On the Move: What Causes Animals to Disperse?

Mayukh Chatterjee

The phenomenon of dispersal has been defined in many different ways, of which one of the oldest definitions was the one given by Lidicker in 1975 [1]. He defined dispersal as"*...any movement of individual organisms or their propagules in which they leave their home area, sometimes establishing a new home area. This does not include short -term exploratory movements, or changes in the boundaries of a home range, such that the new range includes at least part of the former. Dispersal thus produces homeless travelers (vagrants) who are in search of a new home.*" Dispersal has been at the forefront of research involving animal behaviour and ecology for a very long time.

Mayukh Chatterjee received his MSc in Anthropology from the University of Delhi, and is currently pursuing his doctoral research on primate behavioural ecology at the National Institute of Advanced Studies, Bangalore.

In a more general sense, dispersal speaks of the tendency of some animals to move away from their existing groups or from their former territories. The most common and simple aggregation found in nature is the nest site of birds. Hatching juveniles or fledglings leave from a concentrated place and attempt to find a site that they might live in for most part of their life. In the case of birds and certain mammals, large distances may be covered as a result of dispersal, sometimes reaching up to almost 1000 km. The entire process of dispersal usually involves several risks faced by individuals who disperse; for instance, the severe energetic cost involved in long distance dispersal. Why then do most animals disperse? What are the rewards or benefits that these individuals gain against such severe costs? In this article, we shall examine two different types of dispersals that occur, try to understand the causes behind them and their consequences, and finally look at some practical methods through which the phenomenon is analysed.

Keywords
Animal dispersal, causes of dispersal, breeding and natal dispersal.

Dispersal is an essential part of the life history of most living organisms, with a profound effect on populations of the respective species. Its impact on populations is manifold; while, on the

Dispersal may occur at different points in an organism's life history, and due to different causes; for these reasons it has been categorized into breeding dispersal and natal dispersal.

one hand, it influences the dynamics, distribution, population structure and continuity of populations, it also, from a genetic point of view, determines gene flow between populations, and further affects more complex processes of adaptation, speciation and evolution of traits. Dispersal may occur at different points in an organism's life history, and due to different causes; for these reasons it has been categorized into breeding dispersal and natal dispersal. However, it must be remembered that the phenomenon of dispersal stands apart from the phenomenon of migration, with which it is often confused, particularly as both processes may involve certain common factors (*Box* 1).

Breeding Dispersal

Breeding dispersal refers to the movement of individuals from one territory to another *after they have already reproduced at least once in the previous territory*. Thus, it is mostly the adult individuals who actually carry out this form of movement. It is represented by the movement of sexually mature individuals, away from the group, in-between breeding attempts, and would be marked as a successful breeding dispersal attempt only if the dispersing individual has reproduced in the former and latter groups, before and after movement, respectively. Often, a skew is observed in the dispersal of either sex within a specific population or species. Accordingly, breeding dispersal is categorized as male-biased, female-biased or both-sex breeding dispersal.

Causes of Breeding Dispersal

Breeding dispersal refers to the movement of individuals from one territory to another after they have already reproduced at least once in the previous territory.

Although not a very consistent phenomenon, breeding dispersal occurs in numerous species of animals (*Figure* 1), many of which also show natal dispersal (see below) as a regular phenomenon. This phenomenon, however, is thought to be influenced by the reproductive success of individuals involved, for studies have shown that subordinate individuals with lower reproductive opportunities in a group are the ones that usually disperse in order to find better oppor-tunities. For instance, in gorillas, certain females who have given birth in a group, but are not very

Box 1. Dispersal and Migration

Although migration and dispersal both involve movement of animals from one territory to another, and also individual survival as a proximate causative factor driving the phenomenon, they are two distinct phenomena. Migration refers to movement of entire groups or geographic populations of animals from one region to another for very specific needs, which can be either favourable environments for breeding, richer seasonal food resources, or favourable climatic conditions, to survive during a specific phase of the life cycle. For instance, wildebeest in Africa have huge annual migration patterns that are typically cyclic in nature. It is also important to note that in the process of migration the intervening areas that are covered are not exploited in most cases for the specific purpose behind migration. Migration is thus a cyclic process that would occur for any species that migrates, at regular intervals of time, which could be annual or seasonal. Well-known examples of such species include the Monarch butterflies and the wildebeest.

Dispersal, on the other hand, is usually once in a lifetime event, at least as far as 'natal dispersal' is concerned. It involves the movement of animals from one group to another, or rather one territory to another, where it will usually reside for the most of the rest of its life. Evidently, a species may be characterised by both phenomena; thus, individual wildebeests may disperse (natal or breeding) and join other populations or groups, and may also migrate together within the larger population as a whole when survival conditions become adverse. The important distinction is that migration is a group or population typical phenomenon, while dispersal is not. Although dispersal may involve the movement of a sub-set of a group or population, it does not indicate the cohesive and coordinated movement of entire groups or populations, as in the case of migration.

Wildebeest *(Gerald and Buff Corsi)*

Green Sea Turtle *(Caroline Kopp)*

Monarch Butterfly *(Dr L Loyd Glenn Ingles)*

Sockeye Salmon *(Jeremy Sarrow)*

All images in Box 1 ©California Academy of Sciences

Tree Swallow
© George W Hartwell

Western Lowland Gorilla
Gerald and Buff Corsi
© California Academy of Sciences

Great Gray Owl
Gerald and Buff Corsi © California Academy of Sciences

Figure 1. Species with breeding dispersal.

preferred as mates by the dominant 'silverback' male, tend to move out and join other groups, where they may have a better chance of reproducing. Thus, the immediate driving force responsible for such dispersal may include individual survival or deprivation of food or mates; the phenomenon may have ultimately evolved, however, because dispersing individuals survived better and were able to pass their genes, responsible for this behaviour, to succeeding generations.

The study by Sinha *et al* [2] reported a high incidence of female emigration, which occurred primarily from the unimale troops, a form of social organisation that appears to be of recent origin in the study population of bonnet macaques.

Another possible cause of breeding dispersal is lack of mate choice. Sinha *et al* [2], have reported unusual trends of both natal and breeding dispersal in one particular bonnet macaque population in the Bandipur and Mudumalai wild life sanctuaries of southern India. Macaque societies, in general, are characterised by polygynous/promiscuous mating systems with males as the usual dispersing sex. This population now has two kinds of troops – multimale-multifemale troops, typical of bonnet macaques elsewhere and unimale-multifemale, in which a single adult male monopolises reproduction within the troop. The study by Sinha *et al* [2] reported a high incidence of female emigration, which occurred primarily from the unimale troops, a form of social organisation that appears to be of recent origin in

the study population of bonnet macaques. Thus, some females of unimale troops, who were forced to mate with the single dominant male of the troop, moved out of the troop and joined multimale bisexual troops, were they had better mate choice. These unimale troops also showed a high incidence of natal dispersal by juvenile males, possibly because of increased aggression from the single adult male; such aggression may be driven by perceived sexual competition for the troop females. In the multimale troops, however, males who formed the predominant dispersing sex sometimes stayed back in the natal troops and, in some cases, became the most dominant males of the troops. This recent emergence of unimale troops in the population and the subsequent increase in female immigration possibly represent a case of evolution of novel social strategies in which dispersal seems to be mediated by a complex of factors including mate choice, resource distribution, and perhaps individual temperament as well.

Natal Dispersal

Natal dispersal typically refers to the movement of animals from their natal territory, the area where they were born, to either a new region, which they would eventually occupy, or into the territory of other individual/s. The former is seen to be more prevalent among species that are not very gregarious, while the latter is seen in species that are relatively more gregarious. As can be expected, it is usually the juveniles or subordinate individuals that move out. For instance, in species like African wild dogs, naked mole-rats, meerkats or several fox and wolf species, it is usually a breeding pair (the dominant male and female) that monopolizes the activity of reproduction while the other members usually disperse or help in raising the breeding pair's offspring; the latter however, lose out on their own reproductive option.

Species exhibiting natal dispersal can be broadly categorized on the basis of the predominant sex of the individuals that disperse, just as in the case of breeding dispersal. Therefore, one can

Natal dispersal typically refers to the movement of animals from their natal territory, the area where they were born, to either a new region, which they would eventually occupy, or into the territory of other individual/s.

California Ground Squirrel

Ringtailed Lemur

Koala

African Elephant

Figure 2. Species with male-biased natal dispersal.

classify natal dispersal in a species as male-biased (*Figure* 2), female-biased (*Figure* 3) and both-sex (*Figure* 4) dispersal. The sex that primarily does not disperse or is negatively biased with respect to natal dispersal is referred to as the 'philopatric sex', and the phenomenon itself, of residing and spending the entire life in one's own birth group, is termed as 'natal philopatry'. In species that are solitary in nature, juveniles or subadults of both sexes tend to disperse from the natal (mother's) home range, and acquire distinct home ranges for themselves.

Natal dispersal can also be related to species with different mating systems, i.e. monogamous, polygynous or promiscuous species (*Box* 2). For instance, in polygynous species in which both males and females disperse, in most cases it is highly biased towards males while females are the philopatric sex. In promiscuous and monogamous species, however, both sexes may disperse with almost equal frequencies. However, studies on some species of animals like the cheetahs and the bonobos, have shown that the pattern of dispersal is not always so strict. In both of these species, the females are the predominant dispersers while

African Wild Dog *(Dr Robert Thomas and Margaret Orr)*

Chimpanzee
(Gerald and Buff Corsi)

Virignia Opossum *(Alden M Johnson)*

North American Porcupine
(Gerald and Buff Corsi)

Photo Credit: © California Academy of Sciences

Figure 3. Species with female-biased natal dispersal.

the males remain in their natal home range.

Natal dispersal may also affect the demographic patterns of an animal society. An interesting example of this is the Indian wild dog (*Cuon alpinus*) also commonly known as 'dhole'. Studies have shown that a whole range of aspects, both behavioural and demographic were influenced by the pattern of natal dispersal shown by the species. For instance, in the packs studied it was seen that both the sexes dispersed in general, but with a bias towards the female sex. Also the males who dispersed did so at a much later age than the females. Due to this a dhole pack tends to have male-biased adult sex ratios.

Causes of Natal Dispersal

The factors that cause natal dispersal can be described in terms of

Figure 4. Species with both-sex natal dispersal.

ultimate and proximate causations. Several theories have been put forward to provide possible explanations for the proximate as well as ultimate factors that play a role in mediating the process of dispersal.

Proximate Causes

Aggression from Dominant Individuals: This theory holds that aggression shown by dominant animals towards subordinate individuals drives the subordinates to disperse from the natal group. In many animal species, especially the polygynous ones, it is seen that the dominant males often react aggressively towards juvenile males once they approach sexual maturity, in order to reduce sexual competition. Consequently, the juveniles move

Box 2. Mating Systems

Broadly, almost all animal societies can be described on the basis of the type of mating system that is observed among them. In general, all mating patterns are categorized into three types, viz. monogamous, polygynous and promiscuous mating systems.

A monogamous mating system signifies that an adult male and adult female mate to reproduce and sometimes bring up their offspring together. These individuals, often termed as the 'breeding pair', may or may not be accompanied by other individuals of either or both sexes. In gibbons, the basic social unit is just the breeding pair who occupy a territory and raise offspring together. When the offspring attain adulthood, they are driven out of the natal home range. In many canid species, on the other hand, the social group consists of several individuals of both sexes, amongst whom only one female and male monopolize breeding, while the other individuals, some throughout their lives, help in raising litter after litter of the breeding pairs' offspring. African wild dogs are a good example of such a social system.

A polygynous mating system refers to an arrangement where one male monopolizes breeding with several females, at any one breeding season, within the group. Thus, the group may have other males but the dominant male holds sole right to breed with his harem of females. In most cases, this dominant male will drive away subordinate males in order to reduce competition. Hamadryas baboons are a good example of this type of mating system and social organization.

Typical Monogamous Species

Gray Wolf

American Bald Eagle

Typical Polygynous Species

African Lion

Spotted Hyena

Box 2. continued...

Box 2. continued...

Typical Promiscuous Species

Icelandic Sheep

Raccoon

Promiscuity is a system of mating wherein males and females mate with multiple partners of the opposite sex. Promiscuous systems of mating exist in many multi-male bisexual groups, especially those lacking rigid dominance hierarchies, where there are several individuals of either sex and almost all adult individuals have opportunities to mate and sire offspring. A good example is that of the snowshoe hare, a species which tends to lack social complexity and follows a promiscuous system of mating.

out of the natal area and establish their own home range, acquire females, and start their own breeding unit. In species that are characterised by monogamous breeding units within multi-member social organizations, called 'cooperative breeding species' such as African wild dogs, and meerkats, the juveniles of both sexes are philopatric, and help raise the breeding pairs' offspring. However, recent studies on some populations of such cooperative breeding species have revealed both-sex dispersal, although at a very low frequency.

Deprivation of Resources: In many cases it has been observed that subordinate animals are deprived of resources such as food, shelters, and females because of the very fact that they are subordinate, and this may happen even if they are not exposed to the aggressive behaviour of dominant individuals. Consequently, such individuals would have to disperse and gather resources for themselves in order to survive and breed. Although this may not be a direct cause of dispersal, it may nonetheless be an important associative factor, which results in the dispersal of subordinate individuals.

Innate Tendency to Disperse: Intrinsic factors have been found to be responsible for dispersal of individuals in many animal

species. This has been shown by the apparent absence of the above factors and the persistent occurrence of dispersal in many animals unexplained by other causes. In Belding's ground squirrels, for example, individuals disperse in the absence of parental aggression or aggression by other individuals and in the presence of abundant resources. Dispersal in their case was triggered by the attainment of a certain size. Further, in mice, it has been seen that restlessness and explorations out of the natal area increase with approaching sexual maturity and these ultimately lead to dispersal.

Dispersal of individuals probably guards against the possibility of close inbreeding, and is possibly best achieved by the complete dispersal of any one sex, regardless of the population density.

Studies on tigers in India have shown that male tiger cubs, on attaining adulthood move away from their mothers' home range and establish their own range, far away from the natal territories. The female cubs on the other hand usually share the mothers' territory or may establish one of their own, adjacent to their natal territory. This sex biased dispersal pattern, seems to indicate an innate urge to disperse, which is more in males. Whether this difference arises due to genetic or physiological distinction of the males and the females, still awaits investigation.

Ultimate Causes

Inbreeding Avoidance: Inbreeding in its simplest form refers to matings between related individuals. Dispersal of individuals thus probably guards against the possibility of such close inbreeding, and is possibly best achieved by the complete dispersal of any one sex, regardless of the population density.

Close inbreeding leads to increased homozygosity, which is correlated with loss of fitness. Homozygous populations may also suffer due to an increase in the incidence of diseases through the expression of many recessive alleles.

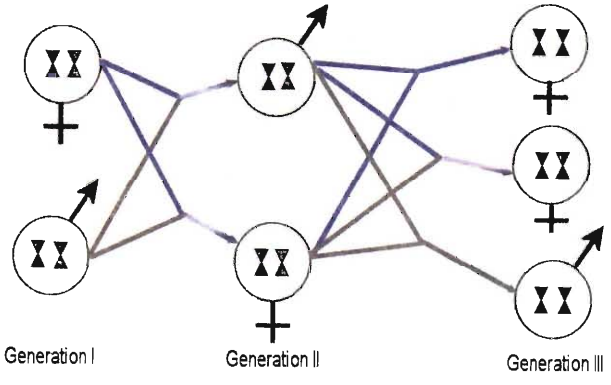
Close inbreeding leads to increased homozygosity, which is correlated with loss of fitness. Homozygous populations may also suffer due to an increase in the incidence of diseases through the expression of many recessive alleles (*Box* 3). Such cases may also lead to population declines if the mutations are lethal or deleterious. The cost of inbreeding must be higher than the cost of dispersal for animals to disperse.

A very interesting study on *Cynopterus sphinx*, a species of fruit bat found in India, revealed an innovative mechanism of avoid-

Box 3. Inbreeding and its Consequences

Inbreeding, in the simplest sense, refers to matings between individuals who have a common ancestor in their preceding generations. In more technical terms, it refers to the coming together of two alleles, identical by descent, on complementary chromosomes. Chromosomes, identical by descent, indicate their emergence from a single molecule of DNA in the near past. Consequently, if the chromosome bears a mutated gene, which is usually recessive, the mutant gene will express itself as soon as it comes together with another identical allele. Inbreeding would thus occur if sibs or genetically close relatives bred, or in other words, through consanguineous matings. Inbreeding is of most concern, because of its positive influence on the coming together of harmful or mutant genes, which are deleterious in nature. In these cases the mutation would express itself phenotypically and thus, reduce the fitness of the individual. In a more extreme consideration, if the mutant gene is a lethal one, it may even result in the death of the individual.

To understand the effects of inbreeding let us consider a progeny bred through the mating of sibs. As in the illustration, we can see that the mother has, say, a recessive mutant allele denoted by the blue cross while the allele complementary to it is the normal allele, indicated by the white cross. Through the different possible assortments, two types of offspring may be born; one that receives a copy of the mutant allele from its mother and the other that does not, irrespective of the sex of the child. Considering the case, in which both children carry one copy of the mutant allele, and in case, these individuals in the second generation inter-breed, we see that their offspring in the third generation can again be of three types: (i) with two copies of the normal allele, (ii) one copy each of the normal and mutant allele, or (iii) two copies of the mutant recessive allele. In the first case, the offspring losses the harmful recessive mutation, in the second case the offspring remains a carrier, while in the third case it becomes what is known as a '*homozygote*' to the mutant trait expressed by the recessive allele. It thus expresses the trait and this may result in reduced fitness in some way or the other. However, the effect of such a combination would highly vary, depending upon the complexity of the mating over generations and also on the type of mutation, as not all mutations are deleterious. Mutations are, however, in most instances harmful and seem to persist in populations only in the recessive state. If a mutation were to be dominant, it would express itself in no matter what combination it occurred and thus would not be hidden and transmitted across generations. The 'chance' of a recessive mutation to express itself is increased through consanguineous matings often resulting in death or loss of reproductive fitness.



Transmission of a recessive mutant allele, through sib-sib inbreeding.

ing inbreeding, through dispersal. These bats form typical harem groups, which are usually monopolized by a single or a small number of resident males. The study showed that effectively both sexes of juvenile pups disperse from their natal territory once weaned. To further reduce the risk of inbreeding, there is a continuous immigration of females into the harems, and an occasional change in the resident males.

Also, Zubiri [3] study in 1995 on Ethiopian wolves showed that in cases where dispersal became far more risky, because of harsh environment and high wolf pack densities, the females (who are the predominant dispersers) often did not disperse, and eventually some became the dominant females of the pack. This would of course bring in a risk of inbreeding, as she would have to mate with usually her sibling in order to raise offspring. The study however showed a high incidence of extra-group copulations wherein a dominant female of one pack would mate with a male from an adjoining pack. This seems to be a new strategy that has been selected to avoid inbreeding, owing to the conditions that bar other ways such as dispersal.

Colonisation: Inbreeding, as proposed, may not be the sole extrinsic factor for natal dispersal. Under certain conditions for instance resource limitations or the possibility of extinctions at a sub-population level, dispersing individuals may be favoured by selection as they would be reproductively more successful in the newly occupied habitats, rather than in a more crowded natal habitat. Consequently, a disperser moving onto an area that is already heavily occupied would have relatively lower success. Studies on newts and other amphibians have shown them to be strict conformees to this theory. For instance, Gill's study in 1985 [4] on the Eastern newt showed that extinction of populations in ponds seems to be a very likely consequence of failure of adults to reproduce successfully over a length of unfavourable years. The study also showed that the newts have developed a phase of dispersal in their life cycles, during which they wander over great distances in order to settle into other available ponds with favourable conditions. In case they do find a pond that is

Under certain conditions, dispersing individuals may be favoured by selection as they would be reproductively more successful in the newly occupied natal habitats, rather than in a more crowded habitat.

It is evident that dispersal, like most natural phenomena, is likely to be caused and/or influenced by a host of factors and caution must be exercised to ensure that all such factors are considered when studying it.

near empty and have at least one mate, they are likely to have a very successful reproductive phase and consequently colonize that pond. In such a case, the phenomenon of dispersal seems to have been definitely favoured simply because colonization of new and empty habitats proves to be reproductively beneficial.

Other Factors

It is thus evident that dispersal, like most natural phenomena, is likely to be caused and/or influenced by a host of factors and caution must be exercised to ensure that all such factors are considered when studying it. Sinha *et al.*'s [2] study on the bonnet macaques, for example, revealed a novel factor – mate choice – that possibly influences the pattern of breeding dispersal in females, while several factors such as competition avoidance and inbreeding avoidance may together influence natal and breeding dispersal among the males. Why some bonnet macaque males fail to disperse remains unknown and further studies may reveal other hitherto undiscovered factors that influence such decision-making. The point to be kept in mind is that very few of such phenomena can be pinned down on any single causative factor, and extensive studies may be needed to understand the different possible causes of any phenomenon. Such novel data also subjects much of the existing theories to reassessment. Referring to Sinha *et al*'s. [2] work again, what are the strategies that males that fail to disperse have evolved to avoid inbreeding? Or, is it that in-breeding does not lead to deleterious effects in populations such as this, as is the case with the cheetah in Africa. One therefore needs to take a more synthetic and relativistic approach while trying to understand natural phenomenon such as dispersal.

Measuring Dispersal

To understand the process of dispersal, the first thing one has to do is to identify the process of dispersal, subsequent to which one may record it for further qualitative or quantitative analyses. Since the occurrence of dispersal is rare, especially those over

long distances and it is also difficult to determine which individuals will disperse, it becomes imperative to devise and use certain strict techniques that will allow the identification and recording of the phenomenon with a substantial level of confidence. Nathan [5], proposed the categorization of techniques to measure dispersal into the following three broad categories.

To understand the process of dispersal, the first thing one has to do is to identify the process of dispersal, subsequent to which one may record it for further qualitative or quantitative analyses.

Biogeographic Methods: These methods mainly involve the observation and comparison of existing distributions of biota in distinct locations. It works on the idea of homological similarities that suggest one population to be the founder of another. For comparison all aspects of phylogeny are usually considered and sometimes, molecular markers are also employed. For instance, Raxworthy [6], studied chameleon phylogeny based on multiple morphological and molecular markers and found that chameleons arose in Madagascar and dispersed repeatedly to locations such as mainland Africa and the Seychelles Islands, which they subsequently colonized. However such data generally tells one of effective dispersal (the inference that dispersal has taken place, although it may not be able to assert other details about the phenomenon), rather than dispersal per se. Further, such data becomes insufficient for quantifying the phenomenon, because it lacks information on both the location and strength of members of the dispersed population.

Movement/Redistribution Methods: This involves the actual observation of the dispersal process, mainly by observing the movement of marked individuals over time and space. Populations are marked using various techniques such as radio collaring, tagging, dyeing, etc, and their movement over different periods observed and recorded, thus providing a first-hand view of the phenomenon in continuum. Turchin [7] proposed a classification of these set of techniques into two further subcategories, Eulerian and Lagrangian. The former, i.e. Eulerian techniques, basically deal with a source population and a resultant population, thus giving the distance of dispersal along with the direct evidence of dispersal. Various markers such as dyeing, tagging, or even the stable isotopes of elements such as hydrogen

Suggested Reading

[1] W Z Lidicker, *Small mammals: their Productivity and Population Dynamics*, Cambridge University Press (Book), 1975.

[2] A Sinha, Not in their genes: Phenotypic flexibility, behavioural traditions and cultural evolution in wild bonnet macaques, *Journal of Biosciences*, Vol.30, pp.51–64, 2005.

[3] C S Zubiri, D Gottelli and D W Macdonald, Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (Canis simensis), *Behavioral Ecology and Sociobiology*, Vol.38, pp.331–340, 1996.

[4] E Gill Douglas, Interpreting breeding patterns from census data: A solution to the husting dilemma, *Ecology*, Vol.66, No.2, pp.344–354, 1985.

[5] R Nathan, G Perry, J T Cronin, A E Strand and M L Cain, Methods for estimating long-distance dispersal, *Oikos*, Vol.103, pp.261–273, 2003.

[6] C J Raxworthy, M R J Forstner and R A Nuss-baum, Chameleon radiation by oceanic dispersal, *Nature*, Vol.415, pp. 784–787, 2002.

[7] P Turchin, *Quantitative analysis of movement*, Sinauer Associates. (Book), 1998.

and carbon in the animals' tissues are employed to identify individuals of specific source populations to be subsequently matched with other sample populations. These techniques however, lack the ability to acquire more precise information about dispersal such as exact distance covered during dispersal, intermediate home range establishments by dispersers, etc.

Lagrangian methods, on the other hand provide a more detailed picture of the process of dispersal as it crucially employs techniques such as radio telemetry, GPS-tagging and satellite-tracking, where animals are radio-collared, fitted with GPS (Global Positioning System) tags or satellite transmitters. The movement of animals is tracked over regular short intervals through radio signal receivers, satellite receivers or through the GPS tags when they are recovered from the study subjects. The results are incredibly detailed, but the techniques are very expensive and are difficult to deploy when dealing with large populations.

Genetic Methods: The use of genetics in understanding dispersal in different species of plants and animals employs certain genetic markers, which are inherited and passed on over generations, and therefore enable the detection of even long-lost genetic relationships between distinct populations. Such evidence may suggest that one population was formed through the dispersion of individuals from another, over a long period of time. Genetic markers, besides varying as to how they are obtained, also vary as to how they are inherited. For instance cytoplasmic markers, such as mitochondria are inherited from a single parent, unlike the bi-parental inheritance mode of the nuclear genome. Usage of such specifically selected markers not only allows the understanding of long-term or short-term dispersal consequences, but also enables the identification of other parameters with regards to dispersal, as for instance, the predominant sex that disperses. Further, genetic markers can be utilized not only to see movement patterns within a generation but also over several gaps of generations; in the latter case, however, it is mostly the relative dispersal effect that emerges, and not the actual process of dispersal.

Future Research

Understanding the process of dispersal requires long-term studies on different species of animals and comparisons across different taxa are essential if one needs to understand the evolutionary benefits and consequences of such a complex phenomenon. Although majority of studies on dispersal has been conducted on wild species, domestic species also offer good opportunities to understand the evolutionary causes that moderate dispersal patterns in animals. Pal, Ghosh and Roy [8], who conducted a three-year study on free-ranging domestic dogs in India, found that juvenile males were the predominant dispersers in the packs they studied. Also males dispersed in greater numbers during the late monsoon, leading the authors to conclude that this dispersal was most probably to avoid competition for mates and to reduce inbreeding. The study of dispersal dynamics in specific species, aided by modern technological advancements like GPS tagging, could provide a wealth of detail that could be used to update our knowledge and theories explaining the phenomenon. It would also help in predicting future consequences of dispersal for different populations, particularly of endangered species, thus enabling us to devise population-specific-management strategies.

India still remains a treasure trove for wildlife biologists and all that is required is to have motivated and highly dedicated investigations to fathom all this treasure. While many studies have been conducted on the ecology and behavior of wild animals, very few studies have focused on intricate aspects such as dispersal that have major impacts at the population level. Studies on such critical phenomena would not only provide a deeper insight into the life of our wild neighbours, but would also enable a better understanding of these species as biological entities, and thus aid in developing better strategies to conserve them.

[8] S K Pal, B Ghosh and S Roy, Dispersal behaviour of free-ranging dogs Canis *familiaris* in relation to age, sex, season and dispersal distance, *Applied Animal Behaviour Science*, Vol.61, pp.123–132, 1998.

[9] D Berteaux and S Boutin, Breeding Dispersal in Female North American Red Squirrels, *Ecology*, Vol.81, pp.1311–1326, 2000.

[10] F S Dobson, Competition for mates and predominant juvenile male dispersal in mammals, *Animal Behavior*, Vol.30, pp.1183–1192, 1982.

[11] F S Dobson, Multiple causes of dispersal, *American Naturalist*, 1985.

[12] P Ferreras, M Delibes, F Palomares, J M Fedriani, J Calzada and E Revilla, Proximate and ultimate causes of dispersal in Iberian lynx *Lynx pardinus*, *Behavioral Ecology*, Vol.15, No.1, pp.31–40, 2004.

Address for Correspondence
Mayukh Chatterjee
National Institute of
Advanced Studies
Bangalore 560 012, India
Email:
mayukh@nias.iisc.ernet.in