



Emergence of games from ecological trade-offs: longevity changes strategies for extra-pair mating in birds

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Abstract

Each member of a breeding pair benefits if the other does more of the parental investment, so there is scope for behaviours that can be interpreted as both cooperative and competitive games between males and females. Extra-pair mating, widespread among socially monogamous birds, adds extra conflict but also potential opportunity to these social interactions. We analyse an individual-based model of a social environment with simple behavioural strategies where game-like patterns and cooperative outcomes emerge. The model focuses on three evolving traits: female propensity for extra-pair copulations and male investment in territorial behaviour and care. Male traits are reaction norms that use experienced within and extra-pair copulations as information input. We found that female extra-pair mating provided incentives for males to reduce territorial aggression and increase care for offspring. However, when adult survival was higher, male investment in care and territoriality changed from being negatively to positively correlated. This happened because longer life expectancy gave more behavioural opportunities for males, where nest desertion maximises lifetime male fitness when female extra-pair copulation is high. This outcome evolved gradually, with stable periods of intermediate extra-pair mating and low territoriality. These were punctuated by cycles of high extra-pair mating, nest desertion, reduced extra-pair mating and relapse to aggressive territoriality before a new stable phase was established. Each successive trait cycle was faster and smaller, indicating that through evolution of reaction norms, the gene pool has a long history that canalizes the evolution of behaviours, which can be interpreted as emergence and refinement of frequency-dependent games.

Significance statement

Most birds that mate in monogamous pairs engage in extra-pair copulations. Males of some species invest (in varying proportions) in offspring that are genetically related only to their social female. The great variability of extra-pair mating levels among different species and populations, supported by numerous field studies, indicates that social and ecological factors play a crucial role in shaping the behaviour. We analyse a computer model in which extra-pair mating evolves concurrently with male reproductive investments in territory defence and offspring care and show how common ecological trade-offs may change the social dynamics within a breeding population and lead to the emergence of complex social interactions between males, females and their neighbours.

Keywords Extra-pair mating · Cooperation · Game theory · Birds

Introduction

It is striking that about 80% of all socially monogamous bird species engage in considerable levels of extra-pair mating that leads to genetic polygamy (Brouwer and Griffith 2019). This happens in a context where the socially mated pair works together over brooding, feeding and protecting the young, for which paternity uncertainty may cause significant conflict (Trivers 1972). At the same time, social pairs compete for nesting sites and food resources with

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neighbours, with males typically performing most of the territoriality. It has been suggested that females who mate outside the social pair-bond may incentivise males to cooperate with other males over vigilance and defence (Eliassen and Jørgensen 2014; Krams et al. 2022) or reduced aggression and increased resource sharing (Gray 1997; Eliassen and Jørgensen 2014; Rumińska et al. 2023). The underlying logic is that extra-pair mating results in a male's offspring being spread across several nests, so whatever benefits the breeding neighbourhood is also likely to positively affect his individual fitness. Thus, when females engage in extra-pair copulations, they may affect the fitness of both within-pair and extra-pair males, and even that of other females in the neighbourhood. Such an entangled web of social interactions among multiple players harbours potential for both cooperation and conflict and is a rich playing field for the evolution of reproductive strategies (Trivers 1972).

One way of making sense of such frequency-dependent behaviours is game theory, which has a long history in biology (Trivers 1971; Maynard Smith 1982). It has achieved great successes through identifying a game in naturally observed behaviours, defining roles, actions and pay-off matrices, before putting players against each other and applying mathematical analysis to predict evolutionarily stable strategies (reviewed in e.g., McNamara and Leimar 2020). Although some interactions that typically occur during a breeding season could be portrayed as biological "games" (such as male-male conflict over access to mates or female-male conflict over parental care), their complex embedding defeats the methods of classical game theory (Maynard Smith 1982; McNamara and Leimar 2020). Methodologically, it becomes challenging when the same action may have implications for several other players, when pay-off matrices may shift because traits are continuous or when life history trade-offs imply that some of the consequences of an action may occur long afterwards, for example if intensive reproductive effort compromises subsequent survival.

The shortcoming of common methodologies led McNamara and Leimar (2020) to argue in their recent book on game theory in biology that classical game theory relies too much on idealized assumptions and needs to be updated to reflect simultaneous evolution of multiple traits, realistic levels of variation, local processes of sensing and limited cognition and consequences on multiple time-scales. A recent review (McNamara 2022) similarly called for better integration of game theoretic models with all four of Tinbergen's (1963) questions, with emphasis on proximate mechanisms for decision-making (e.g. Budaev et al. 2019) and a richer complexity of the environment. The review argued that evolution repeatedly has led to emergence of simple and robust strategies that perform well in the messy and complex "real world", while game theory (as well as optimisation models) tends to find complex strategies that excel in overly

specified environments of low complexity. What are needed are models of simple strategies that may evolve robustness to work well across more complex and open-ended settings (McNamara and Houston 2009). We therefore started from the opposite end compared to what is normally done, by considering typical social behaviours and modelling those with agent-based methods and evolving strategies, before we aim to interpret the evolving behaviours in light of game theory. Such evolving agent-based models have been used widely, e.g. to model behaviour (Strand et al. 2002), life histories (Dunlop et al. 2009) and resource management (Enberg et al. 2009). Here, we focus on how the evolving behaviours lead to population-level patterns of interactions that resemble classical games from game theory.

An extension of game theory that allows for greater environmental complexity is adaptive dynamics (Dieckmann and Law 1996), which permits integration with life history trade-offs. A limitation of adaptive dynamics is that it assumes monomorphic populations with separate timescales for ecology and evolution, thus emphasising ecological equilibria and stylised feedbacks between strategies. The same perspective was implemented in the model of McNamara et al. (1999) for parental investment, where individuals had a negotiation rule that they applied repeatedly to adjust their final level of parental effort. Such rule-based games can incorporate some individual differences (for example individual quality as in McNamara et al. 1999), and while they address how individuals may use local information to inform decisions, deriving the behavioural rule itself may require unconstrained information and cognitively demanding computations.

A model linking extra-pair mating and neighbourhood cooperation was first proposed by Eliassen and Jørgensen (2014). The version analysed here was developed as an evolving individual-based model in Rumińska et al. (2023) where individuals vary, and social interactions are therefore richer than in the first version of the model (Eliassen and Jørgensen 2014) that was based on adaptive dynamics. Using a genetic algorithm (Holland 1992), we study evolving populations of individuals with genes that specify key behavioural traits that affect reproductive success. We detailed multiple trade-offs, and many of them depend on the actions of others, so just like Trivers (1972) described, there is a rich background for competitive and cooperative interactions. Males need to invest in territorial behaviours to defend resources around the nest, and whoever invests more in defence ends up with a larger territory and more resources for chicks in the nest. At the same time, males may invest in care to utilize those resources and protect the young. The model is based on the assumption that males trade their investments in care and territoriality in the current breeding attempt against prospects of future breeding opportunities. Females produce eggs and also care for the

chicks, and if their social male has secured more resources through territoriality, their provisioning is more effective and offspring success higher. Crucially, the degree of extra-pair copulation modifies the male trade-offs, because territoriality benefits all the chicks in his nest, but takes resources away from extra-pair offspring in neighbouring nests (Eliassen and Jørgensen 2014).

The model describes male behaviours as evolving reaction norms that permit adjusting behaviours according to a male's copulation rate with the social and extra-pair females. This in turn creates additional trade-offs for females as their rate of extra-pair copulation has consequences for access to resources as well the care contribution provided by their social mate. In this evolving individual-based model, the strategies in the gene pool have been under selection in specific historical settings, may recently have recombined and mutated, their effects are tested against specific neighbours with their own independently evolving traits, and each individual finds itself in complex social interactions with several members of the same and opposite sex. We have previously shown that for this model, considerable levels of female extra-pair mating evolve, which incentivise reduced male territoriality together with increased levels of male-provided care (Rumińska et al. 2023). It has been noted how this is a mechanism for evolution of cooperative neighbourhoods (Eliassen and Jørgensen 2014), and it has been dubbed the nicer neighbourhood hypothesis.

There has been a decades-long search for “good genes” effects suggested by Trivers (1972), where females seek extra-pair mates with superior genes that should confer advantages only to their extra-pair offspring. Such genetic benefits are sometimes detected (e.g. Foerster et al. 2003), but recent reviews conclude that good genes effects are too weak to underlie the high and widespread levels of extra-pair copulation in birds (e.g. Akçay and Roughgarden 2007a; Brouwer and Griffith 2019). By instead focusing on the hard work involved in successfully raising offspring, we return to Trivers' (1972) often overlooked focus on the effort involved in being a “good parent”, and how female reproductive strategies may trigger high male investment in the brood. Although our model includes only very simple behaviours, an important inspiration has been Hrdy's thoughtful analyses with particularly broad views of parental care and their intertwined relations to mating strategies among primates and humans (e.g., Hrdy 1981, 2009). She linked multiple mating with fitness benefits to mothers explicitly with the infanticide hypothesis (Hrdy 1979), which is qualitatively similar to the mechanisms in our model — but here extended to larger social groups and production of benefits rather than merely avoiding costs. Although Hrdy's focus has been on primates to varying degrees capable of deliberation, many of the evolutionary facets exposed in her writing could be applied to birds. Extra-pair mating has been linked to cooperation also

in previous game theoretic studies (Roughgarden et al. 2006; Akçay and Roughgarden 2007b), and although these studies were criticized for being based on contract-like negotiations rather than individual fitness (McNamara et al. 2006), the focus beyond sexual conflict to potential roles for cooperation during breeding was perhaps too easily overlooked.

In Rumińska et al. (2023), we showed how this individual-based model reliably converged to the same broad solutions as in the previous version that used adaptive dynamics (Eliassen and Jørgensen 2014), even when abundant ecological noise was added to mimic real-world ecological and individual variability. Just as important as this recurrent gravitation towards the same outcomes, however, was how the model exhibited evolutionary trajectories with fluid and dynamic equilibria that fluctuated constantly, but to varying degrees. Here, we focus not on the endpoints but analyse these fluctuations underway, which, when picked apart, point to new games becoming important as longevity makes trade-offs between current and future reproduction more consequential. Our aim is to illustrate how insights from the long history of game theory can be used to analyse evolutionary trajectories of behaviours in individual-based models and highlight the particular implications of this model for the interpretation of empirical studies of extra-pair mating.

Methods

We use an agent-based model with individual genes coding behavioural responses to study adaptive evolution of mating and breeding strategies in birds. The model is a representation of breeding pairs within social neighbourhoods, focusing on the effect of extra-pair mating on resource defence and offspring care. The general structure of the model is the same as in Eliassen and Jørgensen (2014), and the individual-based version used here is the same as in Rumińska et al. (2023); here, we briefly explain its main characteristics and where the analysis in this study differs from previous versions.

Population

The model focuses on a breeding season, during which mated pairs build nests close enough to each other that there can be frequent interactions among neighbours. We assumed that each neighbourhood consists of 24 nests arranged in a circular configuration and connected with exactly three neighbouring nests (Fig. 1). This represents implicit spatial location and thus defines the first-order neighbours with whom the breeding pair may interact. For each neighbourhood, we used a circular network to avoid unnecessary complications that could appear on the network edge. The organisation of the breeding territories was inspired

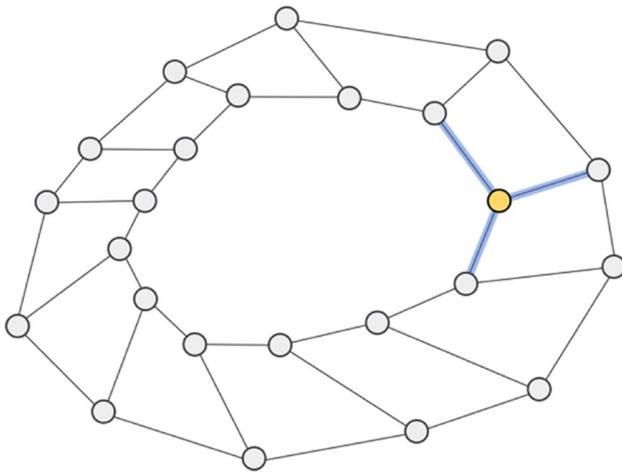


Fig. 1 Example of a neighbourhood. Breeding pairs are arranged in circular networks of 24 nests, where space is implicit and connections between nests represent possible interactions among individuals. Each nest (node) is connected to the same number of neighbouring territories. In the focal nest (highlighted in yellow), within-pair copulations ($WPC = 1 - EPC$) and care strategies are performed; territorial defence and extra-pair copulations (EPC) happen on the network edges, between adjacent territories (marked in blue). The entire population consists of 220 such neighbourhoods. Individuals are randomly assigned to one of these available nests in each iteration of the simulation; if an individual survives to the next year, it will be surrounded by different phenotypes

by aggregations that many wild bird species form during a breeding season (e.g. Bouwman et al. 2006). The whole population consisted of 220 such neighbourhoods of 24 nests, thus totalling 10,560 individuals. These individuals were randomly assigned to nests and neighbourhoods, and if they survived to the next breeding season, their breeding position was again drawn at random.

A time step in our simulation represents a breeding attempt that happens once a year. While running the simulation, we repeated breeding attempts for a set number of years and tracked evolutionary changes of the three traits: female extra-pair copulations (EPC, denoted by x), male care (C_m) and male territorial defence (D). For the first year in the simulation, we initialised all 10,560 individuals with identical genetic setup. All females started with $x = 0$ or 0.6 depending on simulation, and all males expressed the same amount of care and territorial defence. Due to stochasticity in mutations, inheritance and reproduction, these genes gradually evolved, and the ensuing strategies in the gene pool could be identified as engaging in various forms of cooperation or competition, within the sexes or between males and females.

Strategies

The incredible diversity of extra-pair paternity (EPP) levels among species (Brouwer and Griffith 2019), populations

(Gray 1998) and even consecutive breeding attempts (Menerat et al. 2018) suggests that whom to copulate with partly reflects the changing conditions in which the individuals find themselves, and potentially acts as a flexible response to external stimuli. In wild species, the sexes typically differ in reproductive behaviours and the strategies available to them. In this model, females have a mating trait that determines their propensity to engage in extra-pair copulations, while males vary in their investment in defence of resource territories. In addition, both parents have traits that determine how much care they provide for chicks in their nest. This differs from previous modelling approaches (e.g., Kokko and Morrell 2005; Roughgarden et al. 2006; Akçay and Roughgarden 2007a; Liedtke and Fromhage 2012) mainly because it focuses on the ecology of breeding with behavioural strategies that are flexible and reflect adaptations to many types of interactions. We achieved this by using the concept of reaction norms (Sultan and Stearns 2005) that represent how individuals make decisions. Reaction norms allow males to flexibly adjust territorial behaviour and care investment based on local EPC information. Technically, the reaction norms are functions with coefficients defined by evolving values (representing genes) that determine the degree to which locally available information affects decisions. We provided details for calculating core behaviours used in the model in Table 1. These terms are further explained in Rumińska et al. (2023).

For parameters relating to reproductive biology and ecological relationships (survival, reproductive success functions), Eliassen and Jørgensen (2014) performed a rigorous sensitivity analysis and found that qualitatively, the adaptive outcome of female extra-pair mating and reduced male aggression was stable across a large parameter space. New parameters include genotypic strategies, expression of the behavioural phenotype, mutation and inheritance and pairing and positioning in the social network. During model development and testing, we came across no simulations that eroded our confidence that the overall ecology in this individual-based model remains the same compared to the results of the adaptive dynamics model of Eliassen and Jørgensen (2014), and that the model equations converge to common solutions even when started with different initial values (Rumińska et al. 2023). Simulations presented in this paper, however, represent only a small fraction of all possible mortality scenarios; therefore, extrapolation of the results to other parameters should be done with caution.

The model assumes extra-pair behaviours can be performed only between first-degree neighbours, and if the female engages in EPC, she does so with equal probability with each of them. For example, if a female has strategy $x = 0.3$, then the fraction 0.7 of all copulations is with her social partner and 0.1 of copulations with each of her extra-pair partners. EPC is assumed to be a female-driven trait that

Table 1 Model overview. The evolving strategies are modelled as polygenic, quantitative traits, where offspring inherit the mid-parental value with random noise added to account for mutation, segregation and recombination. The lower indices refer to males (*m*) and females (*f*) or indicate the position in the network (*i* — focal individual; *j* — first-order neighbour). Indices *i* and *j* are omitted when the equation considers only individuals from one social pair (i.e. occupying the same position in the network)

Symbol or function	Description	Parameter values/range
Evolving female strategy: propensity for extra-pair mating		
x	Proportion of copulations performed with extra-pair males	[0,1] Initial values: $x=0$ and $x=0.6$
Evolving male strategies: care and territorial defence		
$C_{m,i} = c_{1,i}x_i + c_{2,i}$ $\delta_{i,j} = d_{1,i}x_i + d_{2,i}(1 - x_i) + d_{3,i}$ $D_i = \frac{\sum_{j=1}^z \delta_{i,j}}{z}$	Male care ($C_{m,i}$) reaction norm may adjust to information on EPC of the social female (x) Territorial aggression, $\delta_{i,j}$ towards neighbour j is a reaction norm informed by copulation frequency with the social female ($1 - x_i$) and extra-pair female in nest j (x_j). D_i is mean investment in territorial defence of male i	Initial values: $c_1 = d_1 = d_2 = 0.0$ and $c_2 = d_3 = 0.5$
Male territoriality secures resources to the nest		
$\rho_{i,j} = \frac{z}{z + \delta_{i,j}S_{m,i} + \delta_{j,i}S_{m,j} + f}$ $R_i = \sum_{j=1}^z \rho_{i,j}$	A male's territorial aggression towards his neighbour j determines the share of resources $\rho_{i,j}$ he secures (with some additional challenges f from floaters). Within-season survival S scales the probability that each male is around to defend his territory R_i is the sum of resources controlled by male i summed over the z borders	$z=3$
Adult survival within and across breeding seasons		
$P = e^{-(m_0 + m_R I^\beta)}$ $S = e^{-0.3(m_0 + m_R I^\beta)}$	Survival probability of adults until the next breeding season: P and survival through the breeding season: S . Total reproductive investment of females $I_f = E + C_f$ where E is cost of producing eggs; for males, $I_m = C_m + D$	$\beta = 3.0, m_R = 0.1$ Parameters used in different longevity scenarios: $m_0 = \{2.0, 0.4\}$, $C_f = \{0.9, 0.6\}$, $E = \{0.9, 0.6\}$
Reproductive success		
$W = R^\alpha (S_f C_f^\gamma + S_m C_m^\gamma)$	Number of surviving offspring from a nest (W) depends on resources R and care provided by the female C_f and social male C_m . Provision of care also depend on the parent's likelihood of surviving the breeding season (S_m, S_f)	$\alpha = 0.7, \gamma = 0.7$ (diminishing return on investments)

is not affected by male mating solicitation, mate guarding or other counter-strategies. The final distribution of paternities in the neighbourhood, however, depends not only on the female EPC rates and predefined network structure, but is subject to stochasticity in fertilization and offspring survival.

Investment in offspring care is modelled as a quantitative gene, fixed in females and variable (evolving) in males. The male reaction norm for care has two heritable genetic components, one setting the level and one defining the slope of the reaction norm, using information on experienced copulation rate with the social female as proxy for within-pair paternities (Table 1). Offspring survival, the key to reproductive success, depends on resources available in the territory (R), care investments from both parents (C_m, C_f) and the probability that each of them will survive to provide care for offspring throughout the breeding season (S_m, S_f) (Table 1).

The amount of resources a male monopolises is determined by his territorial investment relative to that of his neighbours' and is calculated border by border with each of the first-order neighbours. Males may adjust the level of territorial defence based on both the social and extra-pair females' mating behaviour. The reaction norm for male territorial behaviour has three heritable genetic elements, with one gene setting the overall level and two genes defining the slopes using information on experienced mating frequencies with the social and extra-pair females (Table 1). A male can thus tailor territorial investment to experienced copulation rate across each of his territory borders, but the reaction norm coefficients are gene values not influenced by the territorial behaviours of other males.

The resulting model permits flexible male and female reproductive strategies to emerge as responses to local

information and behaviour of others in their neighbourhood. Differences in expected offspring survival result from variation in allocation to paternal care and resource defence, as well as stochastic processes. They determine which breeding pairs will produce viable offspring, and through inheritance, they influence the genetic composition of the future breeding population. When a new offspring is created, each gene is drawn from a normal distribution with a mean equal to the mid-parental value (average of maternal and paternal gene values) and a standard deviation set to 0.05, representing mutations, recombination and segregation. Individuals are therefore haploid and have genes for each trait, but express only the strategies that apply to that sex (Table 1). No differences are assumed between within-pair and extra-pair offspring, except the genes they inherit from different male sires.

Survival of the breeding pair

Literature suggests that life expectancy may influence the rate of extra-pair mating (Griffith et al. 2002; Crouch and Mason-Gamer 2018) and could be a predictor of social monogamy (Arnold and Owens 2002). For males, the tolerance for EPP in the social nest is predicted to reduce their current effort if they can expect higher paternity in future reproductive bouts (Mauck et al. 1999; Houston and McNamara 2002). We incorporated this factor in our model to see how longevity would modulate the evolved levels of EPC, male care and territorial defence.

Successful reproduction is influenced by the parents' investment in care and securing of food resources. In males, reproductive investment is the sum of care and territorial defence; in females, it is the sum of care and egg production. The parent's life expectancy depends on ecological parameters determining the background mortality rate that may differ across locations and species biology, e.g. due to predation pressures. In addition, a parent's reproductive strategy affects outcome, as high reproductive investment in the current brood reduces the probability of surviving the season and experience future breeding attempts.

Males experience immediate trade-offs between care and territoriality, where fitness outcomes are influenced by the territorial behaviours of the neighbouring males and the mating behaviours of the within-pair and extra-pair females. The total reproductive investment of males is also subject to a trade-off with within-season survival, which determines the likelihood that they can be around to provide care and defend the territory. Across seasons, the same trade-off between total male reproductive investment and survival determines the likelihood the male will have subsequent breeding opportunities (see Table 1).

The overall driver of survival is the background mortality rate set in the model, whereas the exact longevity

value emerges based on evolved reproductive strategies of males and females. By varying one of the model parameters responsible for the mortality risk (see Rumińska et al. 2023), adaptive strategies evolve to new trait distributions, and in this way, we can simulate populations that vary in expected longevity. In a high-mortality scenario, individuals live for on average 1 year with a small survival probability to the next breeding season. For the more longer-lived variant, some, but not all, individuals live up to 2, 3 or 4 breeding seasons. Individuals that survive to the next breeding season have a higher chance of establishing a nest and finding a partner than 1-year-olds; the number of offspring produced in each breeding round is adjusted to the size of the population (5280 territories in total).

A numerical laboratory to study selection gradients

We focused on investigating the out-of-equilibrium dynamics of the evolving traits as they continually changed from the naïve initial conditions until the more stable evolutionary outcomes. We did so with four distinct cases: two short-lived populations, one initiated with no female extra-pair mating ($x=0.0$) and the other with high EPC ($x=0.6$), and two long-lived populations with the same initial EPC values. Initialising a simulation with $x=0.6$ means that all females mate extra-pair 60% of all copulations, which implies that males have 40% chance of siring within-pair young so that on average, they have more offspring outside their nest. When EPC is 0%, females show no extra-pair activity and mate exclusively with their social partners (genetic monogamy). To study selection gradients in more detail, we stopped simulations when rapid changes in traits occurred to investigate how particular genetic values were correlated with fitness and other traits. In these experiments, we extracted the set of genes and traits of all individuals in a selected year and repeatedly mated these individuals to simulate the average effect of their genotypes on fitness. This was performed 1000 times with randomly assigned partners and breeding positions to sample how these selected genotypes would perform on average across different social contexts of mates and neighbours.

Results

Longevity influences evolution of traits

In all simulations, traits evolved to relatively stable values after some thousand generations but kept fluctuating for as long as populations were simulated. Larger deviations from the long-term mean were common early in each simulation and weakened with time. The fluctuations happened at different time points but had similar characteristics across all

runs. In Fig. 2, we present selected simulations, each initiated with different parameters, to show the general pattern of trait evolution.

There were no qualitative differences in evolutionary endpoints or dynamics when similar populations began from different initial conditions of the female extra-pair copulation trait (top versus bottom rows in Fig. 2). What had large consequences was the general level of mortality (left versus right columns in Fig. 2), which lead to specific adaptations among both females and males. When we simulated populations with a lower mortality rate (Fig. 2b, d), traits generally had different equilibrium values, took longer to stabilise, and large fluctuations were more common. Interestingly, male traits (care and defence) were negatively correlated when life expectancy was short (left column in Fig. 2, care generally went up when defence went down) but positively correlated in more long-lived populations (right column in Fig. 2, care and defence moved up and down together).

Selection gradients at different stages of the simulation

By pausing the simulation in specific years and repeating matings of the individuals with reshuffled neighbours (1 000 times), we obtained a cleaner view of the role of trait distribution and fitness consequences in our population. Figure 3 shows a typical evolutionary course of the investigated traits (top panel) along with several time points to examine trait consequences for fitness (i.e., mean offspring production per individual, on a relative scale). Bottom panels of Fig. 3 shows distribution of traits in the whole population (x -axis), averaged over 1000 independent breeding attempts, and their lifetime (across multiple seasons) reproductive

potential (fitness, y -axis). Note how the clouds moved between selected time-points, indicating changing distribution of phenotypes in the population.

Out-of-equilibrium trait cycles dampening over time

While the trait trajectories in Fig. 2 may look chaotic, phase diagrams of male versus female traits revealed a recurrent cycle that dampens over evolutionary time (Fig. 4). A main difference was caused by varying longevity (left versus right columns in Fig. 4), but the initial EPC value did not alter the position of endpoints (white dots) in the phase space (compare top versus bottom rows in Fig. 4). Time is indicated by the colour-coding in the scale bars to the right, which reveals that early cycles had large magnitude and that later in time, oscillations dampened. A striking difference between the longevity scenarios is how care and defence diverged from the initial values and oscillated around their equilibria at different places in the phase space for the short-lived populations (Fig. 4a, c), but cycled in parallel in the longer-lived populations (Fig. 4b, d). In the short-lived populations, evolution towards high EPCs happened together with high male care and low male defence — high care benefits the female's offspring and low defence makes it possible for males to invest more in care. Importantly, when EPC exceeded 0.5 in the longer-lived populations, male care dropped drastically, and so did territoriality, leaving the females worse off. It thus seems that stable and productive social neighbourhoods, characterised by high male contributions towards care, repeatedly broke down but went through a cycle and rebuilt. For each round, the cycle narrowed, indicating that the evolved strategy set in the population was becoming more robust to change or perturbation.

Fig. 2 Evolutionary trajectories of behavioural traits: female EPC (red line), male territorial defence (blue line) and male care at his social nest (yellow line). Simulations **a** and **b** started from EPC=0.6; **c** and **d** started from EPC=0.0. In **a** and **c**, life expectancy was ca. 1 breeding season; in **b** and **d**, life expectancy was higher and allowed for surviving to 2, 3 or more breeding seasons for some individuals

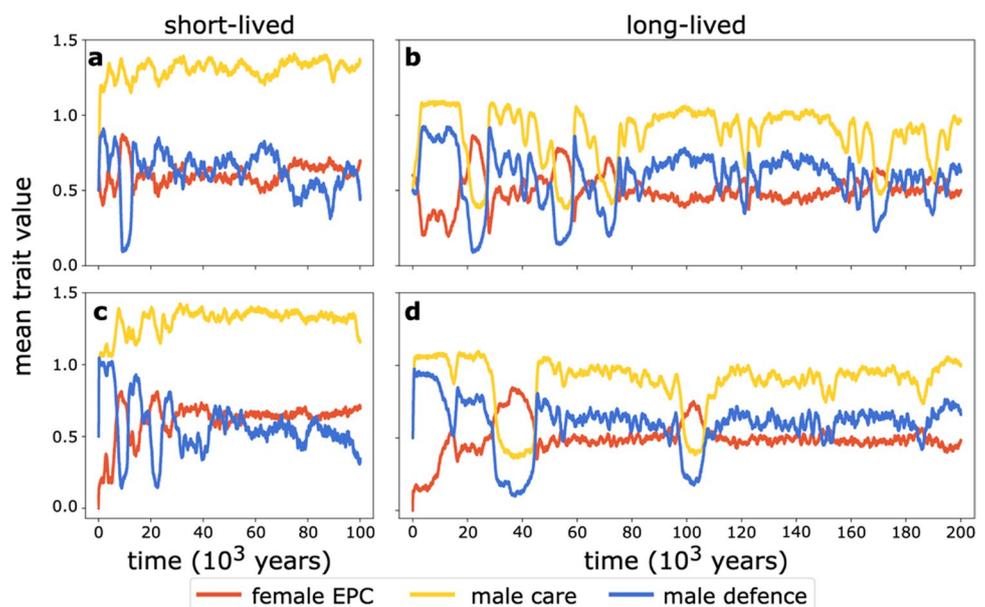
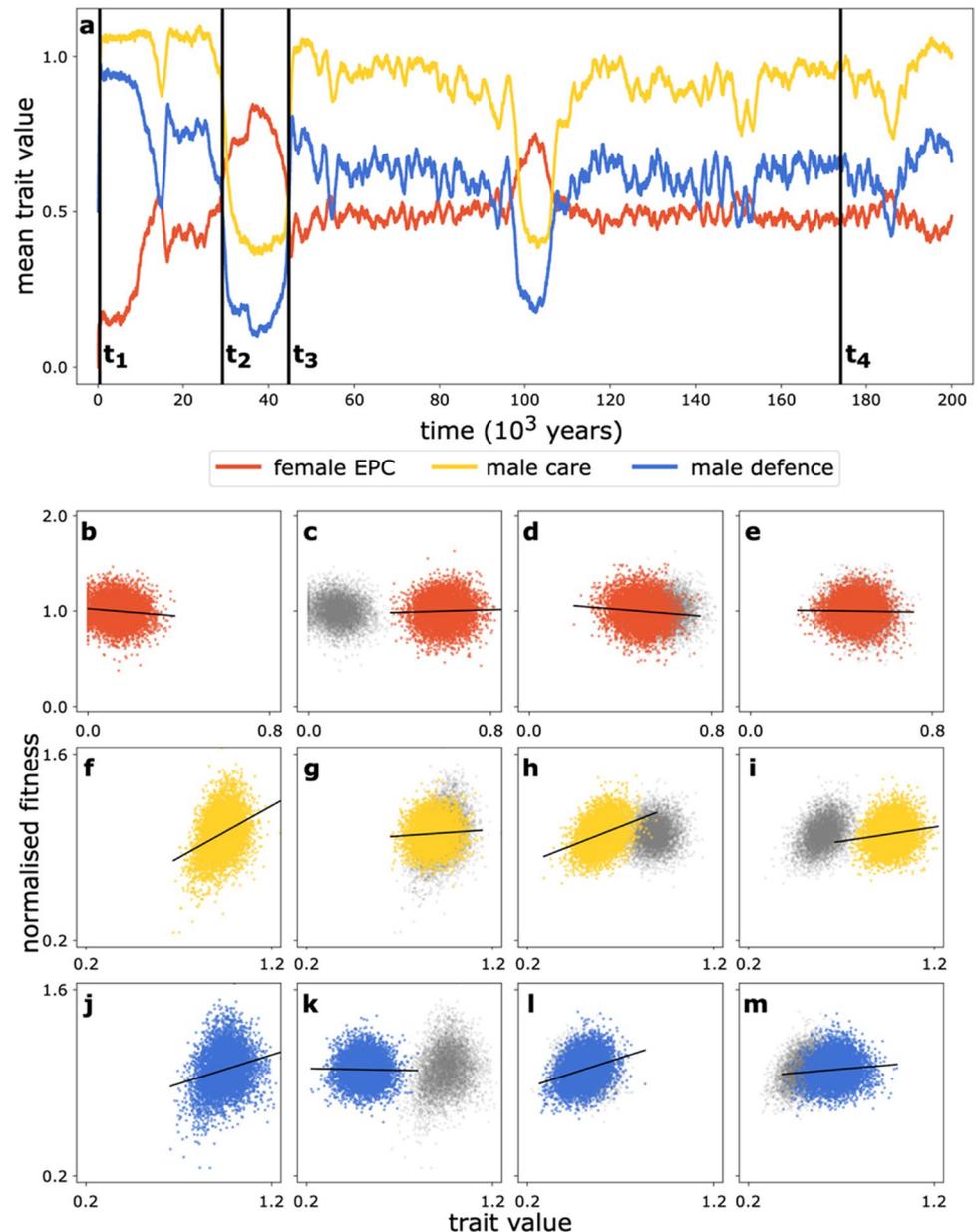


Fig. 3 A detailed look at trait evolution and selection gradients in long-lived species. The top panel shows a long-lived population starting from an initial EPC value of 0.0 (same simulation as Fig. 1d). In the years indicated by black vertical lines (t_1 – t_4), population-level distributions of traits and fitness are shown in the panels as follows. Y-axes in panels **b–m** show normalised number of surviving hatchlings, as a function of female extra-pair mating probability (**b–e**, orange), expressed male care in social nest (**f–i**, yellow) or expressed male territorial defence (**j–m**, blue). Axis scales in the lower panels are conserved to show how phenotype distributions were shifting during the simulation. Grey clouds in the background in **b–m** show fitness distribution from a previous time step to help assess changes in trait distribution over time. Regression lines were added on top to show selection gradients



Evolution is slow but follows recurring patterns

A more detailed look at one cycle of break-down and re-establishment of a productive and social neighbourhood is shown in Fig. 5. The highlighted trajectory shows the first out-of-equilibrium cycle from Fig. 2b to Fig. 4b, starting from around year 29,000 in the simulation (red triangle) and lasting 13,000 years (until the red cross). Red dots indicate the timescale — they are placed on top of the trajectory for every 2500 years. Figure 5 also contains some numbered arrows to help understand the course of evolution during the first cycle. In the beginning, when EPC had climbed to a value of 0.5, males had evolved to provide abundant care, which benefitted the female. (1) Caring males were

common, but an extra benefit could still flow to females with high EPC values because neighbouring males then refrained from territorial defence and channelled more resources to her nest. (2) Next, as males had very few genetic offspring in their social nest, strategies evolved that prioritised extra-pair offspring and saved male investment for future breeding attempts. This was achieved through caring (and defending) less, thus lowering total reproductive investment and increasing survival. (3) In essence, males partially deserted the nests, leaving females with high EPC with virtually no parental help. (4) Then, females with lower EPC provided more incentives for social males to invest in her nest again, and low-EPC genotypes became more and more abundant. (5) This leads to a gradual climb towards higher care as EPC

Fig. 4 Phase diagrams showing how male care and defence (y-axis) co-varied with female extra-pair copulation propensity (x-axis) in simulated social evolution. Panels show short-lived (a, c) and long-lived populations (b, d) starting from EPC = 0.6 (a, b) or 0.0 (c, d). Colour bars on the right indicate timescales for each trajectory (blue for territorial defence and orange for care); white dots mark the endpoint of each simulation after 100 or 200 thousand years

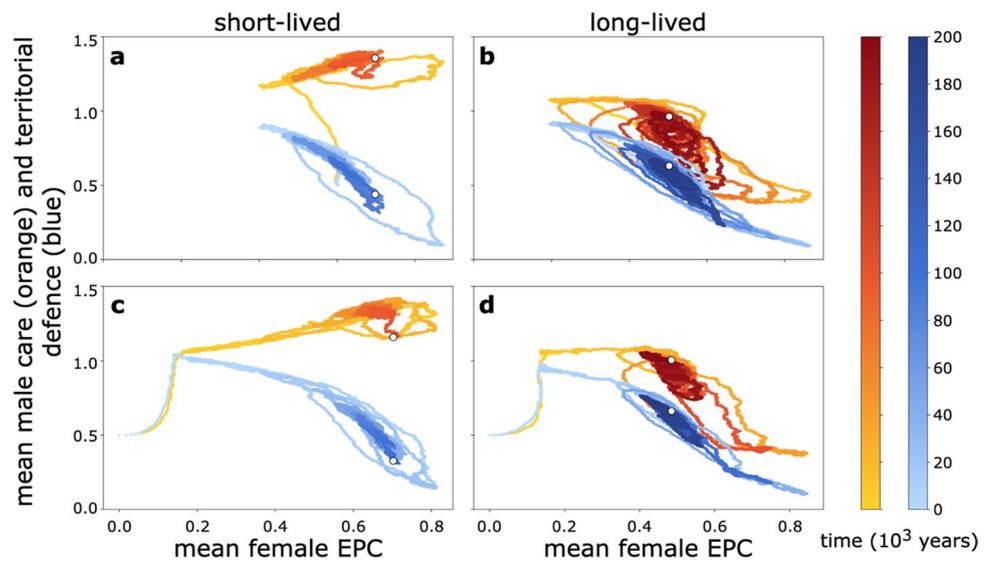
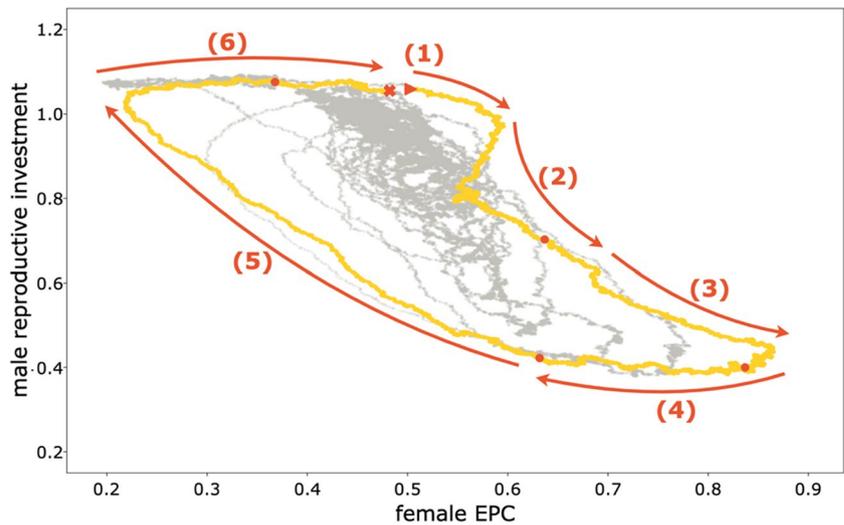


Fig. 5 The first out-of-equilibrium cycle of increasing then decreasing female extra-pair copulation strategy (x-axis) and reduction then rebuilding of male care (y-axis) of the simulation shown in Fig. 4b. Numbers in parentheses relate to explanations in the text. The red triangle and cross mark the beginning and the end of a highlighted circle. The distance between red dots is 2500 simulation years — we can see that evolution was slow at first, and then it sped up towards the end of the cycle



evolved to lower levels. (6) Finally, when male care was at a high level again, females gradually evolved higher EPC, which incentivised reductions of wasteful aggression in the neighbourhood. This was stable until females evolved higher EPC again and a similar cycle followed. As the male reaction norms evolved stronger responses each time, this cycle was repeated with smaller amplitude and faster turnover.

Male tolerance for EPC varies with longevity

The way male care and defence changed from being negatively correlated in short-lived populations to becoming positively correlated in longer-lived populations (e.g. Figure 2 a vs b) had consequences for total reproductive investment. We investigated the average male response to different values of female EPC in Fig. 6. For the short-lived males, total

reproductive investment stayed relatively constant across wide variation of female EPC behaviour (Fig. 6a), indicating a high tolerance for females with high EPC. Short-lived males had low chances of surviving to a second breeding season; therefore, strategies evolved where they invested a lot in care or defence even when they sired few of the offspring in their nest. Towards EPC = 0.6, short-lived males showed reduced defence but still invested in care. The observed drop in defence at high female EPC had the consequence that total reproductive investment went down and increased the probability that the male was around to provide care and defence towards the end of the breeding season too.

In long-lived populations (Fig. 6b), survival to the next breeding season was more likely, so here, any compromise to survival from investing too hard had tangible fitness consequences for the coming years. This trade-off, between total

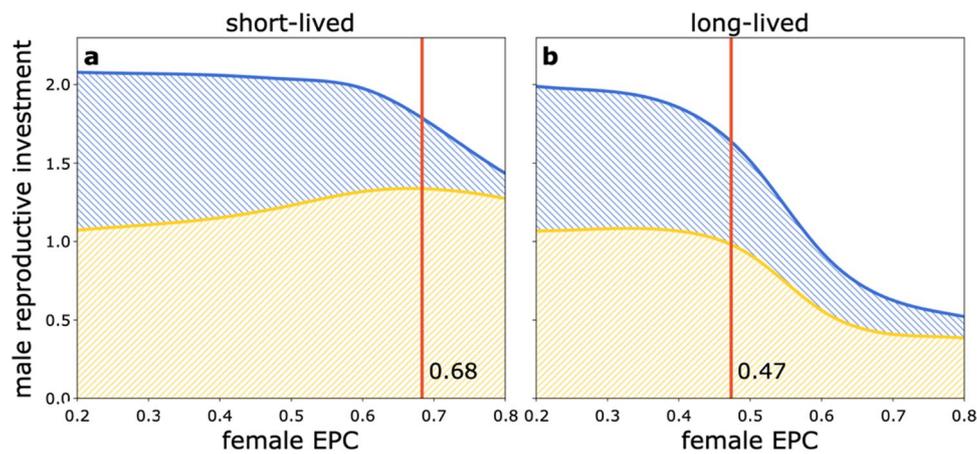


Fig. 6 In longer-lived populations, a new trade-off between total reproductive investment and future breeding changes the male–female social game. This figure shows the mean investment of males in care (yellow) and defence (blue) derived from Fig. 4 c and d but stacked so that the total area depicts total reproductive investment of an average male. Panels show differences in reproductive investment in short-lived (**a**) and longer-lived (**b**) breeding males. There is a trade-off between total reproductive investment and survival so that lower total investment towards the right, particularly in **b**, implies a higher

probability of surviving to breed in the following year. Red vertical lines indicate average female EPC that eventually evolved in each longevity scenario (compare with Fig. 2c, d). Male responses were calculated based on average genetic values recorded in the population as a response to female EPC levels in different time points. Data have been interpolated using `scipy.interpolate` tools (Python) for EPC ranging from 0.2 to 0.8, where the most changes in the female–male dynamics can be observed (compare with Fig. 4)

reproductive investment and survival to the next breeding season, thus began to matter in the long-lived population. In a sense, this weaponised males in the long-lived population, where they evolved a strategy that withheld care if mated with a female with high EPC. Such a strategy in the short-lived population would only worsen the situation for the few within-pair offspring without having a considerable effect on survival to next breeding. Large changes in male total reproductive investment therefore had consequences for population dynamics and age structure, because in this scenario, more males survived when their mean reproductive investment was lower. The age profile of each sex, shown in Fig. 7, illustrates this. In periods when male total reproductive effort was low (Fig. 7a, e.g. around 20,000 years), the male population was dominated by older individuals (Fig. 7b), while the average female population was slightly younger (Fig. 7c).

Discussion

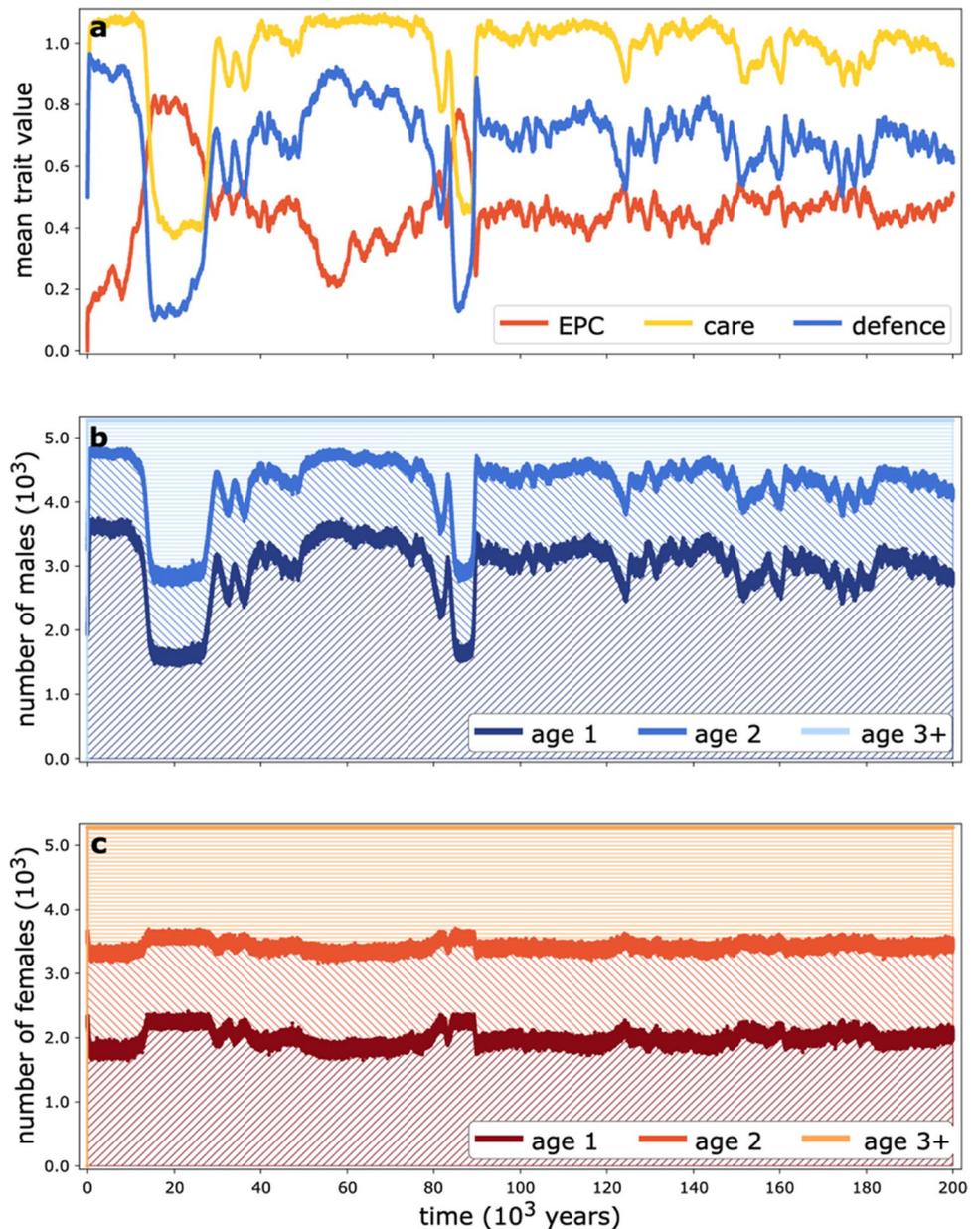
Trivers’ landmark 1972 paper detailed the evolutionary logic of why the sexes differ in expected parental investment. He also outlined the potentially complex games when both sexes invest considerably in offspring, but each individual would benefit if they did a bit less and others a bit more. His analyses successfully achieved clear qualitative predictions because he deliberately adopted a biologically inclusive but empirically problematic definition of parental investment

as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring” Trivers (1972). Because it is easier to follow individual long-term consequences in a model, we examined some of these aspects of parental investment by simulating an artificial population with genes responsible for coding EPC, care and territorial defence, and their impacts on life histories and social interactions. By specifying key trade-offs, the games verbally described by Trivers (1972) emerged as behavioural strategies in our simulated populations, and they changed qualitatively when a basic ecological parameter as predation rate varied.

Ecological trade-offs and the emergence of games

In game theory, the term “game” is used as a tool to interpret and make sense of frequency-dependent behaviours where an individual’s best option depends on the actions of others (Trivers 1971; Maynard Smith 1982; McNamara and Leimar 2020). Although our model is not a game theoretic model, it has the characteristics that McNamara and Leimar (2020) call for as an update to game theory in biology. Specifically, (i) we consider the simultaneous evolution of multiple traits, where female extra-pair mating and the two male traits of territoriality and offspring care may have consequences for each other. (ii) Through inheritance, the genetic algorithm ensures rich individual-level variance, and stochasticity and noise have also been added to mate choice, nest localization,

Fig. 7 The evolutionary trajectories of male reproductive behaviours have consequences for male demography through the trade-off between total reproductive investment and survival. During the pronounced increase in female EPC between ca. 10,000 and 20,000 years into the simulation, males invested less, survived longer, and females became the limiting sex. **b** and **c** show age distribution of breeding males and females, respectively, with the top lines denoting total number of nests in the population. **a** shows trajectories for mean male care (yellow line), male territorial defence (blue line), and female EPC (red line) over time (as in Fig. 2d)



fertilization, hatching and survival (see also discussion in Rumińska et al. 2023). (iii) The males make use of local information available through low-level sensing that feeds into simple reaction norms that require only limited cognitive capabilities. (iv) Consequences emerge on multiple time-scales, both within the season but also by affecting survival to subsequent breeding seasons and thus includes elements of life history theory. In sum, the model represents fairly simple strategies that are evolving in socially variable and complex environments where consequences appear on multiple timescales, in contrast to the often cognitively demanding strategies in simple environments that are common in game theoretic models (McNamara and Houston 2009; McNamara 2022).

When we evaluated the behavioural dynamics of this evolutionary individual-based model, it became clear that individuals were engaged in behaviours that resemble typical games from game theory. Some of these apparent games were multidimensional, both in terms of the number of players and because multiple actions had cumulative impacts with consequences only much later in the season or in life. A strength of this approach is that we avoid having to assume beforehand which responses are beneficial or detrimental to the simulated individuals. A problem is that rigid specification of model rules could have the undesirable side effect of flattening the complexity inherent in natural systems to just one or a simple set of strategies. Using reaction norms and the possibility of flexible behavioural strategies opens

up for additional evolutionary outcomes (McNamara et al. 1999). For example:

- Recognisable from game theory is how males invest in territorial defence at shared borders, where the male who invests most in territorial behaviours gets a larger share of the resource benefits
- Highly territorial males have, however, comparatively less effort to put into parental care. This trade-off is influenced by and embedded within another game, where females who mate extra-pair incentivise neighbouring males to relax territorial defence so resource flow to his extra-pair offspring. Spending less time on territoriality frees time for providing care. This can thus be thought of as a game where females benefit if they can make males work harder for offspring production (Trivers 1972). Conversely, if matings are mostly within-pair, the female provides her social male with incentives to be strongly territorial as that secures resources to the many offspring he has in their shared home nest, but potentially at the cost of reduced care. This game depends on the way the male reaction norms evolve — in our simulations, males defended more with increasing within-pair paternity and decreasing extra-pair paternity
- The next level is a game among females, where a group of females who all mate extra-pair with roughly the same probability can incentivise a neighbourhood where males evolve to invest even less in defence. Because the male now shares borders with less aggressive neighbours, everyone can invest less in defence and still retain nearly as much resource. This is due to tug-of-war dynamics, where the outcome is shared equally when contestants fight equally, no matter whether they fight hard or hardly at all. In other words, stabilising selection on females to promote diffuse paternities makes males waste even less effort on aggression, which frees time for males to care, which eventually benefits females
- Finally, a game emerges across breeding cycles in the low-mortality scenario. Here, male reaction norms have evolved to react to high female EPC rates with reduced overall reproductive investment as a means to prioritise survival to future breeding attempts. Thus, instead of accepting a bad paternity deal this year, the males may reduce on overall investment, increase future survival and breed again

One can also see how there are apparent games in wild populations that are not included in this model, and that future work would need to address. For example, when it comes to information, females may want to signal high within-pair paternity to their social partner and simultaneously high extra-pair paternity to their male neighbours, thus securing maximum investment in their nest from many

males. Concealed and quick copulations could play into such a game, and sperm selection is one dimension of this game that has been widely studied (Birkhead 1998). Another example is the well-studied competition and positioning among both females and males for pair-bonding in species with bi-parental care (Kokko et al. 2003). Furthermore, extra-pair copulations are not randomly distributed as in this model, and there are individual differences among both males and females that affect the likelihood of an extra-pair copulation taking place (Houston et al. 2005).

Males and females coevolve

During the mating season, females and males may adjust their efforts to balance their own survival with the prospects of their offspring, as shown in Figs. 5 and 6. In Fig. 5, we have plotted as a phase diagram the trajectory of population means in male care versus female EPC, which shows cyclical changes indicating that there is a certain balance between what females and males do. Our model did not find a single and stable optimal solution for the trait values in the tested time scale, but an oscillating equilibrium around a certain gravitational point in phase space.

Although the male reaction norm may evolve to withhold care from social females with high extra-pair copulation rate, this is a toothless response when survival to future breeding attempts is low (Mauck et al. 1999; Houston and McNamara 2002). Its main effect would only be to lower the fledgling success of within-pair offspring, while any benefit to future offspring would still be close to zero. Not so when predation mortality is reduced; then reaction norms withholding care from social females with high extra-pair copulation rates evolve because increasing the probability of future breeding seasons with higher expectations for paternity has positive effects on lifetime fitness (Fig. 6). This again can be interpreted as a game between the sexes that results in different allocations within male total reproductive investment. The possibility of deserting the nest effectively puts a check on the maximum extra-pair copulation rate that evolves among females, but only after initial cycles where the male reaction norms slowly evolve the ability to make use of information in this way. That the rate of extra-pair copulation is lower and prevalence of male counter-strategies higher in the population with lower mortality aligns well with observations. Longevity has been identified as one of the most important correlates of extra-pair copulation rate across species (Griffith et al. 2002). In a quantitative review, Arnold and Owens (2002) found that adult mortality was a significant predictor of interspecies variation in extra-pair paternity rate, with a considerable drop in extra-pair paternity when adults were expected to breed twice or more. Short-lived species in general have high and long-lived species have low levels of EPC, suggesting this mating strategy might be an evolutionary adaptation that enhances

their success. For example, in the short-lived tree swallows *Tachycineta bicolor* EPP stabilises between 50 and 87% (Barber et al. 1996; Kempenaers et al. 1999). In contrast, long-lived saddlebacks *Philesturnus carunculatus* (expected life span: 17–21 years) and robins *Petroica australis* (up to 14 years) have EPP rates of 0–2% (Taylor et al. 2008). The parent–offspring conflict, evoked first by Trivers (1972), extends this to multiple mating seasons when males have a chance to save their investment for later.

Male reproductive investment and emergent sex ratios

For the case of the short-lived population in our model, the problem of explaining high female EPC levels has a fairly simple solution — the EPC reaches relatively stable values over several thousand years, and the final fluctuations, at least in our simulations, are relatively small. Males, deprived of the opportunity to leave, put a large part of their energy into raising their young, so that at least some of the individuals will carry their genes into the new generation. Things start to get complicated when males live longer, which effectively introduces the option of leaving the social female for the benefit of potential future broods, and it is when interesting co-evolution of male and female reproductive strategies can be observed.

Temporal variations in reproductive investment also have consequences for population structure, through trade-offs with survival. Trivers (1972) noted how the unbalanced number of males and females is closely related to their role in the adopted strategies in raising offspring. When more females engage in high EPC, males invest less, live longer, and more older males appear. Because the model prioritises older males as mates, young are produced only in numbers to fill the remaining empty nests (the total number of nests is constant over time), and older males represent a larger percentage of the breeding population in this phase of the simulation. It is a reasonable biological assumption and observed in many species (Forslund and Pärt 1995) that older males are more successfully mated. Studies of social behaviour reporting how familiar birds retain social relationships from breeding to wintering grounds (Beck et al. 2020), or pairs that breed together in consecutive years, speak to mating advantages of experience or old age.

Conclusions

In this model where key breeding behaviours were given flexible formulations and a genetic underpinning so that they could evolve, it was interesting to see how many games could be identified from the emerging behavioural strategies among different constellations of individuals, and how these changed over time. The successive cycles of extra-pair

mating and male care and territoriality that became progressively smaller and faster (Fig. 5) demonstrated how genes of males and females form a gene pool that is tightly interconnected and co-evolves so that changes in one trait have consequences for the rest of the genes and determine likely evolutionary paths ahead. In our case, the specific mechanism was the male reaction norms, which may take a long time to evolve: in each breeding season, the male only experiences one value for the within-pair copulation rate, so it takes many years before different parts of the reaction norm have been subject to selection. Meanwhile, mutations and genetic mixing may have changed the genetic strategy. To fully appreciate the potential and resilience of natural selection, one therefore would need to think beyond the individual and the strategy to consider the history of the gene pool in conjunction with the current population-wide selection acting on it.

Author contribution AR, SE and CJ conceived the study and designed the model. AR coded the model, analysed the results and made the figures with input from SE and CJ. AR and CJ wrote the paper with input and edits from SE.

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Data availability The code and data analysed in this study are available publicly in the online repository: <https://github.com/aruminska/EPP>.

Declarations

Ethics approval The study presented in this manuscript is purely theoretical, and no animal experiments or field observations were performed.

Consent for publication The authors agreed to publish the manuscript.

Conflict of interest The authors declare no competing interests.

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