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A Critical Analysis of Unusual Prey Predator Relationships with Regard to their Exclusive Evolutionary Advantages

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Abstract

Objectives: To study unusual prey-predator relationships and generalize them to include behavior reversals and to find out whether they are actually role reversals or mere misnomers. **Methods:** Meta-evolutionary Analysis of various cases of role reversal *e.g.* plant parasitism, plant Carnivory, prey-predator role-reversal and cannibalism to find out their exclusive evolutionary advantages for the species involved. **Findings:** Most cases of role-reversal are, strictly speaking, not role reversals at all. Rather, such unusual prey-predator relationship is part of their natural method of survival or reproduction. The nomenclature of role-reversal on the basis of just their relative size is thus not proper. S*antalum,* wrongly designated as an obligate root-parasite is rather a self-sacrificing species for its evolution by purposive association without harming the host plants. Similarly, plant carnivory also is a kind of role-reversal, since plants are thought to be preyed upon by animals and not the converse. It is proposed that a proto-instinct has developed in these plants. Prey-predator role-reversals are studied most commonly under role-reversals, but we find that they may not be fit to be called role reversals at all, if that method is the part of the obligatory fulfillment of the survival and reproductive urges. **Applications/Improvements:** Generalization of role reversals to behavior reversals and their meta-evolutionary analysis.

Keywords: Cannibalism, Evolutionary Urge, Meta-evolution, Plant Carnivory, Plant Parasitism, Prey Predator Relationship, Role Reversal

1. Introduction

Organisms interact in a variety of ways, one of which is through food consumption as in predator-prey interaction. In most cases in the animal world (~ 90%), it is the large-sized predator that consumes the smaller prey[1,2]. Predators have evolved various mechanisms by which to catch their prey and the prey have developed mechanisms to avoid being caught by the predator[3]. In insects, for example, predator avoidance includes morphological (e.g. camouflage, warning colors and mimicry), physiological (e.g. chemical defense), and behavioral adaptations (e.g. aggregation, avoidance and counter-attack[2,4-5]. An extremely rare anti-predator behavior is that of role reversal. Up until now, role reversal has been attributed to cases in which a prey actively confronts its predator. In these interactions role reversal either ended with no feeding by either side or involved cases of competition between two predators, in which the larger organism preyed on the smaller one[6-10].

Prey-Predator Relations (PPR) have been widely studied in the last hundred years though it has been in existence since times immemorial[11]. The role of the individual species in terms of their interactions can change with time. Role exchanges or role reversals are specific deviations from the general track of PPRs. In these cases, prey species may confront predators in a size-dominant manner size-recessive manner, by changing population

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densities, or without specific trophic interactions[6-7, 10, 12-13]. Also it is known that adult prey of some species attack vulnerable young predators, where prey recognize the species of predators they were exposed to during juvenile stages, and effectively attack their offspring[14-15]. Some authors describe regarding ratio-dependent predation, but they are not related to the possibility of role-reversals[16].

We have recently proposed a generalization of PPR as a core mechanism of evolution[11]. In this work, for the sake of completeness of that generalization, we wish to focus on some unusual PPRs such as: (a) Plant parasitism (b) Plant carnivory (c) Prey-predator Role reversal and (d) Cannibalism. The basic standpoint of the generalization is that the evolutionary urge acts through all species including those related by PPR by the law of purposive association, which guarantees survival and evolution of all species involved. Going beyond the confines of prey-predator reversals, we propose a generalized behavior reversal where cooperation and competition are exchanged.

2. Plant Parasitism

Santalum Album is wrongly designated as an obligate root-parasite which draws nitrogen and phosphorus through supposedly parasitic action by attaching its root to that of a host plant, usually a *legume*. It may be noted that nitrogen and phosphorus are available in the soil which the host plant can draw as an autotroph, while *Santalum* cannot. Further, its distinguishing characteristics are its aromatic compounds which require more nitrogen and phosphorus than is necessary for normal nutrition and growth.

To quote Benton, "By certain criteria, flowering plants are more progressive than many animals"[17]. How? And, what explains this progressive evolution of flowering plants than that of animals? What are those precise criteria on the basis of which this progressive evolution can be explained?

In case of *Santalum* is it (obligate as a parasite) a higher state of evolution or is it an inability to be taken care of in its future evolution? The second question is what is the evolutionary advantage for *Santalum* to have its characteristic aroma?

Its obligacy as a root parasite can be gauged from the fact that the *Santalum* sapling would die without support of a host plant in about one to two years[18]. It means that if it cannot be fragrant, it would rather prefer death! The fragrance and oil of *Santalum* have medicinal and religious significance for humans. Thus, by developing these additional characteristics, it gains evolutionary advantage of coming in contact with the highest evolved *Homosapiens*, bypassing the intermediate contacts with herbivores etc. Sensation which is common to all plants regulating their behavior seems to be evolving towards some kind of a proto-instinct in *Santalum*. This is indicative of a higher kind of evolution compared to other plant species.

Now comes the question of the evolutionary advantage of the host plants. By serving as hosts for *Santalum*, which has utility for humans, the host plants ensure their own self-propagation for as long as *Santalum* would be required, so long they will also be cultivated. Thus they develop the ability to draw more nitrogen and phosphorus compared to other plants, which cannot serve as host for *Santalum*[19].

Santalum, though designated as a parasitic predator, is actually a self-sacrificing species which would survive only with its fragrance so as to serve the human requirement by voluntarily opting to be preyed upon for the purpose. Similarly, the host plant sacrifices its extra nitrogen and phosphorus drawn from the soil to let the *santalum* grow at its expense thus establishing another rung in the chain of sacrifice. Now question is: Should a self-sacrificing plant like *Santalum* be called a parasite to be bracketed along with the likes of *cuscuta*?

This analysis shows that each species, whether it is a prey or a predator, adopts a characteristic evolutionary trait by which its association with the higher evolved species will be guaranteed, which in turn would ensure its evolution into those higher species rather than surviving as the fittest in own level indefinitely or riding slowly along the tree if evolution across intermediate stages. This is precisely the law of purposive association at work[20].

3. Plant Carnivory

The emergence of carnivory in plants begs an explanation that is beyond Darwinian evolution[21]. It is stated that the carnivorous plants developed this trait to have nitrogen and phosphorus from the insects that they prey upon, since they evolved in soils lacking these two ingredients which are very essential for their growth and survival[22].

The first question is: why at all these plants grow in such nitrogen- and phosphorus-deficient soils? Secondly, how the plants deficient in nitrogen and phosphorus

sense or know that the insects are a ready source for them, since..... plants do not have a nervous system that can store and process information for prey recognition, as is the case with ordinary carnivorous animals? On the basis of cost-benefit analyses, it has been proposed that the modification into effective carnivorous systems developed in course of adaptive evolution as the soil became increasingly deficient in nitrogen and phosphorus[23-25].

We have proposed that due to the evolutionary urge acting cosmically in and through all species, by their association with herbivores, the plants evolved into them[11]. But here, there is a role reversal as the nectar-seeking (herbivore) insects themselves become the prey, trying to forage as predators. Nevertheless, here also the emergence of some kind of proto-instinct in carnivorous plants can be assumed to have been an intermediate step in moving from sensation in plants to instinct in animals. Here the characteristic sensing ability of plants for abiotic factors such as light, heat, sound (vibration), humidity, ground water and mineral availability etc. are developed to a maximum, so as to enable them to successfully sense and prey upon animals. Such heightened sensing abilities are thus apt to be called proto-instincts.

4. Prey-Predator Role Reversal

The phenomenon of prey predator role reversal, though rare, requires a special attention in view of the proposed evolutionary hierarchy. In the case of role reversal the usual prey becomes the predator, feeds on its potential predator even if the predator is exceptionally large sized compared to the prey[12].

Amphibians make predatory decisions relying primarily on prey movement and secondarily on prey size, with prey color being less important[26-27]. They respond to moving objects in two ways: small moving objects elicit the orientation of the amphibian towards the object and trigger predation, while large moving objects (antennae or mandible etc.) trigger avoidance behavior[28]. But, in case of role-reversal, the predation techniques of relatively smaller-sized predators are different from that of large-sized predators. In particular the *epomis* larva preys on amphibians such as frogs and the praying mantis preys on large ones such as snakes as an ambush predator.

- ***Epomis*-Frog Role Reversal**

When an amphibian is predated by the *Epomis* larva, it does not have a sense of being predated, but surprisingly, *Epomis* is able to sense and target its amphibian prey perfectly, even though it is a larger one. Here the question is: why do the movements of the *Epomis* larva provoke amphibian predation? And, why is it successfully able to predate on the large amphibian?

We have proposed that evolution occurs by the law of purposive association by which there is an evolutionary urge in the less evolved to become more evolved by an association with the latter, especially through the PPR[20]. The recognition of the amphibious prey is ingrained in the larva genetically. Its enormous food requirement in the short lived larval stage; is the urgency to get into the next instar and the obligatory requirement of the amphibian prey are the factors that have made the larval attack become infallible. The qualities and form of the amphibian prey is lodged in the instinctive memory of the beetle, which operates in the larval stage to aid prey recognition and successful predation. On the other hand, the amphibian prey has lot of food options to prey upon and thus is not able to sense this *Epomis* larva (morphologically similar to other prey larvae) as its predator and thus not able to get success against the *Epomis* larval attacks.

It is to be noted that if such a defense successfully evolves, the *Epomis* beetle may very well face extinction unless its entire instinctive memory and genetic makeup changes to something else. This conclusion is arrived at because the larvae have no other food option. In the third instar the larva requires a many as nine amphibian preys to molt into the pupal stage. Also the grown up *Epomis* beetle, though a generalist, has a special liking for preying on frogs and toads. All this goes to prove that by such continuous instinctive concentration on the amphibian prey, the arthropod beetle truly achieves its goal of evolving into the next higher stage of the amphibian. The amphibian on its part, by being preyed upon by the beetle, may undergo retrogression to arthropod by fearful concentration on the larva at death, in contrast to those amphibian that are preyed upon by reptilian or higher species.

Another important question which arises out of this discussion is that mere "survival of the fittest" may not be as important a criterion as progressive evolution for a fundamental understanding of the structure and the function of species in the living world. In case of *Santalum*, if it cannot have its characteristic fragrance by drawing additional nitrogen and phosphorus from a host, survival no longer carries any worth for itself. It is the urge for forward evolution *e. g.* in case of *Epomis*, it seems Arthropod wants to evolve into amphibia by PPR, that is

working in a hidden manner as a powerful determinant of its evolution bypassing several intermediate phyla[11].

- **Praying Mantis-Snake Role Reversal:** Prey-predator role reversal has been proposed to be of reproductive advantage by disproportionate allocation of energy resources[22,29]. Female mantises are observed to catch big prey like frogs, lizards, birds and even snakes[30]. We propose that the female praying mantis (*Mantis religiosa*), in order to satisfy the reproductive urge in the absence of a male, goes for parthenogenesis and in the process requires a big prey, which can be any of the large-sized predators. The offspring in this case are females only. It is observed that it preys upon the predator, but does not actually eat it whole, and eats only the blood by making incision at specific locations (on the back for snakes, and head for birds) while it is still alive and gasping for breath. Seeing its skillful predation, one wonders whether this ambush predator should be rechristened "preying" mantis rather than "praying" mantis! But nevertheless, this so called role reversal requires explanation from a meta-evolution perspective[31].

In meta-evolutionary analysis, the animals have minds filled with very strong instinctive requirements of food, mate and sleep etc. and accordingly, their instinctive minds are filled with corresponding images which gain in strength with increase in the intensity of the requirement. In addition, the fear of death or of predators is also a constant factor occupying their minds and when it is in the grips of the predator, the image of the predator gets strongly imprinted in its mind and by that, each of its cells (including the reproductive cells) gets the "strong imprint" of the form of the predator.

The female mantis, by preying on the snake, "charges" each of the latter's cells with the imprint of its form. By eating the blood charged with its form imprinted in every cell, it ensures the maturation of the unfertilized eggs in its reproductive tract for parthenogenesis which will result in growth of female forms out of her eggs. It is as though the being of the snake itself got birth as so many female mantises!

5. Cannibalism

Cannibalism is an unusual behavior of intra-specific predation where members of a species prey upon members of the same species, eating whole or part of the individual, thereby manifesting an extreme form of role reversal.

More than 1500 animal species show cannibal behavior[32]. Mostly observed in nutritionally poor environments, it helps regulating population by decreasing completion for the limited resources such as food, mate and territory. It is most prevalent in aquatic ecosystems where about 90% of the species show cannibalism at some point of their life cycle[33]. The praying mantis shows sexual cannibalism, in which the female cannibalizes the male before, during or after copulation[34-37]. Sibling cannibalism and filial cannibalism are other forms observed in different species. Kin recognition (e.g. in tadpoles) is one factor that reduces these forms to some extent[38]. But it is resorted to by the species primarily due to the urge for survival playing a dominant role above all else.

However, cannibalism may not always succeed in population regulation by reduced competition, as the rate of disease transmission within the species and genetic inheritance of the diseases increases by inbreeding, with decrease in population, though in some cases, the diseased ones are cannibalized to reduce the spread of the disease within the species.

The whole point of our analysis is that cannibalism is but another form of role reversal, or rather behavior reversal, where the behavior of nurture, care, filial bonding, friendliness and sexual love are reversed and replaced by hostile behavior, enmity and predation. But in every case, our analysis shows that it is for evolutionary purpose only, though the success rates may differ[39].

We now generalize the scope of role-reversal to include any kind of mutual interaction beyond the narrow confines of the prey-predator kind.

6. Behavior Reversal

Any reversal of behavior in any mutual relationship between individuals or species is a behavior reversal.

Any relationship is defined by the role played, or behavior shown, by the participants in their mutual interaction. Any reversal of that role is a role reversal *e. g.* from cooperation to competition and vice versa in presence of insecurity. The cooperative behavior is manifest as group formation, social behavior, friendliness, helpfulness, commensalism and symbiosis etc. while competitive behavior is marked by enmity and hostility.

Prey-predator role-reversals are special kinds of behavior reversals where prey and predator interchange their roles. However, looking at the success rates of predation by the preying mantis and the *epomis*, it seems

that they may not be role reversals at all! Calling it role-reversal would mean that in an earlier era they were the prey of what they currently prey upon. But there is no such evidence. The assumption that it is a role reversal is based only on the assumption that the larger one should be the predator and the smaller one, the prey. Rather, such predation may be the rule and they were never the prey, but have always been the predators for their respective prey, as an essential mechanism of satisfying their basic evolutionary requirements of the urges for survival and self-perpetuation by reproduction. This further supports the meta-evolutionary paradigm shift towards urges being the driving forces rather than any other factor.

7. Progress in Evolution

Progress in evolution has been defined as 'systematic change in a feature belonging to all members of a sequence in such a way that posterior member of the sequence exhibit an improvement in that feature' and others have argued that it is not possible to identify examples of uniform progress[40-42]. However, there have been many suggestions as to how progress in evolution could be assessed[41,43-48]. Criteria include measures of the relative information content of DNA, ecological dominance, invasions of new environments, expansion of life, replacements, improvements in adaptation or adaptability, the possibility of further progress, increased specialization, increased complexity, increase in general energy, and increase in the range and variety of adjustments to the environment. Are these standards of measure sufficient to determine and explain the status of evolution universally?

Severe difficulties with a number of these measures have been pointed, out[40,45-46,49]. Do all organisms have a progressive evolution as Dobzhansky et al. note, 'Organisms are more or less progressive depending on what criterion of progress is used? In modern Darwinian evolutionary theory it is only a post hoc adaptive story, and it is in no way predictive of future trends'[40].

Many of the definitions of 'progress' involve a belief that there has been an overall improvement in competitive ability in course of time; that different lineages improve their chances of survival during evolution, either relative to each other, or relative to their forebears. Four definitions of progress in evolution are particularly relevant here; increase in morphological complexity, the expansion of life, evolutionary trends, and the increased effectiveness of adaptation[17]. The specialized cases discussed in the present article can hardly be explained under these heads.

Whether it is PPR or role reversal, it is an adaptation that arose from within the individuals involving some form of biological improvement for the same or new way of life[50]. The process of evolution is always a progressive mechanism and competition is a uniform process that occurs within the species and among the different species too. Evolution is driven by biotic factors and competition[51]. No organism, except perhaps the human being, ever recognizes that it had an evolution or devolution and it is the human beings who fix criteria and differentiate between progressive or regressive evolution on the basis of increase in morphological complexity. But by loosing morphological complexity, if the organism is better adapted to the environment, then that is progressive for that organism, though it seems regressive to the taxonomist! It is hard to quantify the complexity to define criteria of progression and regression, and it has been noted that increase in morphological complexity is not a necessary correlate of improved competitive ability[46,50].

Improvement in adaptation has been defined in terms of those features that reduce the likelihood of the extinction of a population through time[52]. Any kind of competition causes genetic changes through epigenetic changes and finally by mutations[53]. This change may be produced by more or less continuous inter-specific interactions or by the cumulative effects of competition on a much larger scale as in case of extinction or major replacements. However, Darwin viewed the history of life as progressive and believed that all places in the economy of nature are filled at any time ('the principle of plenitude'). Thus, species always evolve progressively as a result of biotic interactions and co-evolutionary effects on Prey and Predator both and even in role reversal cases.

The independent cosmic force of evolution does not act differently in the case of role reversal. The evolution progresses always, though the reason ascribed for evolution may be different such as competition, adaptation, speciation, extinction, replacements, and changes in physical environments and so on. Stanley argued that mammals have higher rate of evolution than bivalves because of their higher degree of inter-specific competition[54-55]. Our analysis shows that the reason behind competition is the urge to survive and the different modes of interaction are but a manifestation of the evolutionary urge that includes, but transcends the urge for survival, and which runs of its own as an independent conscious force.

8. Conclusion

We have analyzed unusual PPRs in many distinct situations and come to the conclusion that, they are not actually role-reversals because contrary roles were never seen in all those cases. There is no evidence of *epomis* larva failing and being eaten by a frog, nor of mantis failing and eaten by its chosen prey, nor of any carnivorous plant being the food of the insects it preys upon. It seems that only in cannibalism there is something that can be called role reversal, and it is better instead even to call it behavior reversal, as we have proposed.

In our view, to be precise, true prey-predator role reversal would occur if deer really started preying upon tigers for food! But, this can happen only in a mythologically correct sense if the tiger is born as a deer and vice versa by some queer mechanism, as yet unknown! But within the ambit of the scientific domain, the only clear cases where role reversal occurs are those where the young of the carnivorous predators are preyed upon by adult carnivorous prey, usually when the latter have the advantage of larger population strength to attack and finish the predation process.

However, behavior reversals, proposed here as a generalization of role-reversals, are rather common. They occur in cannibalism and also in the case of poultry-farming and pisciculture and other such activities where animals are nurtured only to be used as food later on when they grow up. Such behavior reversals are clearly for the satisfaction of the urges for survival, and in which the hunger instinct overpowers another instinct like the mother instinct.

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