

Non-reproductive males as an evolutionary stable strategy: Insights for social species

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Abstract

We present an evolutionary account for the emergence of non reproducing males (NRM) in biological populations, potentially extensible to any range of non-monogamous social species. Accordingly, NRM is to be viewed as an evolutionary stable strategy (ESS) which works by improving inclusive fitness through the luring of more and better quality mates, directed by the NRM individual. Female preferences have been shown to be amenable to NRM associated behavior, which is also correlated to lower perceived threat by other males, resulting in decreased aggression and allowing for a longer actuation range. Using a mathematical model, we demonstrate that much like bonobos are matriarchal societies and chimpanzees are male centered, humans are a NRM-centered species, with NRM clustering working as female/male clustering in these species. Finally, we review how humankind history has been firmly steered by NRM, from the Greeks to the Church to Newton, and show how the modern occurrence of NRM can be rationalized if being triggered by diverse demographic access from early age, consistent with evolutionary scenarios.

1 Introduction

As Darwin outlined in *The Descent of Man* [3], reproduction is the engine of evolution. Sexual selection favors traits that increase an organism's ability to reproduce relative to alternative traits. Given the primacy of reproduction, seemingly counter reproductive traits such as the occurrence of non-reproducing-males (NRM) in biological populations pose an evolutionary puzzle [9]. Why would selection have fashioned behavioral mechanisms to forego mating?

The complex nature of the occurrence of NRM indicates its inheritance is not a simple Mendelian trait, making the issue difficult to attack from a genetic mapping standpoint alone. Moreover, little exists in the sense of demonstrating NRM as an evolutionary stable strategy (ESS), owing in part for lack of existing suitable data. To the best of our knowledge, few mathematical analyses of NRM have been realized [4, 5].

The notion that NRM may act by increasing inclusive fitness is not new, having been supported by studies with human populations [2] showing a correlation between kin fecundity and the occurrence of NRM. We advocate that NRM inclusive fitness does also work through male kin fitness enhancing. Namely, the absence of deceptive mating motivation on NRM may facilitate their approximation to females and influence on mate choice, due to the absence of competing interests or competition when compared to other males or females respectively. This proposal has been recently tested on human populations, with supporting results [13]. We propose that this kind of thought may be potentially extended to any social species. In particular, the bigger the population, the greater the effect a NRM may have on kin fitness. This strategy would probably not work as well on small, monogamous populations, where the the cost of foregoing reproduction may outweigh the benefits of inclusive fitness, due to reduced kin number and reproductive potential.

We also put forth a thermodynamic model, based on two dimensional molecular dynamics to capture the essential features of a biological population on the surface of earth subject to social interaction with differing individual evolutionary strategies.

Finally, we propose that humans are a NRM-centered species, with NRM clustering and conflict of interests playing a steering role on the recent history of humankind, which we support with a brief historic review.

2 NRM mechanisms for inclusive fitness

NRM usually baffles evolutionary theorists as one of those kind of behaviors one does not expect evolution to forgive, much like altruism would. Kin selection theory [6], not without its detractors [1], is often invoked as taking care of such embarrassments. NRM may be able to bolster their own inclusive fitness by improving the fitness of their own kin, which could be an advantageous strategy if the boost is large enough or if enough kin is benefited. There are two proposed mechanisms by which this could occur towards male or female kin.

The existence of fundamental biological differences between genders has given rise to competing heterosexual mating strategies. Females have a finite supply of eggs, and very limited reproductive potential compared to males. Moreover, the parental investment required by females to endure pregnancy, and rear offspring is considerable. Evolutionarily, females have been selected to put a premium on quality mate choice, maximizing fitness by seeking a high quality, long-term, committed mate willing to provide protection and resources to support her offspring and her. Therefore, females should be inclined to postpone mating until able to assess these qualities in her potential mate.

In contrast, for males, sperm are plentiful, and parental investment virtually non-existent. Males can thus maximize their genetic legacy by pursuing relentless mating with as great a number of mates as possible [8].

Towards females, inclusive fitness enhancing could happen if a NRM is able to improve their offspring survival chance, a form of parental investment (though

it may be better called kin investment).

Towards males, the NRM should improve their mating chances. To that end, the NRM must be able to influence female mate choice, and prompt earlier, more frequent mating towards his own kin. We propose the following mechanism for this: NRM individuals have better chances of socially relating to females than other males, due to the absence of deceptive mating motivation. They also have the upper hand when compared to other females due to the absence of competing sexual interests, given females compete for parental investment of the better males, a very scarce resource. This suggests that if female mate choice is influenced by social factors, NRM should rank high on the list.

Moreover, NRM related behavior signals no sexual competition with other males, meaning reduced aggression and social threats. This adds for range both in the NRM social reach, as well as lifetime, which can translate to invaluable investment on kin.

Through expanded social reach, NRM individuals gain on fitness enhancing power (towards kin males), meaning, the more females within reach, the more NRM kin matters. This implies NRM incidence should be correlated to female availability. Therefore in small populations or with monogamous species, NRM might not be as good a strategy as straight reproduction.

The mechanism through which the NRM may come to recognize kin is open to debate. It is likely that as in the Westermarck effect [10] this occurs through imprinting on early age. In larger social clusters then, it is probable that NRM individuals provide more indiscriminate assistance.

An immediate corollary from the two previous paragraphs is then derivable for the human society: given the explosive growth of our social group sizes, with virtually no evolutionary time to adapt our ESS, we should experience a sizable rise in NRM incidence in our societies. Moreover, given the almost universalized collective care individuals experience from early age, socializing closely to large numbers of unrelated individuals, it is only logical that these NRM individuals will tend to realize in a growingly indiscriminate manner their hard wired inclusive fitness enhancing behavior. The consequences of this realization and more are fully explored on section 4, after we present a mathematical model to corroborate these propositions.

3 A model for NRM on populations

We have developed a thermodynamic model, based on two dimensional molecular dynamics [7] to capture the essential features of the evolution of a biological population on the surface of earth subject to social interaction with differing individual evolutionary strategies. We understand that the genetic elements associated to NRM behavior are complex, and should be treated as a continuum rather than in a boolean manner.

Social interactions have been modeled using potentials with varying equilibrium distances between individuals, as a function of their NRM-ness. The idea to use atomic potentials to model social interactions is not new [14], although

to our knowledge this is the first such simulation.

Let there be a population of N individuals. Each individual has a position vector in the Cartesian plane, $X_i = (x_i, y_i)$ and a velocity, $v_i = (x_i, y_i)$. Moreover, each individual has an associated NRM coefficient, $G_i \in [-1, 1]$. G_i is negative for females and positive for males, thereby its signal accounts for the individual gender.

In each time-step Δt individuals move a distance $v_i \cdot \Delta t$, and their velocity is re-scaled towards a baseline velocity v_o by making $v_i \rightarrow \sqrt{v_o/v_i}$ (any thermostat could be used, but this is the simplest).

During each time-step their velocity is also changed by $v_i \rightarrow v_i + \sum_{j=1}^N F_{ij}$, where F_{ij} is a Lennard-Jones like potential, whose equilibrium distance, $Q_{ij} \in (0, \infty)$ is a function of both individuals NRM coefficients and genders, $Q_{ij}(G_i, G_j)$. Q_{ij} should be low for two high NRM coefficient males, high for two low NRM coefficient males, and low for male-female interaction.

At any moment, a female may be a pregnant or not. If the female i is not pregnant, it may become pregnant by a male j with a probability $P_i(\vec{X}, \vec{G})$, dependent on the positions of other individuals, \vec{X} , and on \vec{G} , the NRM coefficients of all other individuals. P_i should favor males by closeness, lower NRM coefficient, and by having high NRM coefficient males close by the male and female.

When a female becomes pregnant, she stays so for a period of τ time-steps, during which she cannot become pregnant again. After the pregnancy period, a new individual appears at female i position with initial velocity v_o randomly directed. This new individual, k has equal chance of being a male or female, and a NRM coefficient given by a probabilistic function $G_k = (G_i, G_j)$, his NRM coefficient is a function of his parents NRM coefficients, proportional to these NRM coefficients average plus a random fluctuation. Moreover, a newborn individual has a childhood period of C time-steps, during which it cannot mate.

Finally, at any given time, an individual may die (i.e. simply disappear), with a probability dependent on its age (the number of time-steps since birth), $K(T_i)$, and should increase with age.

4 NRM on human species

We'd now like to turn our attention to the role NRM individuals play on the human species. As with any species, one of the vital viewpoints one must address is the evolutionary one. As such it is necessary for us to take a few steps to take a few steps back in order to be able to frame humans and NRM in the bigger picture. In particular, it is useful to reach back to our two closest living relatives - the Bonobo and the Chimpanzee - in order to gain some evolutionary vantage point. Analyzing the social structure of these two species can yield valuable insights for our own.

Chimpanzees are a male-centered species. Bonobos are female-centered [11]. On chimpanzees, social interactions are marked by a high level of aggression and threats, and controlled by dominating male clusters. On bonobos, they are

marked by social bonding fostered by sexual behavior, and controlled by females. The strong affiliative relationships between unrelated female bonobos provide an alternative model from which predictions for bonding among human NRM individuals can be generated. We propose that humans are a NRM-centered species, with NRM clustering playing the same mediating role in social interactions as male/female clusters do in chimpanzees/bonobos. Likewise, we propose that part of the behavioral repertoire of NRM individuals was re-purposed for social bonding among NRM individuals. This suggests that we are to expect similar behavior among NRM individuals as we see among female bonobos. It's likely that reproductive drive and associated behaviors have been redirected towards NRM bonding and social influence, resulting in NRM clusters steering the groups social dynamics, directing benefits towards kin. Given the large resources allocated to reproduction, it's conceivable that this relocation of efforts by NRM individuals could be very effective indeed.

On an eusocial species with such complex and vast social networks as ours, this kind of influence would be greatly amplified on networks larger than those common during the shaping of our species on the Pleistocene. Although it is hard for us to assert the exact nature of social relation among human predecessors during the Pleistocene, if NRM influence is nearly as close to what we propose it is, examples of NRM individuals in history should abound.

Regarding NRM individuals in human history, we provide here a small example set of individuals whose actions had decisive historical influence, ordered chronologically: Epanimodas, Alexander the Great, Leonardo da Vinci, Michelangelo, Sir Isaac Newton, Gottfried Wilhelm von Leibniz, Oscar Wilde, Fritz Krupp, Nikola Tesla, Alan Turing, Godfrey Harold Hardy, Adolf Hitler, Tim Cook [12].

The lasting influence of NRM individuals on human organization is also clear, as just about every major religion is heavily based on NRM figures, Jesus and Buddah being the most prominent ones. Finally, in regard to the definite importance of NRM clustering in steering human society, it is only necessary to point out that the largest, oldest and most influential institution of human history is essentially comprised of NRM clustering: the Church.

5 Conclusion

An explanation accounting for the occurrence of NRM behavior in social species has been put forth, together with a thermodynamic model allowing for computation simulation of different social scenarios based on inheritable NRM behavior. Possible scenarios have been explored, the NRM incidence being dependent on kin number and demographic horizon and turnover rate.

Possible NRM dynamics on human society have been suggested using comparative ethology with our closest evolutionary relatives, and it was proposed that humans are a NRM-centered species. Supporting that, a brief historical review of NRM individuals on human history was discussed, and the importance of NRM clustering.

Finally, we conclude that through the mechanisms explored, modern humans extremely enlarged social circle is a trigger for the incidence of NRM. Coupled with reduced family size, this implies that modern age NRM will tend to favor kin surrogates (i.e. close friends), leading to a unique social organization. NRM is not only an evolutionary stable strategy, it tends to become the dominating strategy as social group size and demographic horizon event increases, and as social contact becomes ever briefer and the impact of immediate influence in mate choice grows, empowering NRM individuals ever more.

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