Ecological, evolutionary and ecosystem consequences of animals managing risk

Animals live in an extraordinarily complex world. The nature of their interactions with conspecifics and heterospecifics dictates their survival and how many offspring they leave behind. As an ecologist, I'm interested in how animals manage risk of predation and the consequences of their defence responses on mating patterns, evolutionary processes, and ecosystem function. To address these questions, I perform innovative experiments on arthropod study systems, in the laboratory under controlled conditions, in semi-natural mesocosm experiments, and in the field with natural populations in their native habitats. Arthropod systems allow me to manipulate conditions and contexts to ask directed questions while concurrently addressing underlying mechanisms – techniques which are difficult to employ with vertebrates. Moreover, arthropods are often so abundant in most biomes that they are crucial parts of food webs and hold ecosystems together. Any change, therefore, in their abundance, physiology or behaviour can have far-reaching cascading effects on the ecosystem. My empirical work is guided by formal mathematical theory of species interactions. Since many animal traits are condition-dependent, changes in the environment can alter their expression and consequences for interactions between individuals and species. My overarching long-term goal is to predict how species interactions will adjust to rapidly changing climate. To do so with adequate predictive power, it is important to gain mechanistic insights while developing novel conceptions of the natural world. For achieving that, I will exploit my strengths of simultaneously examining patterns and underlying mechanisms to develop novel theory.

<u>Over the next 5 to 10 years, my research programme will investigate how nutrition, habitat and climate regulate species interactions, specifically predator-prey interactions, and the cascading consequences for ecosystems</u>, in the following four broad themes. a) *Conceptual unification of fitness consequences of prey responses:* Two broad fitness consequences of responding to predation risk – fewer foraging opportunities and fewer matings – have been surprisingly studied separately. By integrating them, I aim to conceptually unify fields addressing reproductive ecology and nutritional ecology of prey. b) *How does climate affect interactions between and among species?* Environmental fluctuation across years may alter intra- and inter-species interactions. By long-term monitoring of prey mating patterns near and away from predators I will investigate how climate drives the strength and direction of such interactions and their evolutionary consequences. c) *Phenotype-environment matching in a landscape of fear:* To understand whether and how organisms can shape their own evolutionary trajectories through behaviour, I plan to investigate causes and consequences of phenotype-environment matching in a heterogenous environment of risk – where prey individuals coerce competitively-weaker conspecifics to occupy risky habitats. d) *Ecosystem consequences of predation risk and intraspecific competition:* Predators shape ecosystem nutrient dynamics indirectly by altering prey behaviour and physiology. As prey with certain phenotypes covary in specific environments, I aim to focus on the role of interindividual variation in prey phenotypes in ecosystem function.

Overall, in addition to my research programme advancing conceptual boundaries, I am keen on working on exciting concepts using understudied species and landscapes of India, and popularising them to invoke a sense of pride in laypersons, locally as well as nationally. I am particularly passionate about drylands, and plan for scientific insights from my work to aid efforts to conserve vital function and services that species in ecosystems provide to humankind. I consider this important since drylands cover about 30% of the land surface worldwide and are expanding rapidly due to unsustainable land-use and climate change. Below, I elaborate specifics of my research programme.

a) Conceptual unification of fitness consequences of prey responses

Predators impact prey fitness not just by eating them but also by scaring them[1]. Fear of predators influences prey traits that help acquire mates and nutrition, a phenomenon termed non-consumptive effects[2]. Traditionally, fitness costs of prey responses have been studied separately in the context of reproduction and foraging, with respective ultimate goals of understanding trait evolution and demographic costs (Fig. 1). It is important to reconcile the conceptual divide because access

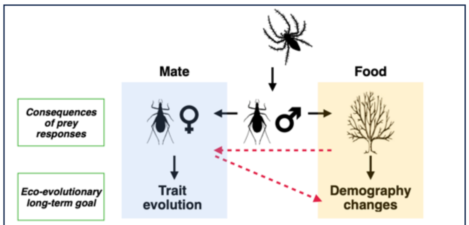

Fig. 1: Two broad fitness consequences of prey responses (cricket) to predation risk (spider) – fewer matings (blue box) and fewer foraging opportunities (yellow box) – have traditionally been studied separately with each field fostering different eco-evolutionary long-term goals. I will conceptually unify these fields by integrating reproductive ecology and nutritional ecology of prey (red arrows), since access to nutrition often drives expression and success of labile reproductive traits.

to nutrition often drives expression and success of labile reproductive traits involved in sexual signalling, courtship, nuptial gifts, and intrasexual competition. In my short-term goals, I will leverage my experience in performing enclosure experiments[3,4] to closely monitor how fear-driven diet choices of prey affect expression of reproductive traits and their fitness consequences. Specifically, I will examine how fear-driven microhabitat changes can influence acoustic call features through restricted access to nutrition. Further, alteration in quality and quantity of nutrition may also affect composition of nuptial gifts – nutrition offered by individuals of some species to their mates before or during pair formation – potentially affecting reproductive success. Bush-dwelling herbivorous tree cricket and their well-studied spider predators[5] found in and around Bangalore offer an excellent opportunity to investigate these patterns. Firstly, tree crickets are known to move lower and deeper into the bush in the presence of their spider predators[6], a microhabitat further away from the nutritionally-rich food at the top of the bush. Secondly, the nuptial gift offered by male crickets – a glandular secretion that females feed on during copulation – is allocated differently based on male diet[7]. Since duration of female staying mounted is associated with male reproductive success, altered diet choices can not only affect nutritional benefits to females but also male reproductive fitness. Such a mechanistic approach to reconciling reproductive and nutritional costs of predator-prey interactions will help generate a more unified behavioural ecological theory. I am currently working on a meta-analysis quantifying the direction and strength of non-consumptive effects on prey fitness via alteration of reproductive traits, in collaboration with Dr. Liam Dougherty (University of Liverpool, UK) and Dr. Shelby Rinehart (Drexel University, USA).

Animals that exhibit sexual signals benefit by acquiring mates but also experience elevated predatory and energetic costs[8]. Individuals exhibiting alternative reproductive tactics (ARTs), such as satellite behaviour, minimise such costs by moving near signalling conspecifics to intercept attracted mates[3]. However, in species with nutrition-limited signal production, an important question that remains unanswered is whether satellites gain information on habitat quality from consistent signallers and move accordingly. Although ARTs are typically theorised to be sexually-selected traits, I am interested in exploring whether satellite behaviour offers adaptive advantage to trace and access nutritionally-rich foraging patches. This novel approach will address the broader question of why ARTs persist in species over evolutionary time. I'm currently reviewing literature linking nutrition and satellite behaviour in the 'ecological crossover' framework, in collaboration with Prof. Ximena Bernal (Purdue University). Predators too are capable of tracking and anchoring themselves in high quality patches of interest to prey. I plan to investigate how nutrition regulates alternative reproductive tactics and predation risk by quantifying the nutritional composition of diets[9], experimentally manipulating access to and quality of nutrition, and manipulating predator presence in enclosure experiments.

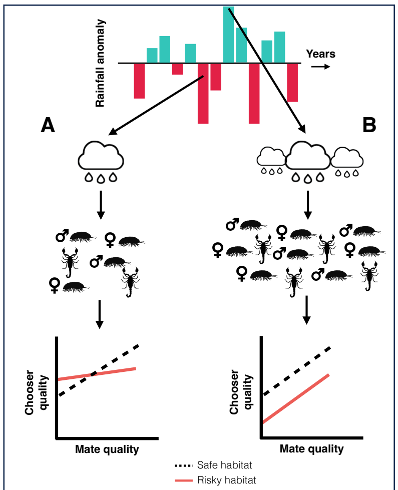

Fig. 2: Variable climatic conditions can alter the fundamental relationship between and among species. Years with deficient (red bars, A) or excessive (teal bars, B) rainfall, may support small or large populations of predators and prey, respectively. The prey population mating patterns in these years may be either (A) disrupted or (B) regulated due to contrasting prey perception of risk (details in Torsekar et al. 2023[10] Fig, 1).

b) How does climate affect interactions between and among species?

Although detrimental effects of climate change on individual species abundance and distribution is attracting much attention, its consequences on species interactions are not well understood. I will examine how climate modulates intra- and interspecies interactions, since ecological interactions are fundamentally tied with climate. Specifically, I will test how precipitation regulates predator-prey interactions (Fig. 2). In arid lands, with low mean but highly variable precipitation, years with sparse rainfall offer fewer foraging opportunities, thereby supporting only small prey and predator populations. Consequently, lower predator-prey encounter probabilities may elicit prey perception of risk that is fundamentally different from that expected in years with high mean precipitation. Varying risk perception can drive temporal variation in strength and direction of prey assortative mating patterns[10], leading to change in frequencies of underlying reproductive traits[11]. Overall, my long-term interest lies in investigating what drives the stability of prey phenotypes - continuously operating stabilising selection versus fluctuating selection. I will test these hypotheses by monitoring prey mating patterns in a manipulated landscape of fear – spatio-temporal variation in predation risk[12] – across multiple years in burrow-dwelling desert isopods and their scorpion predators in the Thar desert. Long-term monitoring will also allow me to track the influence of extreme climatic events such as drought on ecological interactions, especially since the frequency and intensity of such events is expected to increase owing to climate change.

Although catastrophic disturbances such as cyclones are common features of some coastal natural ecosystems, how and the extent to which they reshape animal populations and food webs is still unclear. Cyclones disrupt biota along their path by reducing species richness through local extinctions or drastically reducing population sizes[13]. Bush-dwelling tree crickets, that are distributed along the East coast of India, occupy lower perch heights and centres of the bush in the presence of their spider predators[6]. I'm interested in examining whether by inducing such changes in prey microhabitat use, do spiders facilitate or inhibit the catastrophic effects of cyclones on cricket populations[14]. Further, if phenotype-environment matching drives overlap between spiders and crickets with specific traits (details in next section), I plan to investigate whether predators drive cyclone-induced selection of prey traits. I will do so by enclosing predator-present and predator-absent cricket populations along predicted cyclone paths and censusing and measuring prey traits before and after cyclonic events. With predicted increase in the frequency and intensity of cyclones in the Bay of Bengal due to climate change[15], it is crucial to understand how top-down effects interact with catastrophic events in shaping ecological communities.

c) Phenotype-environment matching in a landscape of fear

Habitat choice driving adaptive change in populations is an under-appreciated mechanism with far-reaching effects[16]. The novel conceptual framework I developed during my postdoctoral work in Israel integrates habitat choice based on predation risk in the process of prey mate assessment with potential to change population mating patterns[10]. For instance, in burrow-dwelling desert isopods, male preference for females was dependent on the presence of a scorpion predator nearby. In my short-term goals, I aim to expand the scope of this framework by testing the generality of the theoretical predictions. First, I will investigate how other prey systems driven by different mating systems (e.g. female competition and mutual mate choice) are influenced by fear of predators leading to altered emergent mating patterns. Further, I plan to augment my novel theoretical framework to include different predator hunting modes. Unlike the sit-and-wait hunting mode of predators such as burrow-dwelling scorpions, actively roving predators are not anchored in space making predator cues unreliable. By investigating whether (field experiments) and how (enclosure experiments) roving predators alter prey mating patterns, I will supplement the theory to include context-dependency of predator hunting modes.

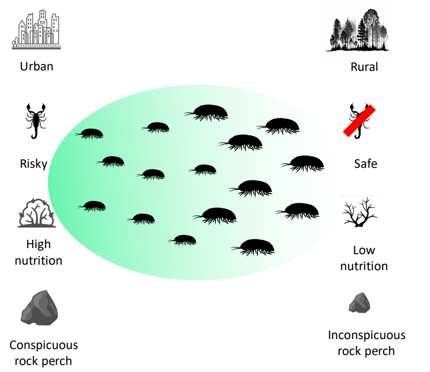

Fig. 3: Illustration of conspecifics with variable phenotypes (two-sized isopods; large vs. small) distributed non-randomly in different environments (green gradient; risky-safe, urban-rural, high vs. low nutrition) driven by intraspecies competition. Such phenotype-environment matching can alter evolutionary trajectories of populations and may also differentially affect ecosystem function.

Previously, I demonstrated that phenotypes covary in a heterogenous environment of risk[10,17]. Moving forward, I will investigate phenotype-environment matching as a potential mechanism for assortative mating, either through intraspecific competition or through 'prudent habitat choice', where individuals disperse to habitats matching their phenotype in the absence of direct competition[17] (Fig. 3). Canonically, assortative mating is predicted to be a consequence of random encounters between sexes followed by mate choice. However, identical habitat choice by conspecifics with similar phenotypes can also lead to assortative mating[18]. I aim to investigate this understudied mechanism in two systems, each with unique advantages – the territorial and stream-dwelling frog species of Western Ghats and the bush-dwelling tree crickets in scrub lands of peninsular India. Specifically, I aim to investigate the drivers of their habitat choice – across potential gradients such as urban-rural, safe-risky, high-low nutrition, and conspicuous-inconspicuous patches – and whether it is different for conspecifics competing for habitats, with the help of field observations and field experiments (Fig. 3). Manipulating predator risk will help unravel whether and how risk disrupts matching habitat choice, emergent patterns, and the fitness consequences. Overall, I'm interested in whether and when habitat choice facilitates assortative mating, and the disruptive role of predation risk.

Dispersal patterns are a key driver of the distribution of genetic variation within and among populations[19]. Over the next 5-10 years, I aim to integrate genomic tools with animal tracking technology, to investigate mechanisms underlying phenotype-environment matching and their population-level consequences. I will test whether individual dispersal decisions are based on their evaluation of their local performances in different habitats and whether they experience higher reproductive fitness based on the phenotype-environment match. Further, in collaboration with population geneticists, I aim to investigate whether non-random gene flow between different habitats due to directed dispersal can drive population divergences. For tracking individuals, I aim to collaborate with movement ecologists to deploy appropriate animal-borne sensors in natural populations (e.g. RFID or Radio telemetry tags). Overall, I aim to better understand whether and how organisms can shape their evolutionary trajectory through behaviour, opening the door to new exciting research directions in evolutionary ecology.

d) Ecosystem consequences of predation risk and intraspecific competition

Just as ecology of a species can mould its evolutionary trajectories, so can evolutionary change in a species shape the ecosystem it inhabits[20]. Traditionally, ecosystem ecologists have considered primary producers and microbial decomposers to be critical drivers of nutrient cycling. But recent work has highlighted the role of animals in altering the rate and intensity of element cycling, especially by predator-induced changes in prey numbers, behaviour and physiology[21]. I'm interested in investigating whether predators can shape ecosystems by selecting certain prey phenotypes predictably occurring in specific habitats in addition to altering prey density and prey trophic function (Fig. 3). By testing the ecosystem consequences of phenotype matching in a heterogenous environment of risk, I plan to direct the field of ecosystem ecology towards considering interindividual variation of prey in shaping the intensity of element cycling. I will conduct mesocosm experiments by enclosing herbivorous prey individuals with extreme trait values with (stress treatment) and without (control) predators, observe their behaviour and diet, and measure cascading effects on soil function and plant leaf litter decomposition. Bush-dwelling tree crickets and their spider predators are an ideal system to address this question. Prey phenotypes inhabiting risky habitats will exert differential foraging pressure leading to changes in quantity and quality of plant litter, and excrements entering the detrital pool, thereby altering the rate of organic matter decomposition in the soil. The answer to this question has critical implications for our fundamental understanding of eco-evolutionary dynamics.

In summary, my core research goals are to better understand how environmental drivers such as nutrition, habitat and climate mediate intra- and interspecies interactions, and their consequences on evolutionary trajectories and ecosystem function. My overarching long-term goal is to understand species interactions to predict how species will deal with rapidly changing climate. I hope for my scientific insights to inform conservation efforts and optimise the interactions between plants, animals, humans and the environment.

My present and past collaborators include researchers from India (Prof. Kavita Isvaran, Prof. Maria Thaker), Israel (Dr. Moshe Zaguri, Dr. Nevo Sagi), the United States of America (Prof. Ximena Bernal, Dr. Shelby Rinehart), and United Kingdom (Dr. Liam Dougherty). In addition to working with them, I will initiate new collaborations at NCBS to expand my research horizons. I will integrate my work with the facilities in the NCBS campus. The mesocosm experiments can be performed in enclosures, and an additional facility to perform semi-natural experiments on campus will be useful. With extramural and intramural start-up grants, I plan to procure instruments including infrared gas analyser, stereomicroscopes, incubators, refrigerators, cameras, and setup anechoic chambers and enclosures.

Mentoring, outreach and institution-building

I believe that research is a social endeavour, making mentoring an essential part of being a scientist. During my PhD and postdoctoral work in India and Israel, I have mentored many undergraduate and graduate students. As a PhD candidate, I worked with undergraduates from neighbouring colleges who helped me with my behavioural experiments. Since many of them were new to research, I ensured that I not only explained details of my specific field research but also broadly described the process of performing science, using ecology and evolution as an example. Many have continued in research as PhD students and by writing recommendation letters for them, I continue to be a part of their academic journey. I have ensured effective mentoring by focusing on transfer of important skills, making sure students learn while conducting experiments, by clearly communicating expectations, and discussing both successes and failures. Overall, by mentoring well, I aim to not only help shape skilled and kind researchers in academia, but also well-informed and problem-solving citizens in society.

Regarding contributions to the organisation, I will exploit my experience organising academic events to coordinate seminars and conferences. As a student secretary during my PhD, I took the liberty to plan and organise departmental symposia, book clubs, social mixers, and weekly seminars. I believe in giving back to community, both locally and nationally. For doing so I will participate in public engagement and outreach to not only explain my research but also to popularise the process of conducting science. Previously, I have complemented my scientific papers by writing blogs and making videos devoid of jargon aimed at communicating my research. Although innovative, I realised early on that my efforts to communicate my own research needed a popular medium. Accordingly, I contacted science journalists and editors of leading newspapers such as The Hindu, Times of India, The Jerusalem Post, Haaretz, etc. and other science communication platforms to reach large audiences. Further, I have enthusiastically participated in institutional outreach events such as Open Day to explain what research in Ecology and Evolution involves. I did so by organising posters, activities, games and even wrote, directed, recorded, and edited a film with a colleague to explain the breadth of research performed at my graduate department. I aim to continue exploring innovative ways to explain not only ideas in science but also the process of conducting it. Especially given that accessing information is rarely a constraint in current times, I hope that popularising how science is conducted will help a wider audience sift through the barrage of information and make informed decisions in their daily life.

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