Complex mating strategies of Santa claus

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Following the initial publication on the endoparasite Santa claus [1], a study that lucidly characterized S. claus transmission from rodent to bird, a question was lingering - how is the mating system organized? Which gender selects the mate? What mating strategies do the males exhibit? In the present study, we will answer these question by supplying unique video-graphic documentation of a courtship scene. The footage include the first observation of the never before seen female S. claus. The evidence is analyzed in the framework of game theory [2] and compared to simulations of the different strategies observed. Thus, we will show that S. claus has reached an evolutionary stable strategy (ESS) [3] composed of Bullies, Gangers and Sneakers. Finally, the evidence strongly support the expectation of such a system: the female role is entirely passive.

Santa claus, game theory, parasite, evolutionary stable strategies

Introduction

Game theory is a frame-work to describe decision making as an abstract tree of branching paths which the players can walk down to optimize their benefit in different type of game settings [3-5]. Types of games include the zero-sum game, the cooperative game, the normal-form game and extensive form game [3-5]. This models have successfully been transposed to a plethora of research disciplines. The adaptation to biology was made by John Maynard Smith [6] in describing the modes *conflict* and *cooperation* from an evolutionary perspective. The males were considered actors that can compete for a limiting resource, the female's womb [6]. Thus, the females can be seen as the biological market [7] to use a metaphor from Economics.

Evolutionary Stable Strategies (ESS), were described as optimizations, on the population level, in frequency distributions of the different available male strategies [6, 8]. The ESS is not necessarily the most optimal state from the perspective of the players. In contrast, it is rather common that each player would have its preference elsewhere, but that the competing players all push towards the ESS from different direction such that the females will benefit from producing offspring reflecting the ESS [8].

Of crucial interest to successfully model the ESS and to understand the mating patterns of a

species, is which gender selects the mate. This has to do with the naturally unbalanced pattern of fitness between the genders where males can supply many females with offspring. In contrast the women, can only hatch one brood at a time. The parallel versus the serial paradigm. It is widely accepted that when the serial gender is the mate selector, evolution will produce runaway mate selection according to the sexy son hypothesis [9]. In contrary, when the parallel gender selects mate, it leads to fractioning of mating type strategies among the actors [9]. In the latter case, there is no need for sexy sons, and thus the male phenotype variation will be operative in contrast to decorative [9].

Materials and Methods

Image Traps

Fifteen image traps equipped with computer vision software was deployed in September 2012 as described elsewhere [1]. The film is supplied along the article as Online Supporting Material

Game Theory Simulations

The Amazon E3 cloud was used. A MatLab-script was constructed with the three observed strategies *Bullies, Gangers* and *Sneakers* coded into it. It was run at 10 000 iterations for population sizes 100, 1000, 10000, and 100000 as well as 2 dynamic populations. The dynamic populations

the preexisting frame-work, such that the populations were allowed to vary in size according to (a) random stochastic extrinsic variables and (b) random stochastic intrinsic variables.

The code is supplied and described in detail in Appendix A.

Results

Analysis of the image trap footage during late December showed a courtship scene where a female S. claus showed herself ready to mate by leaving the home and prancing around outdoors enticing the males.

Three male mating strategies were observed. They were dubbed Bullies, Gangers and Sneakers. Bullies and Sneakers are known from other species to exist. The Bully is a dominant alpha-male that uses its superior strength and size to acquire mates. The Sneaker, also previously known, is like the weasel, a sneaky character that comes in the back-door in a hit-and-run fashion when the Bully isn't watching. Finally, the great surprise is the existence of the Gangers-strategy, small specimens that team up in mobs. Unfortunately, no successful mating was observed for this strategy.



Figure 1: Static ESS Models for 4 populations sizes (0.1k, 1k, 10k & 100k). Bullies (Red line), Sneakers (Green line). ESS marked as star.

are to the best of our knowledge an extension of The static size population models all fell short of reliably maintaining more than two mating strategies at the same time. Specifically, the Gangers were always eliminated from the population (See Figure 1A-D). However both dynamic size models managed to maintain all three strategies (Firgure 2A-B). Further, the intrinsic size model best approximated the frequency distributions observed.



Figure 2: Bullies (red), Sneakers (green), Gangers (blue). ESS marked as star. Panel A shows the extrinsic population model, panel B the intrinsic.

Discussion

To classic game theory, Gangers is an absurd strategy and has previously been dismissed on the face of it being an altruistic behavior. Since it is exposed to *Cheaters*, a very important strategy, that could hide in the flock without exposing itself to the risks of fight. However, since the behavior was observed, it can be inferred that Ganging is a viable strategy among S. claus. One can only speculate about the mating-ritual of successful Gangers and the genetic structures that allow these mutualistic groups to exist.

It comes as little surprise that the Gangers were not maintained in the classic setups of the ESS-models [8], as they would else have been reported decades ago. It is however telling that when the models were made to be biologically relevant, a concept which implications hardly can be said to be understood among the cadre of theorists with little biological training, they all fit the data observed. That the intrinsic model best correlated with the observations has implications on conservation biology, as it suggests that the variation in S. claus is regulated not so much by environment as by unknown underlying genetic factors. If S. claus should be passing a genetic bottleneck, a great loss of phenotypic behaviors

could thus be expected and the *S. claus* population structure could be disrupted an a way that the only known *Ganger* strategy in animalia be lost to the world.

Conclusively, the phenotypic variation displayed among the males/actors clearly fell in the operative category. Decorative variation were small to non-existent. This is strong support for the passive role ascribed to the female *S. claus* in classic literature and illuminates the fallacy of modern writers that wish to transfer the gender roles of an enlightened modern human society onto behaviors of other biological species.

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