Journal of Theoretical Biology 369 (2015) 85–94

Contents lists available at ScienceDirect

Journal of Theoretical Biology

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

A structured population model suggests that long life and post-reproductive lifespan promote the evolution of cooperation

Caitlin Ross [a], Jan Rychtář [b], Olav Rueppell [c,*]

[a] Department of Computer Sciences, The University of North Carolina at Greensboro, Greensboro, NC 27402, USA
[b] Department of Mathematics and Statistics, The University of North Carolina at Greensboro, Greensboro, NC 27402, USA
[c] Department of Biology, The University of North Carolina at Greensboro, 312 Eberhart Building, 321 McIver Street, Greensboro, NC 27402, USA

HIGHLIGHTS

- Traditional view of the relation of sociality and longevity may be too simple.
- Spatial Prisonner's Dilemma model to study life history effects on altruism.
- Complex interactions of duration of life history stages affect altruism potential.
- Long post-reproductive stage and longevity promote the evolution of cooperation.
- Timing of life history may affect the evolution of cooperative behaviour.

ARTICLE INFO

Article history:
Received 22 September 2014
Received in revised form
14 January 2015
Accepted 17 January 2015
Available online 28 January 2015

Keywords:
Aging
Social evolution
Altruism
Lifespan
Game theory

ABSTRACT

Social organization correlates with longevity across animal taxa. This correlation has been explained by selection for longevity by social evolution. The reverse causality is also conceivable but has not been sufficiently considered. We constructed a simple, spatially structured population model of asexually reproducing individuals to study the effect of temporal life history structuring on the evolution of cooperation. Individuals employed fixed strategies of cooperation or defection towards all neighbours in a basic Prisoner's Dilemma paradigm. Individuals aged and transitioned through different life history stages asynchronously without migration. An individual's death triggered a reproductive event by one immediate neighbour. The specific neighbour was chosen probabilistically according to the cumulative payoff from all local interactions. Varying the duration of pre-reproductive, reproductive, and post-reproductive life history stages, long-term simulations allowed a systematic evaluation of the influence of the duration of these specific life history stages. Our results revealed complex interactions among the effects of the three basic life history stages and the benefit to defect. Overall, a long post-reproductive stage promoted the evolution of cooperation, while a prolonged pre-reproductive stage has a negative effect. In general, the total length of life also increased the probability of the evolution of cooperation. Thus, our specific model suggests that the timing of life history transitions and total duration of life history stages may affect the evolution of cooperative behaviour. We conclude that the causation of the empirically observed association of life expectancy and sociality may be more complex than previously realized.

1. Introduction

Most biological species age and different species age at different rates. These observations are explained by the evolutionary theory of aging with the declining force of natural selection at older ages based on extrinsic mortality and reproductive schedule (Hamilton, 1966). For social species, and particularly humans, this basic theory has been refined to account for inclusive fitness effects through resource transfers (Bourke, 2007; Lee, 2003). A specific example is the "Grandmother Hypothesis", explaining the expansion of female post-menopausal lifespan (Hawkes et al., 1998). Transfers can take the form of resources and information and may explain why many social

---

* Corresponding author. Tel.: +1 336 2562591; fax: +1 336 3345839.
E-mail address: olav_rueppell@uncg.edu (O. Rueppell).

http://dx.doi.org/10.1016/j.jtbi.2015.01.020
0022-5193/

species, including humans, are exceptionally long-lived and exhibit post-reproductive lifespans (Carey and Judge, 2001). However, a comprehensive explanation of the association between longevity and sociality may be more complicated (Carey, 2001a; Carey and Judge, 2001) and post-reproductive lifespan may exist for other reasons (Cohen, 2004; Packer et al., 1998).

The inverse causality may have influenced the co-evolution of sociality and longevity: longer-lived species or species with post-reproductive lifespan may be more likely to evolve cooperation and ultimately sociality, creating potentially positive feedback loops in the association between life history and social evolution. The effect of life history on social evolution has been explored by several theoretical studies that mainly focus on the role of age-dependent dispersal [reviewed in (Lehmann and Rousset, 2010)] and the role of local kin competition that may negate kin-selected benefits of altruistic behaviour (Debarre et al., 2014; Taylor, 1992). Increased survival resulting in overlapping generations, has also been demonstrated to promote altruistic behaviour (Taylor and Irwin, 2000). The specific life history of cetaceans and humans have been analysed to explain the emergence of a post-reproductive life span (Johnstone and Cant, 2010). However, we are unaware of a study that systematically explores the effect of the temporal structure of life histories, namely the durations of the pre-reproductive, reproductive, and post-reproductive life span in a simple, general model.

Modelling the effect of particular life history structures on the evolution of cooperation allows for unbiased testing of the separate effects of pre- and post-reproductive lifespan, reproductive stage, and total duration of life without the additional life-history parameters that may influence the coevolution of sociality and longevity in any particular species. Sociality may protect individuals, particularly during maturation, from a variety of factors and thus decrease extrinsic mortality (Keller and Genoud, 1997). Maturation time is correlated with sociality (Hatchwell, 2009) and with longevity (Ricklefs, 2010). In empirical data sets such correlations hinder the investigation of independent effects of specific life history variables. For example, no association between sociality and longevity was detected in North American birds when external mortality and maturation time were statistically accounted for Blumstein and Moller (2008). Prolonged maturation time is also associated with longevity in other taxa (Ridgway et al., 2011) but its effects on the evolution of cooperation and sociality are unclear.

The evolution of cooperation is commonly modelled in the general game theoretical framework by a two-person game called Prisoner's Dilemma (Nowak, 2012). The simple form of the Prisoner's Dilemma (PD) predicts no evolution of cooperation because a non-cooperator (=defector) receives a higher fitness pay-off from a pairwise interaction with another individual than a cooperator, regardless of whether the other individual cooperates or not (Axelrod, 1984). Relative to cooperation, the predicted defection behaviour leads to fitness costs at the group level but persists due to individual selection. However, several extensions of the PD have been developed that can explain the emergence and maintenance of cooperation in a population (see for example Nowak, 2006) and these extensions serve to increase the realism of the underlying model for most biological systems (Lewis and Dumbrell, 2013).

The extensions that generally favour cooperation include repeated interactions (Axelrod, 1984) and the introduction of spatial population structure (Nowak and May 1992; Killingback and Doebeli, 1996; Nakamaru et al., 1997, 1998; van Baalen and Rand, 1998, Mitteldorf and Wilson, 2000; Nakamaru and Iwasa, 2005; Lieberman et al., 2005; Ohtsuki et al., 2006), particularly in the form of scale-free networks (Santos et al., 2006a). In some cases, however, the spatial structure inhibits the cooperation (Hauert and Doebeli, 2004).

Although some exceptions exist, most Metazoans age with important functional consequences (Finch, 1990). Thus, a third biologically significant extension of reiterated PD games that has recently received significant attention is the phenomenon of ageing. Older age may lead to more information that can enhance an individual's strategy transfer capability (Szolnoki et al., 2009). Alternatively, ageing leads to a decrease in vitality and thus increases the likelihood of being replaced (Liu et al., 2012). Both processes promote the evolution of cooperation by increasing the population heterogeneity, particularly when individuals are born young and grow older during the simulation (Liu et al., 2012; Szolnoki et al., 2009). Age as a co-evolutionary process has also demonstrated benefits for the evolution of cooperation when it influences the strategy adoption of an individual's neighbours (Wang et al., 2012). These studies of aging demonstrate an impact of ageing on the evolution of cooperation but allow horizontal transmission of strategies (Liu et al., 2012; Szolnoki et al., 2009; Wang et al., 2012) which is more appropriate for cultural than for genetic evolution (Danchin et al., 2004). Specifically, this approach deemphasizes the role of biological ageing and its link to mortality and reproductive schedules, which are central to the understanding of the evolution of ageing and life-history (Finch, 1990; Hamilton, 1966). The life-history of most biological species can be divided into pre-reproductive, reproductive, and post-reproductive stages that differ fundamentally with respect to fitness consequences and thus their impact on the evolution of cooperation (Finch, 1990) and any other traits.

To specifically investigate the link between different life-history structures and the evolution of cooperation in a general biological context, we constructed a spatial model that relied solely on vertical transmission, replacing individuals that die of old age with young, biological offspring from neighbouring individuals (Ross et al., 2013). We incorporated an age-dependent life-history structure with pre-reproductive, reproductive, and post-reproductive periods of varying lengths and study their effect on the long-term evolutionary dynamics of cooperators and defectors. This biologically realistic division in reproductive and non-reproductive phases resulted in an unsaturated population model that is difficult, if not impossible to solve analytically (Debarre et al., 2014). Our simulation results suggested that the total duration of life and the ratio of reproductive to non-reproductive stages are important for the evolution of cooperation. Furthermore, we found consistent evidence that the duration of post-reproductive and reproductive, but not pre-reproductive life-history stages, favour the evolution of cooperation.

2. Methods

For our simulation analyses we built a spatially organized population model in C++, in which stationary individuals can occupy the nodes of a 128×128 square lattice with periodic boundaries. Each of the 16,384 nodes in this two-dimensional lattice is connected to eight neighbouring nodes (Moore neighbourhood size of one). Although neighbourhood size itself can influence the evolution of cooperation (Zhu et al., 2013) we keep this parameter constant for simplicity. The neighbourhood size of eight behaves more deterministically than smaller neighbourhood sizes (Ross et al., 2013), is biologically relevant and computationally manageable. Cooperative or non-cooperative interactions can occur only pairwise with the direct neighbours (Fig. 1) and lead to fitness payoffs for each of the two interactants. We chose a simplified PD payoff matrix with $1 < b \leq 2$, following Santos et al. (2006b) and (Szolnoki et al. (2009).

$$\begin{array}{ccc} & Cooperate & Defect \\ Cooperate & 1 & 0 \\ Defect & b & 0 \end{array} \tag{1}$$

The model implements a stochastic updating procedure of nodes by randomly selecting one specific node from the entire