Determinants of antipredator behaviour in birds

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Abstract- Predation influences the fitness of prey and leads to antipredator strategies in prey populations. Anthropological changes are also detrimental to birds' survival. Hence, birds have evolved defenses against predation. Prey defenses include a number of components including physical, behavioural and ecological elements that are significant in determining the antipredator response of birds. The anti-predatory response of birds suggests their adjustments towards fear from predation. Study of these factors enables us to understand the selective forces against birds' response to natural predation risk. These components support the animal in immediate survival but they have likely costs on food availability, feeding time, reproductive output and parental care. Identified gaps in the understanding of antipredator behaviour of birds emphasize the need to initiate behavioural studies in different habitats and geographic regions of the country to frame guidelines for conservation of birds.

INTRODUCTION

Most of the animals in the ecosystem are potential prey, except some upper trophic level carnivores. A behavioural adaptation to minimize the chances of being eaten is called anti-predatory behaviour. Various strategies undertaken by animals and birds as anti-predatory behaviour include individual and social strategies. Birds which play an important role in ecosystem often face various types of disturbance stimuli and show different tactics and anti-predator behaviour against it, like escaping, freezing, deception, mimicry, increased detection of predators, etc. Birds are feathered vertebrates and accord to various ecological functions extending over a broad range of positions in ecosystem. The avian habitat is roughly divided into forest, scrub and wetlands, although many species require a mixed type of habitat.[1]

As the prey becomes aware of the predator's approach, it does not fly away instantly; instead it monitors the predator's approach till flying away becomes useful. The cost of fleeing essentially results into loss of opportunities to feed and engage in social activities like courtship, mating, territorial defence, and performing other activities that increase fitness. Energetic costs of fleeing and risk of injury as a consequence of fleeing are other expenses of fleeing. The opportunity cost of fleeing decreases with the decrease in predator-prey distance. Decrease in the predator-prey distance increases the risk of not fleeing due to increase in predation risk. The distance at which birds start to move or flee against intruder is called

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as Flight initiation distance (FID). Similarly, the term escape distance is also used to indicate minimum distance from the invader. It is also called as flush distance or escape flight distance. The distance at which a predator is detected along with the distance at which the prey flees off the predator is called buffer distance. Buffer zone is the gap within which human action is limited to reduce interruption to wildlife. Birds behave in a different manner in areas with varied levels of human disturbance. The flight initiation distance was found to decrease in areas where more people visited the beach, and specifically in a small area near the pier. North Indian resident birds have been observed to be habituated towards people because of non-violent shielding behaviour of Hindus. Samia *et al.* (2015)[2] investigated 96 bird species and observed morphological, life history and natural history traits to correlate with variation in avian escape strategy. Prey initiate flight soon after detecting a predator so as to minimize attention costs related to ongoing monitoring of the location of the predator. Brain mass, body size, habitat structure and group sizes are the main predictors of escape strategy. FID for 2067 adult barn swallows was registered by Moller (2014)[3] from 1983 to 2012. Of these birds, 18 individuals were captured by predators, domestic cats (*Felis catus*) or sparrow hawks. Significantly shorter FID was observed among depredated individuals than survivors. Moller *et al.* (2013)[4] provided estimates of FID in resident and migratory birds before and after a severely cold winter along a latitudinal gradient in Europe. Decrease in FID was evident before and after the cold winter, but only among resident species, and more so for rural than urban populations of the same species. Fernandez- Juricic *et al.* (2005)[5] reported visibility and detectability as important factors influencing a species response to an approaching threat.

In this review, we focus on a number of biological, ecological, antipredator distances and behavioural responses that influence the antipredator behaviour of birds, eventually leading to bird conservation.

Biological factors

Body size

Moller *et al.* (2008)[6] studied 63 species of birds in Denmark to analyze susceptibility of predation by sparrow hawks in relation to mean FID, showing a negative relationship accounting for 13% of the variance after adjusting for body size. Preys of intermediate body size are easier to handle and also yield significant resources and hence are preferred by predators. Blumstein (2006a)[7] found that larger flying birds take longer flight before take-off and longer FID is expected in larger species for this reason alone. Approach towards smaller bird species was easier in suburban than in rural areas. Body size can be considered as the best predictor of FID because it is also the best predictor of life history, anatomy, physiology, behaviour, and conservation status. As the prey's size brings it into the range favoured by the predator, predation risk increases.

Eye size, Lens and tympanic membrane

In an initial study conducted by Blumstein *et al.* (2004)[8], there was no indication that large eyes had evolved in species living in isolated habitats, or in species eating mobile prey. Contradictorily, Moller and Erritzoe, (2010)[9] analyzed eye size in 97 bird species and reported that species with large eyes and higher ability to resolve visual details will have relatively longer FID as mediated by longer alert distances (ADs). Relatively higher AD in birds with large eyes and increased perch height was reported by Blumstein *et al.* (2004)[8]. They found that birds assessed themselves to be at a lower risk of predation when they were 3 m above the ground compared with being <3 m above ground. Birds of perch height 3m off the ground had greater FIDs in six species, but in three species had the opposite response. A significant positive relationship was found between eye size and alert distance in 23 species. Hearing in birds is related to the tympanic membrane in birds. For a given body size, a larger tympanic membrane implies better hearing ability. FID was reported to be related to the size of the tympanic membrane and the footplate of stapes in 37 species of birds. A significant positive correlation was observed between FID and tympanic membrane. This indicates better hearing ability. It may be deduced that auditory information has a remarkable role in predator-prey interface.[10]

Brain size

Analysis of 27 bird species from Australia by Guay *et al.,* (2013)[11] found no significant association between brain size and FID. Moller and Erritzoe, (2014)[12] suggested that a relatively larger brain allows for longer FID because of faster reaction to a likely predator. The intentions of the predator and the chance of attack before fleeing are also assessed by a larger brain. Different results were observed by Cooper and Blumstein (2013)[13] who reported

that in a sample of 107 bird species, FID increased with relative eye size, but decreased with relative brain size. Additionally, FID increased independently with size of the cerebellum, which plays an important role in motor control.

Wing shape

Fernandez-Juricic *et al.* (2006)[14] studied the relationship between body mass and size, indices of wingtip shape and hind limb length, flight initiation distance and landing distance of 83 birds of North America, Europe, and Australia and reported that pointed and concave wingtips and shorter hind limbs make birds more vulnerable to predation. Body mass and size, indices of wingtip shape and hind limb length, flight initiation distance and landing distance of 83 birds of North America, Europe, and Australia. Birds with pointed wings fled at longer distances and landed much farther than species having rounded wings, although hind limb length was not associated with flight initiation and landing distance.

Plumage

The toll of having conspicuous colours of plumage in birds leads to increased predation risk, affecting their anti-predator behaviour. McQueen *et al.* (2017)[15] employed behavioural observations and alarm call playback in Male superb fairy-wrens (*Malurus cyaneus*) to find out how birds adapt responses to predation risk in accordance with their plumage colour. They observed blue fairy-wrens to flee frequently in reaction to alarm calls, emerged from their cover in a longer time, foraged in cover and were more vigilant. Thus, fairy wrens with pronounced plumage were cognizant of being at a higher predation risk and accordingly change their behaviour. Antipredator behaviours of conspecific males within sexes have been shown to escalate with the potency of colour signals exhibited by them.[16,17]

Ecological Factors

Habitat

Adaptation to an urban environment in juncos (*Junco hyemalis*) was reported by Atwell *et al.* (2012)[18] as a rapid change in FID between urban and rural populations. Intermediate to large effects of relationship between FID, habitat openness and habitat diversity have been reported in most studies, although Blumstein, (2006a)[7] reported a small effect. Moller and Garamszegi, (2012)[19] reported that the horizontal component of FID was strongly related to habitat openness as compared to the vertical component. However, a strong relationship between FID and habitat

was found by Valcarcel and Fernandez-Juricic (2009)[20] while testing the safe habitat hypothesis. There is also indirect evidence of predators affecting FID of prey in urban areas as many birds seek shelter near human dwelling where raptors are rare. Guay *et al.* (2013)[11] reported that FID was longer when individual black swans (*Cygnus atratus*) were farther from water, which acted as a refuge. These findings fit well with the predominant role of predation in predicting urbanization of birds.[3] Carrete and Tella (2017)[21] studied behavioural changes like antipredator response and exploration in burrowing owls (*Athene cunicularia*) living in urban habitats in relation to their fear to humans. Their findings suggested that fear of humans is variable in different bird individuals. This is estimated as FID to the advancing human in the way that urban life would select for fearless individuals. Recent work by Jiang *et al.* (2020)[22] suggests that animals avoid predators by gathering information produced by other species. Mixed species flocks (MSFs) of birds are predominant in forest ecosystems and are partly structured around interspecific information transfer, with "nuclear" species providing information that other species overhear and use against predator encounters. Foraging decisions are mainly governed by the predation risk as observed in granivorous bird species in different habitats and microhabitats. The study done in a Nigerian Forest Reserve suggested that a genuine approach for assessing habitat quality as perceived by animals can be an insight into their foraging decisions.[23]

Season

Moller *et al.* (2013)[4] did FID experiments on 207 bird species in 7 pairs of urban and rural areas from northern to southern Europe before and after the extremely cold winter of 2009-2010. FID in different species of birds on an average became shorter after the cold winter, but only in resident urban populations frequently exposed to humans and not in migratory or rural populations of the same species. The difference in FID between urban and rural habitats increased after the cold winter, especially in areas with the coldest winter weather.

Visibility

Influence of habitat visibility on time allocation and escape decisions was studied by Boyer *et al.* (2006)[24] in Crimson rosella as (*Playcercus elegans*). It was found that visibility influenced time allocated to both foraging and locomotion and there was no effect of visibility on FID, latency to detect and latency to flee.

Urbanization

Diaz *et al.* (2013)[25] studied patterns of FID across Europe and found that urban populations had shorter FID than rural populations of the same species. The difference in FID between urban and rural populations decreased with increasing latitude, paralleling trends in raptor affluence. In analyses of sample genes in 12 paired populations of blackbirds (*Turdus merula*), Moller *et al.* (2013)[4] discovered that a gene involved in harm avoidance differed strongly between urban and rural populations. Carrete and Tella (2011)[26] found that urbanization is the most prevailing cause of habitat transformation worldwide. The relationship between FID and relative brain size (RBS) in urban invasiveness was studied by Moller (2009)[27] who found that RBS indirectly influenced urban invasion through its positive effect on inter-individual variability in FID. FIDs were consistently lower in urban than in rural conspecifics. Short FID allows birds to coexist in the proximity of humans. Initial responses to urbanization are defined by behaviour and provide clues about how certain species deal with urban habitats, human presence, and novel resources of food and nest boxes conditions like noise, artificial light and pollution.[28]

Food resources

The link between individual state and responsiveness of turnstones, *Arenaria interpres*, on rocky shores was studied by manipulating condition through the provision of supplementary food by Beale and Monaghan (2004)[29]. They found that birds whose condition had been enhanced showed greater responsiveness to standardized human disturbance, flying away at greater distances from the observer, scanning more frequently for predators and flying further when flushed. An experiment on white-browed sparrow-weavers (*Plocepasser mahali*) was done by Fong *et al.* (2009)[30] to determine the importance of direct and indirect environmental cues in assessing predation risk. Weaver foraging was influenced more by indirect than by direct risk. Distance to cover is much influencing factor rather than availability of food resources. Foraging decisions in weaver are sensitive to variation in risk and indirect cues are relatively more important than direct cues. In a food supplementation experiment conducted on song sparrows, *Melospiza melodia*, Rastogi *et al.* (2006)[31], suggested that daytime nest predation reduced greatly with food supplementation. Fed females exhibited short foraging bouts and time spent in the nest increased. This highlights the fact that food availability guides nest predation through its influence on antipredator behaviour.

Antipredator distances

Effect of Starting Distance (SD) on FID

In a study of 64 species of Australian birds, significant positive relationship between SD and FID was observed by Blumstein, (2003)[32]. He contributed economic models of escape behaviour and predicted that escape decisions are dynamic and will be influenced by both the costs and benefits of remaining. This demonstrates that species generally assess risk dynamically and flush at a greater distance as starting distance increases. Stankowich and Coss (2006)[33] reported that the relationship between SD and FID might be logarithmic or even quadratic due to suboptimal scanning rates by prey. A strong correlation was found by Cooper and Blumstein (2014)[34] between SD and AD with FID. Approaches with longer SD may have shorter FID than those with a SD at the limits of the zone of awareness. A predator begins its approach far enough from prey and the individual also becomes alert far away from predator, resulting in a longer FID.

Effect of AD on FID

Role of physiological cost of monitoring and risk assessment and relation of these factors with AD and FID were observed by Cooper and Blumstein (2014)[34]. With increase in AD, there is an increase in the length of approach and assessed risk at any given predator prey distance. There is a positive correlation between FID, SD and AD. Utilizing data from FID tests, a study was done by Dumont *et al.* (2012)[35] on alpine marmots (*Marmota marmota*) which demonstrated that results on FID are affected by using SD as a proxy for AD. A linear mixed model with covariate AD showed FID to be affected by interaction between previous activity and AD whereas when SD replaced AD as the covariate, no effect was observed in the analysis.

Population trends and FID

Relationship between population trends and FID of 193 species of birds in North America, Australia and Europe was studied by Moller *et al.* (2014)[36]. A negative relationship between population trends and FID was observed in Australia and Europe, rather than North American birds. Strong effects of some variables of population trends such as farmland breeding habitat, FID, body size, migratory habit and continent were observed mostly in European birds. Bolnick and Preisser, (2005)[37]

found that costly defensive strategies reduce population density of animals through indirect effects. Declining population trends were observed among 56 species of European birds' species by Moller (2008)[38]. It was concluded that large body sized species with longer FIDs show declining population trends because humans disturb such species more often. Shorter FIDs have been found to scale down the impact of human disturbance and are acquired in birds in countries with higher human population density. However, Reif *et al.* (2011)[39] reported that stronger effects of brain size on population trends in birds is context dependent in North-Western Germany, compared to an area from Eastern Germany to the Czech Republic. A strong negative correlation between population trend and FID was reported by Diaz *et al.* (2013)[25] after analysis of 329 populations with information on both variables in the same country.

Horizontal and vertical components of FID

FID can be separated into its horizontal and vertical components as reported by Blumstein *et al.*, (2004)[8]. In their studies it was observed that vertical component becomes zero in organisms moving in two dimensions. Moller (2010)[40] did a comparative study of 69 species of birds and reported four times more variance in FID among species to be due to the horizontal than the vertical dimension of escape. Due to this, large species rely more on the horizontal component of escape as compared to small species which are influenced by cost of flight.

Predators' eye contact

Birds respond differently against direct and indirect eye contact of approaching threat. In various studies done by Bateman and Flemming (2011)[41] for *Hadeda ibises* (*Bostrychia hagedash*) and Lee *et al.* (2013)[42] for magpies (*Pica pica*), it was reported that FID or AD significantly increased when approaching humans looked directly at them rather than elsewhere. This was observed to reinforce the hypothesis that many bird species can distinguish between potential predators intently looking at a prey individual and those only looking intermittently.

Speed of predators' approach

Different impacts of slow and fast approaches by predators towards prey were observed by Cooper and Avalos (2010)[43]. FID was smaller for slower approach speed of predator as the prey has more time to reach a refuge than if the predator approaches faster. Lank and Ydenberg (2003)[44] found that if two identical predator approach at different speeds, the risk to the prey at any particular distance is greater during the faster approach. Similarly, Bateman & Flemming (2011)[41] reported that *Hadeda ibises* show lower FID when approached quickly rather than slowly by a human.

Distance from refuge

Refuge is a safe area for prey to hide from predator. Kramer and Bonenfant (1997)[45] reported AD critical as the distance at which a predator approaching at a continuous speed will reach the refuge at the same time as the fleeing prey. Preys flee before the predator reaches ADcritical to allow them a margin of safety (MOS) to arrive at the refuge before the predator. If the prey is between the predator and the refuge, the predicted FID, d*, is ADcritical + MOS − DP, where DP is the distance between the prey and its refuge.

Driving speed and direction

Cars are functional tools for assessing cognitive abilities of birds with respect to risk. Legagneux and Ducatez, (2013)[46] in a study recorded that birds adjusted their FID to road speed limits by increasing FID as speed limit increases, while there was no similar effect of the vehicle speed. This response reduces the risk of collision and decreases mortality. Mukherjee *et al.* (2013)[47] showed that American crows (*Corvus brachyrhynchos*) adjusted their risk-taking behaviour to the driving direction of cars in a particular lane while crows in the opposite lane to that used by an approaching vehicle stayed back.

Direct and tangential approach

Attributes of duration and length of the predator's approach are helpful in risk assessment. These factors lead to assessment of greater risk than that attributable to predator-prey distance alone. This causes increase in FID as AD increases. Various studies done separately[5,48,41] show that birds could distinguish direct and tangential approaches by humans at a fixed distance. Moller and Tryjanowski (2014)[49] found that rural birds were better able to assess the direction of approach by humans in rural than in urban habitats. Interestingly it was reported[50] that blackbirds (*Turdus merula*) fled on foot, when exposed to frequent disturbance by humans rather than engaging in potentially expensive flight.

Behavioural responses

Vigilance

Vigilance is the active behaviour shown by prey against approaching possible threats. In studies by

Stankowich and Coss (2006)[33] it was reported that individuals scan their surroundings for potential threats that might be looming. This vigilance may be shared by members of a group, which would be more beneficial than a solitary animal that must divide its time between scanning and foraging. It is evident that the predation risk is greater to a less vigilant prey. Birds spend much of their time in foraging activities and antipredator vigilance. Proctor *et al.* (2006)[51] explained a vigilance model predicting that birds in the outer region of feeding area are more vigilant as compared to those in the inner region. This testifies to the dominant birds choosing to forage in the centre of the flock. Increased vigilance on exposure to a predator model was reported in Siberian Jay *Perisoreus infaustus.*[52] Jay's breeders retaining offspring were observed to be comparatively more vigilant than breeder groups with no kin. Not allocating time to vigilance can be fatal for a prey, if it fails to detect the predator until captured. Campos *et al.* (2009)[53] studied the relationship between predation risks such as degree of concealment, height in tree/shrub, distance to the forest edge and time allocated to singing and vigilance in a group of 13 passerine species living in an East African Savanna. They found that concealed birds sang more and were less vigilant. Vigilance increased as distance to the forested edge increased. Whether vigilance plays a role in antipredator behaviour and influences escape of animals from predators, a multispecies study was done on wild birds from urban and rural habitats in three European countries.[54] Rural birds were observed to be less vigilant as compared to urban birds. Urban habitat disturbances influence the vigilance behaviour and urban birds exhibit higher perceived predation risk and are therefore better at avoiding predation.

Detection

A game-theoretical model was developed by Broom and Ruxton (2005)[55] that applies specifically to the effect of crypsis on FID. Prey is cognizant of the predator before the predator detects the prey, but as the predator approaches closer, its chance of the prey detection increases. In a detailed study done[7], it was observed that at an isolated island the loss of all predators relaxed selection on predator recognition abilities. Mutation rate and the cost of flight had considerable effect on the average and standard deviation of recognition abilities.

Escape latency

Starting distance and many of the predation risk factors like intruder speed and directness of approach known to affect FID have influence on escape latency.[56] Longer SD and direct eye contact of predator enhance escape latency. Shorter escape latency is observed in the presence of food and familiar female. Escape latency decreases when opportunities to improve fitness are present. A prey is predicted to emerge when the risk of emerging equals the cost of hiding. A waiting game theory between prey and predator given by Hugie (2003)[57] concluded that large differences in fitness consequences for predator and prey lead to a waiting game where prey stays in refuge until after the predator has left the area. Similarly, Cooper *et al.* (2012)[58] reported that cost of fleeing decreases as escape latency increases. Latency to escape is expected to be greater when predation risk is smaller and cost of fleeing is higher because it prevents the prey from obtaining benefits of feeding, social behavior, or other activities that increase fitness.

Loss of predator over long period of time

Escape behaviour and vigilance behaviour reduces when birds are isolated from predators, and insular animals forage more and are less vigilant than mainland ones. In multi predator hypothesis, Blumstein, (2006b)[59] reported that isolation from all predators lead to a rapid loss of antipredator behavior, including loss of the group size effect and breakdown of predator recognition abilities. Studies have shown that local extinction of predators for prolonged periods relaxes natural selection on predator recognition.[60] Over by gone years prey may lose the ability to identify locally extinct predators as dangerous. Experience-dependent behaviour is lost after the first generation in the absence of predators, while more hard-wired antipredator behaviour persists for thousands of years following isolation from predators.

Prey-predator interaction

When a prey is threatened by predators, prey adopts defensive tactics, and its cost affects growth, maturation rates, survivorship, fecundity, or population density. This is known as "trait mediated interaction" (TMI) and effects reflect a balance between the conflicting demands of reproduction vs. predator avoidance. An intermediate positive effect on FID was reported in plover species against abundance of mammalian predators.[10] Predator-prey interactions are dependent on predator's perspective, beginning with detection by the predator, identification, approach, subjugation, and consumption. Weak escape

responses are observed in areas lacking predation and having high exposure to humans.

Habituation

Runyan and Blumstein (2004)[61] reported that moderate degree of pseudo replication of prey did not significantly affect individual identity because rate of habituation varies for different individuals and is evident only when individual identity is known. A weak evidence of habituation with repeated estimates of FID was reported by Blumstein (2014)[62] in 8 different species of ducks and owls to passerines. Impact of habituation and risk allocation on blackbirds (*Turdus merula*) was studied by Rodriguez-Prieto *et al.* (2009)[63]. They found lower FID with higher pedestrian rates, in response to both usual and novel approaches. Jiang and Moller (2017)[64] estimated the FID of 48 pairs of related bird species with different threat status to human proximity and reported longer FID in more threatened bird species. The study revealed that animals become habituated to human proximity through adaptation or through microevolution.

Parental investment

Two parameters, clutch size and fecundity were found to be negatively related to mean FID.[7] Hatching success in curlews (*Numenius arquata*) was maximum at intermediate FID[65], as would be expected if long FID restrained efficient incubation. Seltmann *et al.* (2012)[66] reported longer incubation periods in eiders (*Somateria mollissima*) with longer FIDs. Contradictorily, Moller and Garamszegi (2012)[19] observed that rate of senescence decreased with increasing mean and variance in FID, especially for the vertical component of escape. A positive correlation between FID and corticosterone levels in incubating eiders was found by Seltmann *et al.* (2012)[66]. However, Partecke *et al.* (2006)[67] found lower testosterone and corticosterone levels in urban as compared to rural individuals in blackbirds.

Nesting and Parental nest visit synchronization

Predation is the primary cause of nesting mortality in birds. The antipredatory behaviour of *Cyanistes caeruleus*, blue tit parents was studied by Saavedra (2020)[68]. The blue tit parents were laid bare to predators or their stuffed models having chemical cues. Blue tits responded to the behavioural cues of live predators more than to predator models infused with chemical cues. It was suggested that the blue tits are able to gauge the intensity of predation risk and adjust their antipredator behaviour according to the behavioural, visual and chemical cues of the predators. A number of studies suggest that behavioural changes are exhibited by birds in response to the visual cues of the predator.[69,70]

Birds with antiracial offspring need to feed them at regular intervals, but each feeding visit risks drawing attention of the potential predators to the nest and exposing its location. Synchronisation of visits by both parents has been suggested as a behavioural adaptation to reduce the risk of nest predation. Khwaja *et al.* (2019)[71] investigated this prediction over three timescales using nestling provisioning data from 25 passerine species in Tasmania and New Zealand and estimated the level to which parents actively synchronised their nest visits. They concluded that breeding birds may have some capacity to adapt the synchrony with which they provision over short evolutionary timescales. FID may be used as a parameter of measurement of risk-taking behaviour. Risk taking decisions made for offspring care can influence fitness of breeding individuals. The cost of antipredator behaviour leads to parents' trade off between care of offspring and cessation of care for their lives. Therefore, in order to find a way out, predation risk is needed to be assessed exactly.[72,73] Increase in current reproductive value, nest concealment and costs of lost parental care led to decrease in optimal FID and also the parent to stay back at nest.[74] Some instances of costs of fleeing are so much that staying at the nest becomes optimal strategy for nesting species.

CONCLUSION

The ability of birds to cope with predators is very much dependent on its bodily cues. Studies provide a link between behavioural adaptations and survival success of birds in the wild. These behavioural changes play an effective role in the conservation of birds. The anti-predatory behaviour is modified by the adjustments in the distances at which birds flush after seeing or confronting the predator. Understanding how individuals use biological, ecological, behavioural factors and anti-predatory distances to survive depredation may help us device conservation strategies to the fullest.

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