



Research Article

PRELIMINARY INVESTIGATIONS INTO THE PREDATOR PREY DYNAMICS OF INDIAN DINOSAURS BY AGENT-BASED MODELLING SIMULATIONS

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ABSTRACT

Advancements in computer simulations have facilitated the understanding of paleobiology and paleoecology of extinct animals even in cases of limited paleontological evidence. Two dinosaur species, *Rajasaurus narmadensis* (Wilson), and *Isisaurus colberti* (Jain & Bandyopadhyay) dominated the late Maastrichtian stage of upper Cretaceous Lameta formation in India, whose paleobiology is poorly understood. A preliminary approach to understand the predator prey dynamics of these two dinosaur species is presented in this study using Agent Based Modelling Simulations (ABMs) program *Netlogo* by modelling the agents under three scenarios of varying predator prey ratio (PPR) and analyzing the results. The results revealed that the scenario with the high PPR provided maximal predation success, faster and higher kill numbers and overall predation efficiency, similar to extant predators/ facultative scavengers. Further research including additional key factors in the simulation models are necessary for a better understanding of the paleoecology of these dinosaurs.

Keywords: Dinosaurs, *Isisaurus colberti*, Predator-prey dynamics, *Rajasaurus narmadensis*.

INTRODUCTION

The late Cretaceous, Maastrichtian stage Lameta beds of central India have yielded important fossils of two dinosaur species viz., *Rajasaurus narmadensis* (Wilson), an abelisaurid theropod and *Isisaurus colberti* (Jain & Bandyopadhyay), a titanosaurian sauropod (Wilson *et al.*, 2003; Jain and Bandyopadhyay, 1997). Both the species of dinosaurs shared the habitat with other dinosaurs of the Indian subcontinent, namely the *Jainosaurus septentrionalis* and *Indosuchus raptorius* (Paul, 2011). In contrast to the extensive work on dinosaurs from other parts of the world, a study on the paleoecology and paleobiology of the Indian dinosaurs is lacking. Although, it has been known that *Rajasaurus narmadensis* preyed on *Isisaurus colberti* and *Jainosaurus septentrionalis* (Paul, 2011), studies on the predator-prey dynamics of these species are either extremely rare or rather poorly understood. Since it is impossible to determine interspecific interactions of extinct species by direct observations, other means to elucidate the mechanism of ecological interactions become necessary.

One such method is the adoption of Agent-based Modelling simulations (ABMs), considered to be primary tools in ecological modeling which are computer programs to simulate the target system and its interactions. In ABMs, entities or agents with defined conditions interact in the virtual system allowing researchers to perform tests of interest in a limited timeframe and helps in understanding the nature of the system under study (Pahl and Ruedas, 2021; Bousquet and Le Page, 2004). In this context, this study was designed for elucidating the predator-prey dynamics between *Rajasaurus narmadensis* and *Isisaurus colberti* and to provide a model framework for reconstructing potential paleobiological and paleoecological scenarios for future studies.

MATERIALS AND METHODS

The Agent based Modelling simulations (ABMs) for the present study was designed using the freely available program *Net Logo* (Tisue and Wilensky, 2004) latest

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version 6.3.0 (available at <https://ccl.northwestern.edu/netlogo/download.shtml>). The simulation was designed with the mobile agents, *Rajasaurus narmadensis* and *Isisaurus colberti* placed on a 50 X 50 grid space corresponding to a 2500 sq. km landscape (Figures 1 and 2). The agents were designed to match the specific body proportions per the known estimates to arrive at realistic results (Paul, 2011). All the agents were set to move randomly on the simulation landscape as defined by the program parameters with the agent *Rajasaurus narmadensis* to actively pursue and kill its prey *Isisaurus colberti* and incurring an energy cost of about 10 per cent per predation event. Three simulations

scenarios with Predator/Prey Ratios (PPR) were set as follows: (1) Low PPR = 1:100, (2) Mid PPR = 1:10 and (3) High PPR = 1:2. Each simulation scenario were run for 10 trials each for a total of 30 trials for all three scenarios and each trial lasted for a time frame (in days) when all *Rajasaurus narmadensis* agents died. Data were collected for all the trials and the statistical analysis was done for the consolidated data by incorporating appropriate statistical tests using *GraphPad Prism* version 8.0.2 (263); GraphPad Software Inc., La Jolla, CA, USA (Motulsky, 2007). Statistical significance was set at 5 per cent probability level.



Figure 1. Interface of Netlogo program displaying the simulation space with programmed agents and parameter controls.

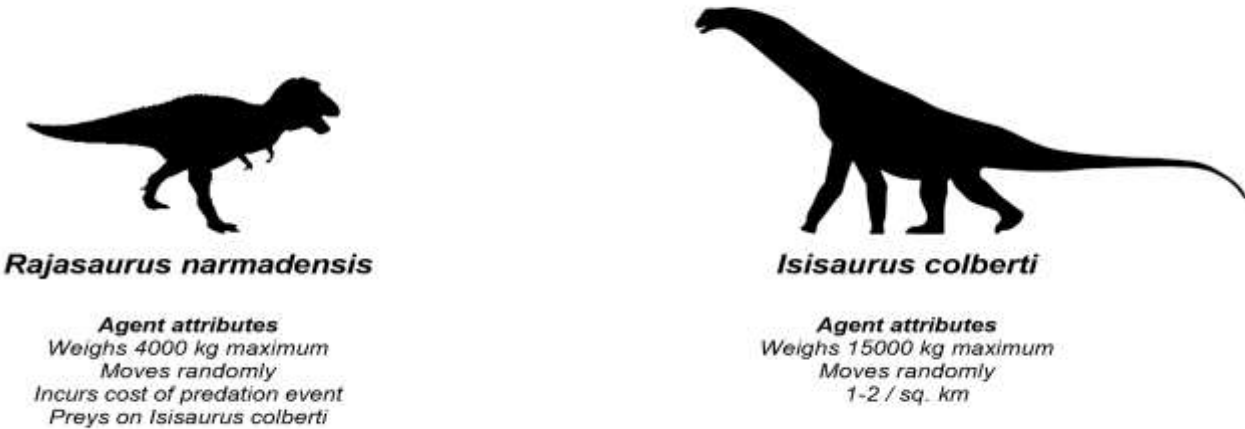


Figure 2. Simulation agent types and their attributes.

RESULTS AND DISCUSSION

The simulation of the different scenarios using the agents, *Rajasaurus narmadensis* and *Isisaurus colberti* revealed several important insights. The efficiency of predation (%) was found to be increased with the increase in predator population and was found to be positively correlated to the number of predator agents available in the simulation landscape (Figure 3). Similarly, the number of days to make the first kill was inversely proportional to the number of available predator agents in accordance to the set PPR and was found to significantly differ ($P < 0.05$) among different scenarios (Figure 4). The number of days of survival of predators and hence survival rate (%) were found to be dependent on the available predator population (Figure 5). Higher predator prey ratio correlated with high percentage of days of survival of predators in the system and decreased in relation to lower PPR. The difference in survival were found to be significantly different ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$) across different PPR simulation scenarios. The total number of kills during the simulation time frame was also found to be significantly ($P < 0.0001$) associated with the given PPR in the different simulation scenarios (Figure 6). It was found that the total number of kills was found to be low at the PPR of 1:100 and a higher kill count value consistent with PPR value of 1:2 was found to be evident from the simulation.

The dinosaurs *Rajasaurus narmadensis* and *Isisaurus colberti* roamed the landscape of the Indian subcontinent 67 million years ago at a time in the earth's history when the

Gondwanaland mass dismembered and the Indian plate drifted northwards. The habitat conditions were similar to an island continent and provided the inhabitant dinosaurs to evolve several morphological features specific to the region and adapted to suit the interspecific interactions among the taxa (Bhatt, 2003). Further, it has been difficult to ascertain the theropod ecology due to the apparent lack of modern analogues necessitating the adoption of recent advances in paleontology and simulation modelling to determine the paleoecology of these extinct animals in terrestrial Mesozoic ecosystems (Kane *et al.*, 2016). While the population density of a species is inversely proportional to its home range consistent with its body size (Brown *et al.*, 1995) there are reasonable expectations that the large predatory dinosaurs should have lower population densities than their prey species. However, it has been found that the gigantism in large theropods is facilitated by lower food requirements and higher reproductive rates (Farlow, 1993; Burness *et al.*, 2001) and a taphonomic census of the faunal assemblages of Upper Cretaceous Hell Creek Formation of northeastern Montana, USA estimated a predator prey ratio of 2:1 with a relative abundance of large predatory dinosaurs (Horner *et al.*, 2011). While detailed estimates on the population densities of the dinosaurs from taphonomic studies in India is currently unavailable, it is reasonable to base our understanding on the population densities of dinosaurs occurring at a similar time period elsewhere in the world to help us draw a picture of the predator-prey dynamics of the ecosystem of interest.

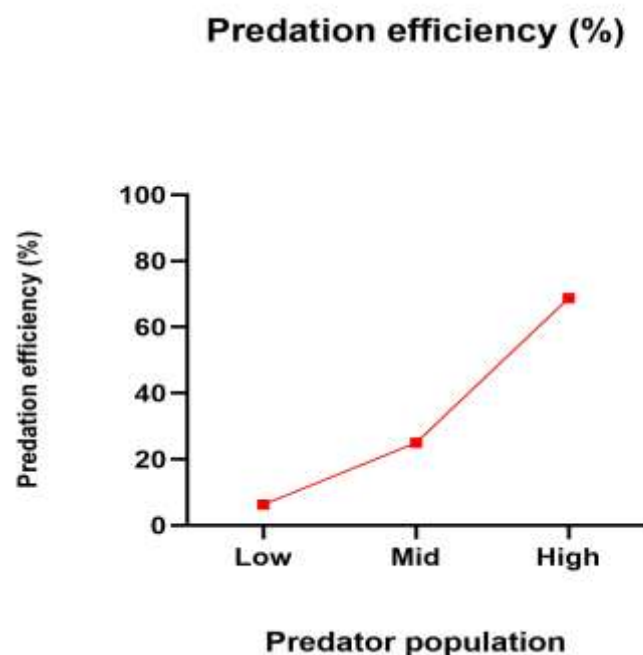


Figure 3. Predation efficiency (%) significantly increased as predator population increases at the set PPR in the different simulation scenarios ($R^2 = 0.98$; $P < 0.05$).

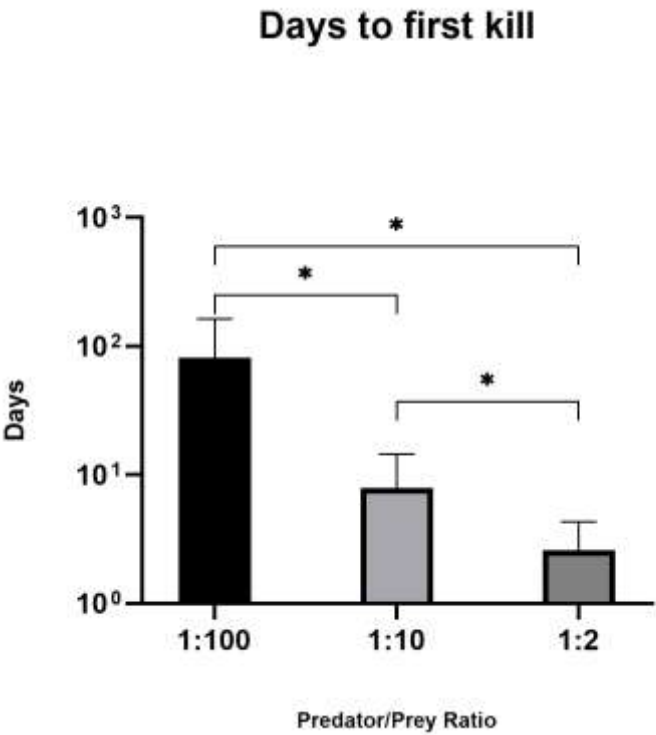


Figure 4. The number of days taken to make the first kill at the given PPR in the different simulation scenarios (* $P < 0.05$).

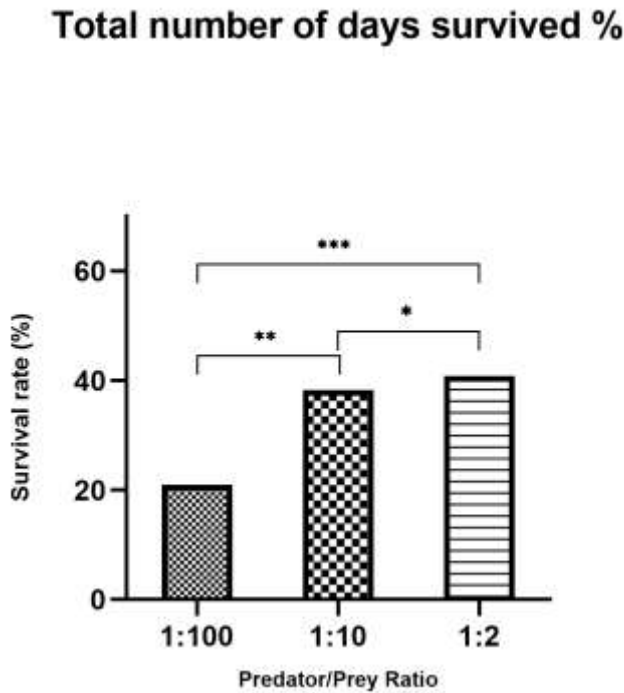


Figure 5. The survival rate (%) of the predators at the given PPR in the different simulation scenarios (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

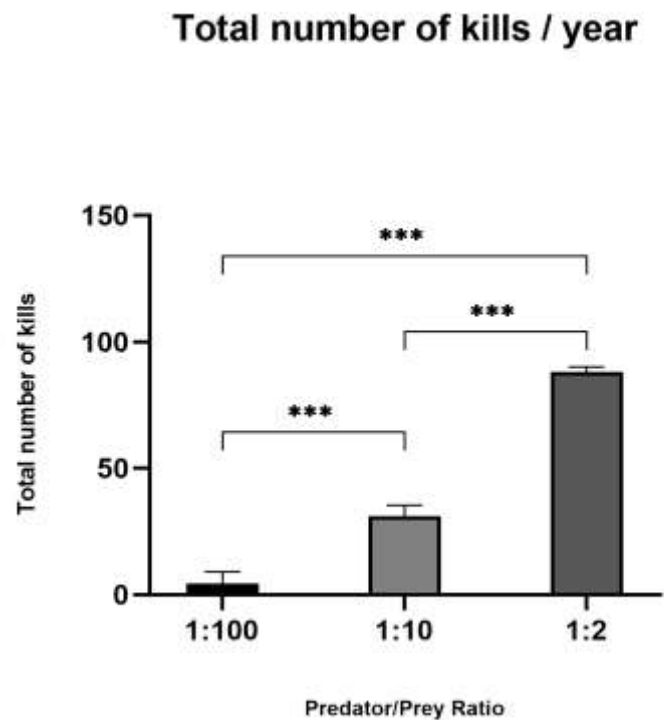


Figure 6. The total number of kills during the simulation time frame at the given PPR in the different simulation scenarios (**P<0.0001).

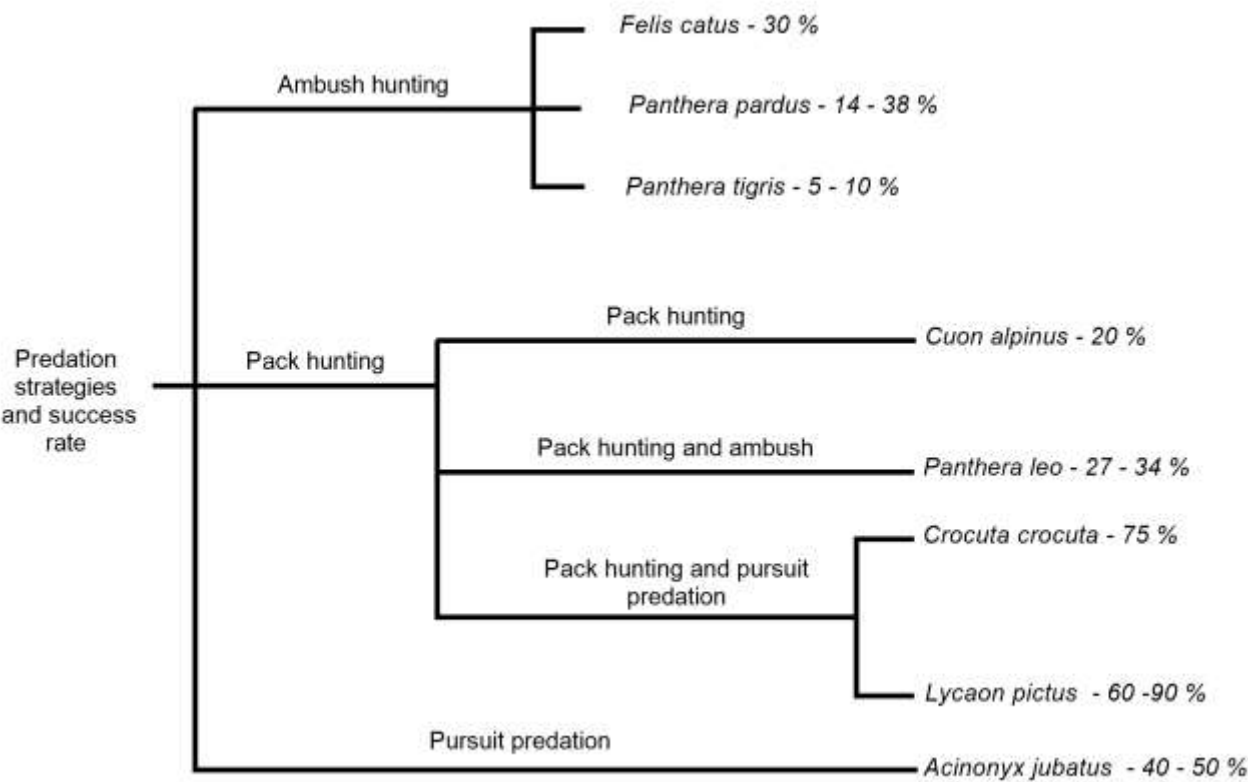


Figure 7. Predation strategies and hunting success rates of extant carnivores.

Another aspect of the ecological considerations of predator-prey dynamics is the hunting success rate of a predator. It is the ratio of successful killing of prey to that of the total number of attempts and is influenced by various factors such as physical features, favorable conditions, temporal state, prey preference, age and experience. While the hunting success rate of most mammalian carnivores falls below 50%, some African wild dogs achieve success rates of over 90% (Smith *et al.*, 2020; Jarvey *et al.*, 2022) and is attributed to the adoption of specific predation strategies (Figure 7). Although it is impossible to determine the hunting success rate by direct observation in case of *Rajasaurus narmadensis* or any other extinct dinosaur for that matter, the simulation results from the present study showed a predation efficiency rate of 68.75% which falls roughly within the subgroup of pack hunting and pursuit predation strategy adopted by hyaenids and canids. It is also interesting to note that, in contrast to other large felids, both the hyaenas (*Crocota Crocuta*) and African wild dogs (*Lycaon pictus*) are facultative scavengers (Pereira *et al.*, 2014).

Given the similarity of hunting success rate of *Rajasaurus narmadensis* with that of hyaenas and wild dogs possibly due to adoption of similar predation strategies, a few important assumptions about the paleobiology of these extinct creatures are drawn as follows. For example, the presence of a frontal horn ornaments as narrowing the binocular field of vision, and bite force similar to that of *Allosaurus fragilis* (Delcourt, 2018; Pahl *et al.*, 2021), it can be speculated that *Rajasaurus narmadensis* was possibly a facultative scavenger like modern day hyenas substituting carrion for fresh kill to meet its energetic requirements. One reason to draw this conclusion is the significant energetic advantage and efficacy that can be brought about by such opportunistic scavenging in intermediary sized theropods (Kane *et al.*, 2016).

Although several key insights were revealed from the present study, it should be noted however, that the model is not comprehensive and several key factors need to be considered before arriving at a deterministic conclusion. For instance, simulating the paleoeco systems are not easy and accurate as several key factors such as the average birth rate and death rate, presence of other biotic agents, non-target prey species, conversion of biomass, migration and epidemic events all contribute to the complexity of modelling a realistic functional ecosystem simulation. Further research will focus on the inclusion of flocking behaviour in the titanosaurid prey species and carcass availability to understand its effect on predator-prey dynamics.

CONCLUSION

This study showcases a preliminary approach to devise and design a model system to understand the predator-prey dynamics of dinosaurs of lameta formation in India and inclusion of additional data derived from future studies would greatly help to improve our understanding of the paleobiology and paleoecology of such extinct ecosystems.

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