative breeding systems, which incorporate vertebrates and invertebrates and scale from helpers at the nest to large eusocial societies, uniquely showcase the diversity of social trajectories both within and across species (see glossary in Appendix 1). In these systems, individuals have two primary routes to maximize their inclusive fitness (Bourke, 2011): through direct reproduction (as either a dominant or a subordinate individual) or through helping to raise nondescendent young. Investment in producing and rearing offspring can be energetically costly (Heinsohn & Legge, 1999) and individuals often face a trade-off between pursuing one or the other fitness option (Cant & Field, 2001). The large body of work to date on the evolution of cooperative breeding has given us a good understanding of how selection can act on the different reproductive strategies, and in particular of why some individuals forgo reproduction entirely in order to help raise relatives (Clutton-Brock, 2009a; West, Griffin, & Gardner, 2007). There is enormous variation, however, in the extent to which individuals specialize irreversibly on distinct life history strategies of helping or breeding and, if they do, in the point during development when the two strategies diverge. At one end of the spectrum, the eusocial species such as honeybees exhibit early and irreversible commitment to worker or queen phenotypes, while at the other end, most vertebrate systems maintain the capacity to breed throughout life (Fig. 1). Even among those systems with flexibility of reproduction, there are varying degrees of specialization at different ages (Carter, English, & Clutton-Brock, 2014; Jeanson & Weidenmüller, 2013).

Here, we provide a conceptual framework to address the variation in the timing and extent of irreversible commitment to specializing as a breeder or nonbreeding helper, using insights from recent theory on developmental plasticity and drawing links across the disparate studies on vertebrate and invertebrate systems. In contrast to decades of research and debates on the developmental basis of cooperation in social insects (Linksvayer & Wade, 2005; O'Donnell, 1998; Schwander, Lo, Beekman, Oldroyd, & Keller, 2010; Wheeler, 1986), there has been far less focus on how the environment experienced during development has shaped life history trajectories in cooperatively breeding vertebrates. Recently, however, there has been growing interest in how early life

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http://dx.doi.org/10.1016/j.anbehav.2015.05.006
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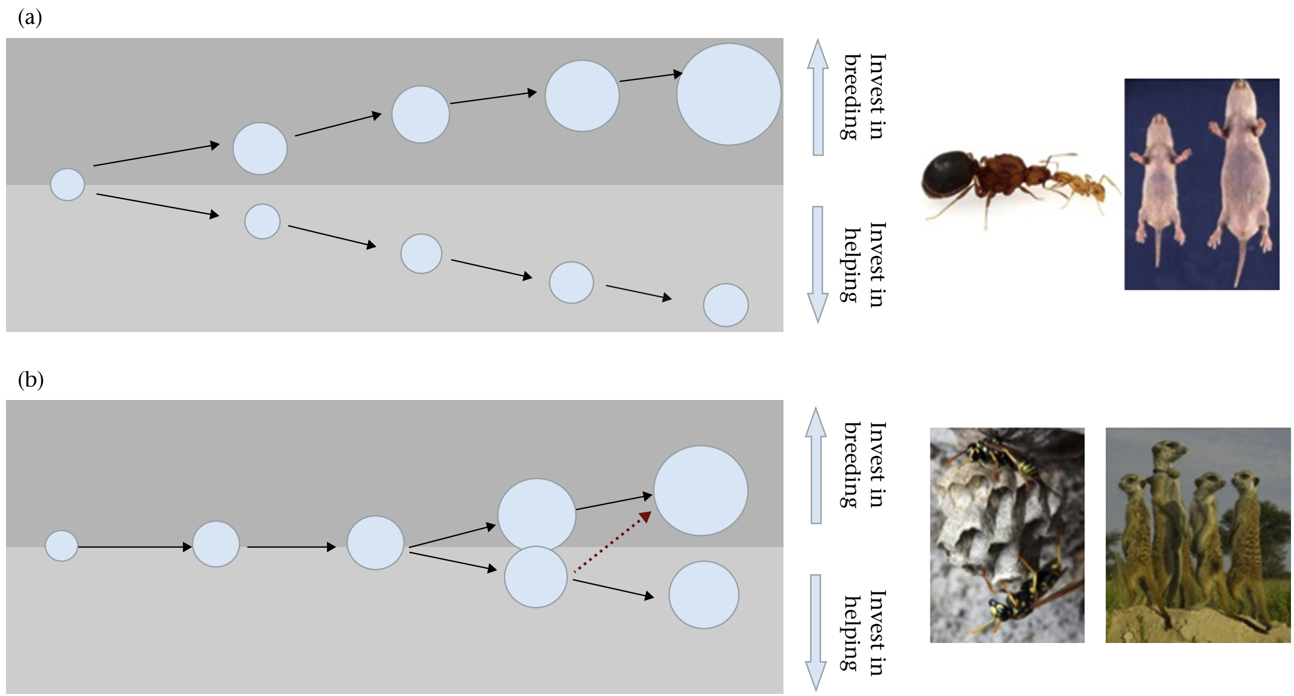

Figure 1. Variation in developmental trajectories across cooperative systems. Two broad types of developmental trajectory are discussed in this review: (a) individuals diverge to develop as breeders or helpers from an early age, with considerable morphological differences between types and no (or very little) plasticity after divergence has occurred; and (b) breeders and helpers follow similar developmental trajectories, are morphologically indistinguishable as adults and helpers can become breeders later in life (red dashed line). Photo credits: Alex Wild, Justin O'Riain, Sinead English.

conditions can have formative effects on cooperation in vertebrate systems, and if and when individuals should specialize or remain flexible along their developmental trajectory (e.g. Huchard et al. 2014). We first describe how individuals might integrate information from different sources (genes, parents and experience) when tailoring their developmental trajectory to generate an adaptive match between selective environment and phenotype. We predict that the reliability of this information at different points of development will be important in determining whether and when individuals specialize as a breeder or helper, or remain plastic throughout life. Second, we consider how constraints imposed by developmental mechanisms and social structures (such as group size, reproductive skew or queue length) might influence individuals' ability to respond to the environment and, in turn, the extent of phenotypic divergence. Throughout, we use this developmental perspective to highlight common patterns and contrasts across vertebrate and invertebrate cooperative systems.

HOW INFORMATION RELIABILITY AFFECTS THE EXTENT AND TIMING OF SOCIAL SPECIALIZATION

One of the most compelling explanations for adaptive developmental plasticity is that genes, parents and the environment of development provide correlative information about conditions under which the phenotype is selected (Leimar, 2009; Leimar, Hammerstein, & Van Dooren, 2006; Shea, Pen, & Uller, 2011). Over the course of development, it would be adaptive for individuals to acquire and use information from these different sources to reduce uncertainty about the environment, and thus to produce a phenotype appropriate for the conditions of selection. The reliability of this information in predicting later selective conditions is a key factor determining when development should be sensitive to the environment (Moran, 1992; Piersma & Drent, 2003; Tufto, 2000). In spite of a growing body of theoretical work on the role of information in shaping adaptive development (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Donaldson-Matasci, Bergstrom, & Lachmann, 2010; Fischer, van Doorn, Dieckmann, & Taborsky, 2014; Frankenhuis & Panchanathan, 2011; Schmidt, Dall, & van Gils, 2010; Stamps & Krishnan, 2014), there have, to our knowledge, been no attempts to apply this theory to explain patterns of developmental plasticity across cooperative systems. Indeed, the role of information on fitness options in shaping cooperation has only recently received theoretical attention, in a model demonstrating that helping is more likely to evolve when individuals can assess their own reproductive value and that of their relatives than when individuals are lacking this information (Holman, 2014). This model makes a valuable contribution to how information on reproductive value affects the evolution of facultative helping, yet does not explicitly address the role of information in generating different patterns of developmental plasticity.

What types of information might individuals use to assess their best developmental route to maximizing fitness in a cooperative system? According to inclusive fitness theory (Hamilton, 1964), it pays individuals to help if the indirect or delayed direct benefits of helping outweigh the costs of lost reproduction. Over the course of development, individuals should therefore assess their opportunities for personal reproduction versus the kin-selected benefits of rearing nondescendent young and allocate their investment in breeding or helping to maximize both direct and indirect components of fitness (Bourke, 2011). Specifically, information about the potential benefits of helping versus breeding independently (i.e. the *r*, *B* and *C* terms of Hamilton's rule), and the reliability of this information, should play a fundamental role in individual decisions to specialize as a nonbreeding helper or to retain reproductive flexibility. This information can in principle come from genes, parents and the social and abiotic environment, and individuals might integrate these separate sources of information when assessing their options about whether to remain flexible in their development or specialize on a particular life history trajectory.