

Feeding behavioural alterations in vultures due to environmental contamination

Annapurna Sahu

Pt. Ravishankar Shukla University, Raipur Chhattisgarh, India

Abstract

Vultures are important scavenger birds that help maintain ecosystem balance by feeding on dead animals and preventing the spread of harmful diseases. They play a major role in cleaning the environment naturally. However, in recent years, environmental contamination has seriously affected vulture populations and their feeding behaviour (Green *et al.*, 2004). Toxic substances such as veterinary medicines, pesticides, heavy metals, industrial pollutants, and plastic waste are becoming major threats to these birds. Among them, diclofenac, a veterinary anti-inflammatory drug, has caused severe population decline in many Asian vulture species after vultures consumed contaminated livestock carcasses (Oaks *et al.*, 2004). Environmental pollution also changes the normal feeding habits of vultures. Many vultures are now forced to feed on garbage dumps, slaughterhouse waste, and contaminated carcasses because of decreasing natural food availability (Carvalho *et al.*, 2022). This increases their exposure to plastics, toxic chemicals, and disease-causing organisms. Contaminants may affect their digestion, foraging movement, scavenging efficiency, and social feeding behaviour. Heavy metals and pesticides can also weaken their health and reduce survival rates (Gangoso *et al.*, 2009). The present paper reviews how environmental contamination alters feeding behaviour in vultures and explains its ecological impacts. It also discusses important conservation measures such as banning harmful veterinary drugs, improving waste management, monitoring pollutants, and establishing safe feeding zones to support long-term vulture conservation and population recovery.

Keywords: Vultures, feeding behaviour, environmental pollution, diclofenac toxicity, scavenging ecology, plastic contamination, conservation biology

Introduction

Vultures are obligate scavengers that provide important ecosystem services by rapidly consuming dead animal carcasses and limiting pathogen transmission (Pain *et al.*, 2003) [12]. Their strong digestive acids allow them to tolerate harmful microorganisms that are lethal to many other animals. Due to this ecological function, vultures are considered key regulators of ecosystem sanitation and nutrient cycling. Despite their ecological importance, vulture populations have experienced dramatic declines over the last three decades due to environmental contamination and habitat disturbances (Shultz *et al.*, 2004) [6]. Industrial pollution, agricultural chemicals, heavy metals, veterinary drugs, and plastic waste are increasingly affecting vulture physiology and behavioural ecology. Among environmental contaminants, veterinary non-steroidal anti-inflammatory drugs (NSAIDs), particularly diclofenac, have caused one of the most rapid avian population crashes recorded globally (Oaks *et al.*, 2004) [6]. Vultures feeding on carcasses of livestock treated with diclofenac suffer acute renal failure and visceral gout, resulting in extremely high mortality rates (Naidoo & Swan, 2009) [10]. Environmental contamination also modifies feeding behaviour by influencing carcass selection, food preference, scavenging efficiency, movement patterns, and communal feeding interactions (Ghosh-Harihar & Ramakrishnan, 2024) [5]. Urbanization and waste accumulation have further forced many vulture species to forage at landfill sites and garbage dumps where they consume contaminated waste materials and plastics (Carvalho *et al.*, 2022) [2].

Objectives of the Study

1. To investigate the impact of environmental contamination on the feeding behaviour and scavenging patterns of vultures.

2. To assess the effects of veterinary drugs, pesticides, heavy metals, and industrial pollutants on vulture health and feeding ecology.
3. To examine how plastic ingestion and toxic substances alter foraging behaviour, food preference, and digestive efficiency in vultures.
4. To analyze the ecological consequences of altered scavenging behaviour on ecosystem balance and disease control.
5. To evaluate existing conservation measures and suggest effective strategies for the long-term protection and recovery of vulture populations.

Environmental Contaminants Affecting Vultures

1. Veterinary Drugs

Veterinary medicines are one of the major causes of vulture population decline worldwide (Green *et al.*, 2006) [7]. Among these drugs, diclofenac has been found to be extremely harmful to vultures. This drug is commonly used to treat pain and inflammation in livestock animals. After treatment, traces of diclofenac remain in the bodies of dead animals. When vultures feed on these contaminated carcasses, the drug enters their body and causes severe kidney failure and visceral gout, often leading to death (Oaks *et al.*, 2004) [11]. Studies conducted in India, Nepal, and Pakistan reported that diclofenac poisoning caused a decline of more than 95% in several *Gyps* vulture species (Green *et al.*, 2004) [6]. Although the veterinary use of diclofenac has been banned in many regions, illegal use of the drug still continues and remains a serious threat to vulture survival (Cuthbert *et al.*, 2015) [3]. Other veterinary drugs such as ketoprofen, aceclofenac, and nimesulide are also considered dangerous because they may produce toxic effects on the kidneys and digestive system of vultures (Swan *et al.*, 2006) [15].

2. Heavy Metals and Industrial Pollutants

Heavy metals such as lead, mercury, cadmium, and arsenic enter the environment through industrial waste, mining activities, pesticides, and contaminated water sources (Pain *et al.*, 2003) [12]. These toxic substances accumulate in the tissues of dead animals, and vultures become exposed when they consume contaminated carcasses. Heavy metal poisoning can affect the nervous system, digestion, and overall health of vultures. Lead poisoning, in particular, has been associated with loss of appetite, weak muscle coordination, reduced flying ability, and abnormal feeding behaviour (Gangoso *et al.*, 2009) [4]. Long-term exposure to heavy metals may also decrease feeding frequency and weaken social interactions during group feeding.

3. Pesticide Contamination

Agricultural pesticides are another important source of environmental contamination affecting vultures. Chemicals used in farming may enter the food chain through contaminated livestock, wild animals, and carcasses (Mateo *et al.*, 2015) [9]. Pesticides such as organochlorines and organophosphates can accumulate in the body tissues of scavenging birds and negatively affect their behaviour and health. Exposure to these toxic chemicals may damage sensory organs, disturb digestion, reduce feeding efficiency, and increase mortality risk. In some cases, pesticide contamination may also affect reproduction and overall survival of vulture populations.

4. Plastic Pollution and Landfill Waste

Rapid urbanization and improper waste disposal have forced many vultures to depend on garbage dumps and landfill sites for food (Carvalho *et al.*, 2022) [2]. While feeding at these places, vultures often swallow plastic materials, rubber pieces, cloth fragments, and other harmful waste products along with food. Plastic ingestion can cause serious health problems such as blockage of the digestive tract, oxidative stress, enzyme imbalance, and neurological disorders (Carvalho *et al.*, 2022) [2]. These health effects may reduce feeding efficiency, weaken body condition, and alter natural scavenging behaviour. Dependence on human-generated waste also reduces the natural foraging habits of vultures and increases their exposure to harmful contaminants and diseases.

Feeding Behavioural Alterations in Vultures

1. Changes in Food Preference

Environmental contamination has significantly influenced the feeding preferences and carcass selection behaviour of vultures across many regions of the world (Ghosh-Harihar & Ramakrishnan, 2024) [5]. Under natural conditions, vultures primarily depend on carcasses of wild herbivores and naturally dead animals available in open landscapes and forest ecosystems. However, rapid habitat destruction, urbanization, decline of wild ungulate populations, and reduction in natural food resources have forced many vulture species to increasingly depend on livestock carcasses and human-generated waste materials. In South Asia, domestic cattle carcasses now form a major part of the diet of several *Gyps* vultures (Ghosh-Harihar & Ramakrishnan, 2024) [5]. Although livestock carcasses provide a regular food source, they also expose vultures to veterinary pharmaceuticals such as diclofenac and other toxic NSAIDs. This shift from natural prey sources to

contaminated livestock remains one of the major causes of altered feeding ecology and population decline in vultures. Recent DNA metabarcoding studies revealed that Indian vultures consume a high proportion of domesticated animal remains, indicating strong dependence on anthropogenic food resources (Ghosh-Harihar & Ramakrishnan, 2024) [5]. In urban and semi-urban areas, vultures are increasingly observed feeding at slaughterhouses, garbage dumps, and landfill sites where food is easily accessible. However, these food sources often contain plastics, industrial waste, chemicals, and pathogens that negatively affect vulture health and survival. Changes in food preference may also influence nutritional quality and feeding behaviour. Natural carcasses provide balanced nutrients required for survival and reproduction, whereas contaminated waste material may reduce nutritional intake and increase physiological stress. Such behavioural modifications gradually weaken natural scavenging instincts and increase dependence on unstable human-associated food resources.

2. Altered Foraging Patterns

Environmental contamination and habitat disturbance have greatly modified the foraging behaviour and movement patterns of vultures (Pain *et al.*, 2003) [12]. Traditionally, vultures used large open landscapes and grasslands for locating carcasses through visual scanning and social information sharing. However, habitat fragmentation, industrial development, deforestation, and reduction in safe feeding grounds have altered these natural movement patterns. In contaminated environments, vultures often travel longer distances in search of uncontaminated food resources. Increased travel requirements result in higher energy expenditure and greater physiological stress. Reduction in natural carcass availability further intensifies competition among scavengers and forces vultures to forage in risky habitats. Several vulture species have adapted to feeding near roadsides, slaughterhouses, dumping grounds, and urban waste disposal sites where carcasses and food waste are easily available (Carvalho *et al.*, 2022) [2]. Although such sites provide predictable food supplies, they also expose vultures to heavy metals, plastics, pesticides, pathogens, and chemical pollutants. Feeding near roadsides additionally increases the risk of vehicle collisions and human disturbances. Satellite telemetry studies have demonstrated that environmental disturbances significantly influence movement ecology and foraging ranges in vultures (Phipps *et al.*, 2013) [13]. Birds living in contaminated or disturbed habitats often show irregular flight patterns, altered migration behaviour, and changes in habitat utilization. Some species have also shifted from natural forest and grassland ecosystems toward urban and semi-urban landscapes in search of food. Altered foraging behaviour may further affect breeding success and population stability because vultures spend more time searching for food and less time in nesting and reproductive activities.

3. Reduction in Feeding Efficiency

Exposure to environmental contaminants can directly reduce feeding efficiency and physiological performance in vultures (Naidoo & Swan, 2009) [10]. Toxic substances such as diclofenac, pesticides, heavy metals, and plastics affect neurological functioning, digestive processes, muscle

coordination, and metabolic activity. Vultures exposed to toxic veterinary drugs often exhibit delayed feeding responses, weakness, lethargy, and abnormal feeding posture. Kidney damage caused by diclofenac poisoning disrupts metabolic balance and reduces the bird's ability to process food efficiently (Naidoo & Swan, 2009) [10]. Affected vultures may consume smaller quantities of food and show reduced participation during communal feeding events. Plastic ingestion is another major factor reducing feeding efficiency in scavenging birds (Carvalho *et al.*, 2022) [2]. Plastics and non-digestible materials may block the digestive tract, reduce nutrient absorption, and damage internal organs. Gastrointestinal obstruction can create a false sensation of fullness, causing reduced food intake and gradual starvation. Heavy metal contamination, especially lead exposure, may impair muscle coordination, vision, and nervous system functioning (Gangoso *et al.*, 2009) [4]. Such effects reduce the ability of vultures to locate carcasses, compete with other scavengers, and consume food efficiently. Chronic toxic exposure also weakens immune response and overall body condition, making vultures more vulnerable to infections and environmental stress. Behavioural observations suggest that contaminated vultures often display reduced aggression and slower reactions during feeding interactions. This may alter competitive hierarchies within scavenger communities and reduce survival chances for weakened individuals.

4. Social Feeding Disturbances

Vultures are highly social scavengers that depend on communal feeding behaviour for efficient carcass detection and resource utilization (Pain *et al.*, 2003) [12]. Group feeding allows vultures to locate carcasses rapidly, defend food resources, and reduce predation risk. However, environmental contamination and large-scale population declines have severely disrupted these social feeding systems. Diclofenac-related mortality drastically reduced vulture population density across South Asia, leading to fewer communal feeding events and breakdown of traditional scavenging networks (Green *et al.*, 2006) [7]. Declining population size reduces the effectiveness of social information transfer that vultures use to locate food sources over large distances. At contaminated feeding sites such as garbage dumps and slaughterhouses, increased competition among scavengers may lead to aggressive interactions and behavioural stress. Vultures competing for limited uncontaminated food resources may display abnormal dominance behaviour and increased conflict with other scavengers such as feral dogs and crows. Environmental stress may also alter social hierarchy within feeding groups. Weak or contaminated individuals often fail to compete successfully during communal feeding, leading to unequal food distribution and poor survival rates. In some cases, reduced group size may lower feeding efficiency because vultures rely heavily on collective behaviour to detect carcasses. Disruption of social feeding behaviour not only affects individual survival but may also influence reproductive success, chick survival, and long-term population recovery. Therefore, preservation of safe feeding habitats and uncontaminated carcass availability is essential for maintaining natural social behaviour in vultures.

Ecological Consequences

1. Carcass Accumulation

Vultures play an essential role in maintaining environmental cleanliness by rapidly consuming animal carcasses before

decomposition progresses (Pain *et al.*, 2003) [12]. Their highly efficient scavenging behaviour helps remove dead animals from ecosystems within a short period of time. However, severe declines in vulture populations have greatly reduced carcass disposal efficiency in many regions. As vulture numbers decrease, carcasses remain exposed in the environment for longer durations, leading to foul conditions and increased microbial growth. Slow decomposition of carcasses attracts secondary scavengers such as feral dogs, rats, jackals, and crows. The increasing availability of carcasses provides these opportunistic scavengers with abundant food resources, allowing their populations to expand rapidly. The rise in feral dog populations has become a major ecological and public health concern in several South Asian countries. Unlike vultures, feral dogs are inefficient scavengers and may leave partially decomposed carcasses exposed for extended periods. This further increases environmental contamination and creates favourable conditions for disease-causing organisms. Carcass accumulation may also contaminate nearby soil and water resources through bacterial growth and toxic decomposition products. Such environmental degradation negatively affects wildlife, livestock, and human communities living near contaminated areas.

2. Disease Transmission

Vultures act as natural biological sanitizers because they consume decomposing carcasses before harmful pathogens can spread within the environment (Markandya *et al.*, 2008) [8]. Their highly acidic digestive system destroys dangerous microorganisms such as anthrax bacteria, rabies-associated pathogens, and other infectious agents that may survive in decaying animal tissues. Declining vulture populations have significantly reduced this natural disease-control mechanism. When carcasses remain unconsumed for long periods, they become breeding grounds for bacteria, viruses, and parasites. Secondary scavengers such as feral dogs and rats feeding on infected carcasses may spread diseases to livestock, wildlife, and humans. Studies suggest that vulture decline in South Asia indirectly contributed to an increase in stray dog populations and associated zoonotic diseases, particularly rabies (Markandya *et al.*, 2008) [8]. Increased dog populations near human settlements elevate the risk of dog bites and disease transmission among rural and urban communities. In addition to rabies, prolonged carcass exposure may increase the spread of diseases such as anthrax, brucellosis, tuberculosis, and botulism. Contaminated water and soil near carcass disposal sites may further facilitate pathogen transmission. Therefore, the decline of vultures not only threatens biodiversity but also creates serious public health challenges by weakening natural disease regulation within ecosystems.

3. Ecosystem Imbalance

Vultures occupy an important position in food webs and nutrient cycling processes because they efficiently recycle organic matter from dead animals back into ecosystems (Shultz *et al.*, 2004) [6]. Their scavenging activity supports ecological stability by preventing excessive carcass accumulation and maintaining balanced scavenger communities. Behavioural alterations and population declines in vultures can disturb trophic interactions and ecological balance. Reduction in vulture numbers allows other scavengers such as feral dogs, rats, and crows to dominate carcass resources. This shift in scavenger

community structure may alter predator-prey relationships and increase competition among species. Changes in scavenger dynamics may also influence nutrient recycling patterns within ecosystems. Delayed carcass decomposition can affect soil quality, water contamination levels, and energy flow across trophic levels. In some ecosystems, reduced scavenging efficiency may indirectly impact herbivore populations and broader biodiversity patterns. Environmental contamination affecting vultures may further disturb migration behaviour, habitat utilization, and breeding success, thereby weakening ecosystem resilience. Loss of vultures from natural ecosystems represents not only the disappearance of a species group but also the breakdown of an important ecological service essential for maintaining environmental health and biodiversity conservation.

Conservation Strategies

1. Ban on Toxic Veterinary Drugs

One of the most important steps for vulture conservation is the strict prohibition of toxic veterinary drugs, especially diclofenac (Cuthbert *et al.*, 2015) [3]. Research has clearly shown that even small amounts of diclofenac present in livestock carcasses can cause fatal kidney failure in vultures after feeding. Although several countries have officially banned veterinary diclofenac, illegal use of the drug still continues in many regions and remains a major threat to vulture survival. To reduce mortality, safer alternatives such as meloxicam should be promoted among veterinarians and livestock owners because studies have confirmed that meloxicam is non-toxic to vultures (Swan *et al.*, 2006) [15]. Government authorities should strengthen drug monitoring systems, regulate pharmaceutical sales, and create awareness programs for rural communities regarding the harmful effects of toxic NSAIDs on scavenging birds. Proper implementation of veterinary regulations and strict legal action against illegal drug use are essential for protecting remaining vulture populations.

2. Establishment of Vulture Safe Zones

The establishment of "Vulture Safe Zones" has emerged as an effective conservation strategy for restoring vulture populations and natural feeding behaviour (Shultz *et al.*, 2004) [6]. These protected areas are designed to provide vultures with safe and contaminant-free food sources by ensuring that carcasses available for scavenging are free from toxic veterinary drugs and pollutants. Vulture Safe Zones generally include monitored feeding stations, breeding habitats, nesting areas, and awareness programs for local communities. Such areas reduce exposure to diclofenac, pesticides, heavy metals, and other environmental contaminants while supporting natural scavenging activities. Several conservation programs in South Asia have reported positive improvements in vulture survival and breeding success within protected feeding zones. Maintaining safe feeding habitats is therefore essential for long-term population recovery and behavioural restoration in endangered vulture species.

3. Monitoring Environmental Contaminants

Regular monitoring of environmental contaminants is necessary to identify threats affecting vultures and reduce toxic exposure (Green *et al.*, 2006) [7]. Scientific monitoring programs should examine livestock carcasses, soil, water,

and waste disposal sites for the presence of harmful veterinary drugs, pesticides, heavy metals, and industrial pollutants. Monitoring helps conservation authorities identify contamination hotspots and implement timely protective measures. Laboratory analysis of vulture tissues, feathers, blood samples, and carcasses can also provide important information regarding pollutant accumulation and health conditions in wild populations. Long-term ecological monitoring programs are essential for understanding changes in feeding behaviour, migration patterns, mortality rates, and breeding success. Such scientific data can support conservation planning and policy development for vulture protection.

4. Waste Management Improvements

Improper waste disposal and increasing plastic pollution have forced many vultures to depend on garbage dumps and landfill sites for food (Carvalho *et al.*, 2022) [2]. Feeding in such contaminated environments exposes vultures to plastics, chemicals, pathogens, and hazardous waste materials that negatively affect their health and behaviour. Improved waste management systems are therefore important for reducing unnatural scavenging behaviour in vultures. Proper disposal of animal carcasses, reduction of open dumping practices, and effective segregation of plastic and chemical waste can significantly minimize contaminant exposure. Governments and local authorities should strengthen landfill management and encourage environmentally sustainable waste disposal practices. Public awareness campaigns promoting plastic reduction and environmental cleanliness can also help protect scavenging birds from harmful contaminants. Reducing dependence on anthropogenic waste sources may gradually restore natural foraging behaviour and improve ecological health in vulture populations.

5. Captive Breeding and Population Recovery Programs

Captive breeding and reintroduction programs have become important conservation tools for critically endangered vulture species (Bowden *et al.*, 2012) [1]. These programs aim to increase population size, preserve genetic diversity, and support long-term species recovery. Under captive breeding programs, vultures are protected from environmental contaminants and provided with safe food and veterinary care. Once populations become stable, selected individuals may be released into protected natural habitats and Vulture Safe Zones. Successful breeding centres established in India and Nepal have contributed significantly to the conservation of endangered Gyps vultures. These programs also support scientific research, behavioural monitoring, and public education regarding vulture conservation. In addition to captive breeding, habitat restoration, public participation, international cooperation, and community-based conservation efforts are essential for ensuring sustainable recovery of vulture populations in the wild.

Conclusion

Environmental contamination has become one of the greatest threats to vulture populations worldwide. Toxic veterinary drugs, pesticides, heavy metals, industrial pollutants, and plastic waste have significantly affected the feeding behaviour, scavenging efficiency, movement

patterns, and overall survival of vultures (Green *et al.*, 2006)^[7]. Among these threats, diclofenac poisoning has played a major role in the rapid decline of several *Gyps* vulture species across South Asia (Oaks *et al.*, 2004)^[11]. Changes in food preference, increased dependence on garbage dumps, altered foraging behaviour, reduced feeding efficiency, and disturbances in social feeding systems indicate that environmental pollution is deeply affecting the natural ecology of vultures. These behavioural changes not only threaten the survival of vultures but also create serious ecological and public health problems. Declining vulture populations reduce carcass disposal efficiency, increase the spread of infectious diseases, and disturb ecosystem balance by allowing secondary scavengers such as feral dogs and rats to increase in number (Markandya *et al.*, 2008)^[8]. Effective conservation of vultures requires immediate control of environmental contaminants and restoration of safe feeding habitats. Strict implementation of bans on toxic veterinary drugs, promotion of safe alternatives such as meloxicam, establishment of Vulture Safe Zones, proper waste management, and regular monitoring of pollutants are essential for long-term conservation success (Cuthbert *et al.*, 2015)^[3]. In addition, captive breeding programs, habitat protection, scientific research, and public awareness campaigns can play an important role in restoring declining vulture populations. Coordinated international conservation efforts are therefore necessary to protect these ecologically important scavengers and maintain ecosystem health and biodiversity for future generations.

References

1. Bowden C, Luthin C, Jakati R, Green R. Recovery planning for endangered *Gyps* vultures in Asia. *Journal of Bombay Natural History Society*,2012;109(3):129-135.
2. Carvalho V, Baptista G, Silva A. Toxicological impacts of plastic ingestion on black vultures (*Coragyps atratus*). *Journal of Hazardous Materials*,2022;424(D):127753-127762.
3. Cuthbert R, Taggart M, Saini M, Sharma A. Continuing mortality of vultures in India associated with illegal veterinary use of diclofenac and a potential threat from nimesulide. *Oryx*,2015;49(1):1-9.
4. Gangoso L, Alvarez-Lloret P, Rodriguez-Navarro A, Mateo R. Long-term effects of lead poisoning on bone mineralization in vultures exposed to ammunition sources. *Environmental Pollution*,2009;157(2):569-574.
5. Ghosh-Harihar M, Ramakrishnan U. Diet composition and continued risk of toxic drug contamination in *Gyps* vultures in India. *Biological Conservation*,2024;289(1):110389-110397.
6. Green R, Newton I, Shultz S, Cunningham A. Diclofenac Poisoning as a Cause of Vulture Population Declines across the Indian Subcontinent. *Journal of Applied Ecology*,2004;41(5):793-800.
7. Green R, Taggart M, Das D, Pain D. Collapse of Asian vulture populations: Risk of mortality from residues of the veterinary drug diclofenac in carcasses of treated cattle. *Journal of Applied Ecology*,2006;43(5):949-956.
8. Markandya A, Taylor T, Longo A, Murty M. Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. *Ecological Economics*,2008;67(2):194-204.
9. Mateo R, Vallverdú-Coll N, López-Antia A, Taggart M. Transfer of pesticides from livestock carcasses to scavenging birds: Implications for conservation. *Environmental Research*,2015;142(1):215-222.
10. Naidoo V, Swan G. Diclofenac toxicity in *Gyps* vultures is associated with decreased uric acid excretion and not renal portal vasoconstriction. *Comparative Biochemistry and Physiology Part C*,2009;149(2):269-274.
11. Oaks J, Gilbert M, Virani M, Watson R. Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature*,2004;427(6975):630-633.
12. Pain D, Cunningham A, Donald P, Duckworth J. Causes and effects of temporospatial declines of *Gyps* vultures in Asia. *Conservation Biology*,2003;17(3):661-671.
13. Phipps W, Wolter K, Michael M, MacTavish L. Do power lines and protected areas present a catch-22 situation for Cape vultures? *PLoS ONE*,2013;8(10):1-10.
14. Shultz S, Baral H, Charman S, Cunningham A, Das D. Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent. *Proceedings of the Royal Society B*,2004;271(6):S458-S460.
15. Swan G, Naidoo V, Cuthbert R, Green R. Removing the threat of diclofenac to critically endangered Asian vultures. *PLoS Biology*,2006;4(3):395-402.