Movement Mechanisms of *Gyps himalayensis* (Himalayan Vultures) in the Central Asian Flyway

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Presented by
Sherub

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Faculty of Sciences
Department of Biology

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Sherub

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Summary

In a space varying from sub-atomic to cosmic scales, nothing is static. As Heraclitus stated half a millennium B.C.: ´Panta rhei´ - everything is constantly on the move.

Seasonal wildlife movements are often described and characterized as migrations, which may have evolved from dispersal movements. Animal movements per se may not have captured human attention from the beginning, but animal migrations have since Aristotle. Apparently, migratory movements were abundant throughout the millennia, and individual survival and population processes depended on them. The magnitude of migration phenomena on earth has dwindled with global species extinction and population decline. Numerous such migration phenomena may become history, and more of them will vanish in case our efforts for species conservation fail.

The phenomenon of animal migration has captivated scientific interest, and mysteries of wildlife movements are being researched, deciphered and understood. In general, wildlife movements are described in the forms of various migration and five movement types: i) dispersal, ii) nomadic iii) pursuing, iv) escape, and v) spreading. Wildlife migrations can also take the form of partial migration, when only a part of a population migrates seasonally. Partial migration can be found both within long-distance and altitudinal migrations.

Movement study in wildlife has begun with simple marking on animal such as with metal or colour bands in early 20th century. In the later part of 20th animal movement studies were performed using satellite tracking, and only recently have GPS point locations been recorded for birds on a global scale. Researcher have now begun to use miniature solar-powered light weight hardware with single to multi-sensor bio-loggers, efficient to collate animal behaviour via recordings of an individual’s activity (mostly through 3D-ACC sensors) and its exact spatial locations (via GPS sensors). Through the use of 3D-acceleration sensors, one can now also estimate the movement energy via the calculation of the overall dynamic body acceleration (ODBA). This measurement is sufficiently correlated to the overall energy expenditure of individuals to allow for comparisons among and between species.
The most modern bio-logging units are remotely programmable which allow researchers to remotely manage sampling regimes. Movement data from bio-loggers that are back-packed on the birds are most efficiently and automatically read out to online database (such as Movebank) via GSM or GPRS mobile network communication systems.

For my movement research, e-OBS GmbH solar-powered tags with GPS and ACC sensors, packaged with GSM and GPRS communication facilities were used. The e-OBS bio-logger can be remotely managed via an internet interface, either to collect low or high resolution (1Hz) GPS point data. Every day the bio-logger relays five GPS fixes to the Movebank online database, whereas with a GPRS package, all onboard data (GPS and ACC) are automatically uploaded to Movebank when the tagged bird is within the mobile network. Along with high resolution GPS data, I have used 13 environmental parameters available from the Movebank’s EnvDATA system which influence the vulture movement.

In the Asian landscapes, data from animal migrations or movement research are very scanty. However, there is outstanding research on Bar-headed Goose (Anser indicus) migration, other notable studies in Asia are: - the migration of Common Cuckoo (Cuculus canorus) and Common Swift (Apus apus pekinensis). Otherwise, movement studies in three major Asian avian migration flyways have been mostly focussed on the understanding of the spread of avian influenza.

Research on vultures across this continent is also scarce. Across Asia, some conservation, pharmacological and mortality studies have been conducted on scavengers, but movement research on Asian vultures is almost non-existing. Otherwise, very little about the movement of vultures in Asia is known.

For the first time, this study focuses on the annual movements of the Himalayan Vulture (Gyps himalayensis). I define annual movements is a composite of biannual seasonal migrations from summer to winter areas, daily survival, locomotion and exploratory or continuous nomadic flight. I have chosen this species to study for manifold reasons. Raptors belonging to the vulture taxonomic group are critically endangered around the world, sixteen of the 23 species are enlisted in the threatened category. Himalayan Vulture is a near-threatened species with existing estimated
population below 334,000 individuals. It is the heaviest (6-12kg) flying bird in Asia which performs biannual seasonal migratory movements across the Himalayas, and an obligate scavenger making it one of the best species to understand flight mechanisms, migration and annual movements. Vultures are soaring raptors popularly known to harvest wind energies, such as thermals and orographic uplifts as well as tail winds for energy conserving movements.

In this study of the Himalayan Vultures, I have assessed the survival and annual movements, flight characteristics and annual movements in relation to environmental factors and flight mechanisms over the Himalayas in the thin air.

I back-packed eObs bio-loggers on 18 free ranging and wild Himalayan Vultures, mostly immatures and juveniles or nonbreeding sub-adults. During the first year of the experiment, five of the 18 Himalayan Vultures died en route to their summer areas during their northward seasonal migration. In the assessment of survival and annual movements, I looked at mortality depending upon environmental parameters and initial departure flight distance from winter areas. I demonstrate that en route, migration mortality in Himalayan Vultures is about 27%. It is observed that those dead individuals during migration flew north directly against the north-south meridional head winds, less able to find and use thermal uplifts, and also remained in high density human settlement areas with high humidity and high temperatures. In contrast, those individuals that survived who were able to find thermal uplifts, maintained optimal flight height above the grounds, chose to stay away from high density human settlement and remained in overall higher altitude locations with low temperatures, and their initial migration distance until their first stopover was > 1500km. Mean annual cumulative distance travelled by Himalayan Vultures is 31578 km, and mean of summer movement range is quadruple times the mean winter movement range. The movement tracks and movement range confirms that Himalayan Vultures are truly a migratory species.

In the analysis of flight characteristics and annual movements, I analysed how flight characteristics are affected by 13 selected environmental factors. Animals are in constant interaction with abiotic environmental parameters in their movements. A movement may entail seasonal migratory movements and daily movements in both summer and winter areas. I provide a descriptive investigation of flight characteristics
of annual movements and annual navigation pathways of the Himalayan Vulture in Asia. I show the environmental conditions that vultures prefer for their living. This examination also demonstrates that vultures migrate to warmer climes in winter, at altitudes below 3800m, and summer in areas of altitudes above 4000m. In the winter, vultures move from lower NDVI to higher NDVI areas. I illustrate that vultures in their summer range are exposed to stronger thermal and orographic uplifts, higher surrounding temperature with drier atmospheric humidity and lower precipitation. Flight height above the ground in summer areas is two times the winter flight height (mean range 180-340m). With this annual movement study, I showcase the north-south and east-west movement range extension of the Himalayan Vultures in Asia.

One of the primary quests in this study was also to understand the flight mechanisms of the Himalayan Vultures over the surging mountains of the Himalayas coupled with thin air. Soaring raptors can fly at high altitudes of up to 9000 meters, and Himalayan Vultures are known to fly at around 7000 meters. Using high resolution circle or thermalling GPS data (1Hz), from 50-6500 meters above sea level, a 2-fold range of air densities, I assessed the *behavioural adaptation to the flight into thin air*. People’s quest to unravel how birds fly long journeys during their migration are still a scientific challenge. While quite a number of studies have been conducted to understand the physiological adaptations of flight mechanisms, the specific mechanisms underlying the behavioural adjustments to high-altitude flights are largely unknown. To create the necessary lift to support the same weight and maintain soaring flight in thin air, birds might modify lift coefficient by biophysical changes, such as wing posture and increasing the power expenditure. Alternatively, they can change their flight characteristics. We show that vultures use the latter and increase circle radius by 35% and airspeed by 21% over their flight altitude range. These simple behavioural adjustments enable vultures to move seamlessly during their annual migrations over the Himalaya without increasing energy output to flight in high elevations.

Finally, I recommend existing movement data sets can be analysed comparatively to better understand annual movement characteristics, migration and navigation, landscape level energetics, daily activity pattern, as well as time and energy budgets. Given its wide range distribution, I strongly suggest and call for collaboration among all the Himalayan Vulture range countries for the conservation management of the species as the species use vast expanse of Asian landscape. I also advice to use
these movement data to proactively plan for infrastructure development and installations. Furthermore, I also recommend immediate future research as to understand the Himalayan Vulture foraging behaviour and herding movement. I propose that cremation of human corpses in sky burials by Buddhist and Parsee in Asian landscape be encouraged and continued with caution of the use of NSAIDs. Attention is also drawn on how bio-loggers with high resolution and multi-sensor capabilities on birds will serve as an independent real-time mobile weather buoy, which in turn can also serve as sentinels for various weather fronts. Similarly, real time analysis of behavioural (ACC) data may eventually be used to predict impending natural disasters.
Zusammenfassung


Eine der wesentlichen Ziele meiner Studie war es auch die genauen Flugmechanismen des Himalaya Geiers zu verstehen, vor allem zu den Zeiten, in denen die Vögel über die höchsten Gipfel des Himalaja hinwegsegeln. Es ist bereits

General Introduction
1.1 The scientific fascination of movements & global migrations

Human researchers are engaged in documenting and understanding various movements within and beyond the space that we as *Homo sapiens* have occupied—from the galactic to cosmic movements, planetary movements in solar systems, day and night rotational movement of the earth, atmospheric and oceanic movements of winds and currents, migratory movements of wildlife on land and sea, flow of blood in circulatory systems in animals, and vertical movements of sap in plant anatomy.

Seasonal wildlife movements are often described and characterized as migrations, which may have evolved from dispersal movements (Alerstam and Christie 1993). Animal movements *per se* may not have captured human attention from the beginning, but animal migrations have since Aristotle (Berthold 2001; Wilcove 2008). Apparently, migratory movements were abundant throughout the millennia, and individual survival and population processes depended on them. The magnitude of migration phenomena on earth has dwindled with global species extinction and population decline. Wilcove and Wikelski (2008) suggested that wildlife migration itself has become an endangered phenomenon. Passenger Pigeons (*Ectopistes migratorius*) in North America have already become extinct and their migrations are gone forever. Numerous such migration phenomena may become history, and more of them will vanish in case our efforts for species conservation fail (Wilcove 2008).

The phenomenon of animal migration has captivated scientific interest, and many researchers have been engaged in deciphering the mysteries of wildlife movements (Berthold, 2001). Berthold, 2001, in his book *“Bird Migration A General Survey”* describes various categories of migration and five movement types: i) dispersal, ii) nomadic iii) pursuing, iv) escape, and v) spreading. Dispersal movement is exhibited by most wildlife species, and primarily by juveniles and sub-adults or by newly bonded breeding pairs. Nomadic movement is observed in species characterised by rapid sexual maturity and without having breeding site fidelity, and dependent on ephemeral food resources (Berthold 1978; Berthold, 2006). An example of such species is the Red Crossbill (*Loxia curvirostra*). Antbirds in South America are famously known for their exhibition of pursuing movement, which primarily follows ant colonies (Touchton and Wikelski 2015). Escape movement is an immediate survival movement shown by wildlife species as a response to severe stimuli such as tsunami, earthquake, risk of
depredation and abrupt changes in weather. Spreading movement is observed in species regardless of age group spread out or expand its distribution to a new area. The Collared Dove (*Streptopelia decaocto*) is the best example of birds showing this movement (Nowak, 1989; Hengeveld, 1993). Wildlife migrations can also take the form of partial migration, when only a part of a population migrates seasonally. Partial migration can be found both within long-distance and altitudinal migrations.

Researchers have discovered phenomenal global scale animal migrations on earth. Some of the most magnificent animal migrations on earth are: the multi-generation migration of the Monarch butterfly (*Danaus plexippus*) in the Americas, Loggerhead turtle (*Caretta caretta*) movement from the islands of Japan to Mexico, polar migration of Arctic Tern (*Sterna paradisaea*) from Arctic to Antarctic, the journeys of White Storks (*Ciconia ciconia*) from Europe to the African Cap of Good Hope (Flack et al. 2016), unguided migration of Common cuckoos (*Cuculus canorus*), and migration of Common Swift (*Apus apus pekinensis*) to Africa from Asian (Akesson et al. 2012) and European landmasses.

In the European continent, the study of bird migrations dates back to bird ringing and retrieval of bands started early in the 20th century. Displacement experiments of Common Starlings (*Sturnus vulgaris*) are one of the classical experiments that used bird ringing with the aim to understand orientation and navigation skills of long-distance migrating birds (Perdeck 1967).

Satellite tracking of wildlife movement has begun in the latter part of the 20th century with collections of very few and only approximate (‘doppler shift’) locations of individuals, sometimes as few as 10 locations per annual cycle. Only recently have GPS point locations been recorded for birds on a global scale (Kays et al. 2016).

1.2 Technological advancements and selection of bio-logging devices

Despite significant technological advancements in recent years, experiments on bird navigation and biophysical flight mechanisms in wild and free ranging individuals have still been scanty. Our knowledge and understanding of avian migration mechanisms still requires further observations, experiments and explorations. In the recent years -
beginning in the early 21st century - dedicated researchers, technology and software (analytical and communication) system developers have come together to produce miniature solar-powered light weight hardware with single to multi-sensor bio-loggers, efficient to collate animal behaviour via recordings of an individual’s activity (mostly through ACC sensors) and its exact spatial locations (via GPS sensors). Through the use of 3D-acceleration sensors, one can now also estimate the movement energy via the calculation of the overall dynamic body acceleration (ODBA). This measurement is sufficiently correlated to the overall energy expenditure of individuals to allow for comparisons among and between species (Wilson et al. 2006; 2008; 2014a; 2014b; 2015).

The most modern bio-logging units are remotely programmable which allows researchers to remotely manage sampling regimes. Movement data from bio-loggers that are back-packed on the birds are most efficiently and automatically read out to online database (such as Movebank) via GSM or GPRS mobile network communication systems. To the GPS positions of a tagged animal movement, remotely-sensed geophysical and atmospheric information can be synchronized in the post data processes. With the advent of multi-sensor bio-loggers, the above mentioned nascent understanding of navigation and movement mechanisms of migrants has become a reality (Nathan et al 2008; 2012). For instance, we can now finally attempt to answer questions such as: Why does an animal migrate? When does an individual migrate? How does a migrant move? What are the energy costs and expenditures? Additional physiological bio-loggers, such as implanted heart rate and body temperature loggers, allowed for even greater insights into the energy expenditure beyond the use of ODBA (Bishop et al 2015).

For my movement research, e-OBS GmbH solar-powered tags with GPS and ACC sensors, packaged with GSM and GPRS communication facilities were used. The e-OBS bio-logger can be remotely managed via an internet interface, either to collect low or high resolution (1Hz) GPS point data. Every day, with the GSM package, the bio-logger relays five GPS fixes to the Movebank online database, whereas with a GPRS package, all onboard data (GPS and ACC) are automatically uploaded to Movebank when the tagged bird is within the mobile network (Flack et al. 2016).
Now, we are already into next generation multi-sensor bio-loggers which can collect spatial, atmospheric pressure (via pitot tube), angular speed (via gyroscope) and true orientation (via magnetometer) data independently. With the existing mobile (GSM & GPRS) networks and satellite telecommunication systems, live updates of animal locations on a global scale are now possible. With the engagement of high resolution, multi-sensor bio-loggers, combined with advance analytic skills, existing theories on bird migration and navigation proposed in 19th are being validated and refined.

Progress in animal movement studies has recently been exponential and new global initiatives such as ICARUS (International Cooperation for Animal Research Using Space) will prominently boost movement studies (Wikelski et al. 2007). ICARUS is an antenna communication system infrastructure to be installed on ISS (International Space Station) solely dedicated for animal or biodiversity movement and behavioural research, and will thus serve as an eye to watching animals or biodiversity around the world.

1.3 Research in movements and migrations in Asia

In the Asian landscapes, data from animal migrations or movement research are very scanty. However, there is outstanding research on Bar-headed Goose (*Anser indicus*) migration which unravels and provides an understanding of physiological and biophysical performances (Hawkes et al. 2011; Bishop et al. 2015) of a species crossing the tallest land barrier to migrants in Asia. Notable emerging movement studies in Asia are: the migration of Common Cuckoo (*Cuculus canorus*) (Buckley et al. 2016) and Common Swift (*Apus apus pekinensis*) (Akesson et al. 2012). Otherwise, movement studies in three major Asian avian migration flyways have been mostly focussed on the understanding of the spread of avian influenza to address human health concerns and to manage avian vectors to avoid pandemic threats from influenza virus (H1N-series virus)(Takekawa et al. 2009; Choi et al. 2016).

Research on vultures across this continent is also scarce. Across Asia, some conservation, pharmacological and mortality studies have been conducted on scavengers, but movement research on Asian vultures is almost non-existing. In contrast, in the west (Americas, Europe, Africa and Asian Middle East) several
migration studies have been performed but annual movement research has barely begun. Life history tracking of wildlife, especially of avian species is now emerging or in the making with the advent of the new technologies described above. Otherwise, very little about the movement of vultures in Asia is known (Swan et al. 2006; Cuthbert et al. 2007).

For the first time, this study focuses on the annual movements of the Himalayan Vulture. The annual movements is a composite of biannual seasonal migrations from summer to winter areas, daily survival, locomotion and exploratory or continuous nomadic or herding flight.

1.4 Selection of EnvDATA parameters and online annotation service
The EnvDATA (Environmental Data Automation Track Annotation) system is an online environmental data annotation service in the Movebank (Dodge et al. 2014). The system offers hundreds of environmental data variables (geophysical, atmospheric and climatic, GIS layers, etc..) that a living individual interact with in its environment in space and time. For the current study, 13 environmental parameters were selected and annotated to the spatial GPS data at temporal scale.
Table 1. The environmental factors used in understanding the annual movements of the Himalayan Vulture.

<table>
<thead>
<tr>
<th>Sl.No.</th>
<th>Source</th>
<th>Environmental Parameters</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Earth surface, land cover, globe cover</td>
<td>Land cover 2009</td>
<td>GlobCover 2009 Land-Cover Classification, GlobCover/Land Cover 2009, Provider: European Space Agency</td>
</tr>
<tr>
<td>2</td>
<td>Earth surface, Vegetation, Leaf area &amp; vegetation, Modis Land, 0.05-deg month, Terra</td>
<td>NDVI</td>
<td>MODIS Land Terra Vegetation Indices &amp;deg Monthly NDVI Description: The normalized difference vegetation index: a measure of the concentration of live plant leaves based on remote sensing reflectance measurements. Higher values indicate more vegetation. Estimate is based on the highest quality image obtained during each 1-month period.</td>
</tr>
<tr>
<td>4</td>
<td>Topography, Elevation, SRTM</td>
<td>Elevation</td>
<td>SRTM Elevation, SRTM90-m DEM; Description: Ground elevation above mean sea level Unit: m No data values: -32768, -9999 (provider), NaN (interpolated)</td>
</tr>
<tr>
<td>5</td>
<td>Weather, Wind, Wind speed, ECMWF, Interim Full Daily at Pressure Level</td>
<td>Vertical velocity</td>
<td>ECMWF Interim Full Daily PL Pressure Vertical Velocity, Description: Vertical velocity of pressure, Unit: Pa/s</td>
</tr>
<tr>
<td>6</td>
<td>Weather, Wind, Wind speed, ECMWF, Interim Full Daily at Pressure Level</td>
<td>U velocity</td>
<td>ECMWF Interim Full Daily PL U Velocity, Description: Velocity of the east-west (zonal) component of wind, Unit: m/s</td>
</tr>
<tr>
<td>7</td>
<td>Weather, Wind, Wind speed, ECMWF, Interim Full Daily at Pressure Level</td>
<td>V velocity</td>
<td>ECMWF Interim Full Daily PL V Velocity, Description: Velocity of the north-south (meridional) component of wind, Unit: m/s</td>
</tr>
<tr>
<td>8</td>
<td>Weather, Temperature, Air temperature, ECMWF, Interim Full Daily at Pressure Level</td>
<td>Temperature</td>
<td>ECMWF Interim Full Daily PL Temperature</td>
</tr>
<tr>
<td>9</td>
<td>Weather, Derived variables, Uplift Velocity, Movebank</td>
<td>Orographic uplift</td>
<td>Movebank Orographic Uplift (from ASTER DEM and ECMWF)</td>
</tr>
<tr>
<td>10</td>
<td>Weather, Derived variables, Uplift Velocity, Movebank</td>
<td>Thermal uplift</td>
<td>Movebank Thermal Uplift (from ECMWF)</td>
</tr>
<tr>
<td>11</td>
<td>Weather, humidity, ECMWF, Interim full daily</td>
<td>Relative humidity</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Weather, precipitation, cumulative Precipitation, ECMWF, Interim full daily</td>
<td>Total precipitation</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Weather, sunshine duration, ECMWF, Interim full daily</td>
<td>Sunshine duration</td>
<td></td>
</tr>
</tbody>
</table>

1.5 Global vulture diversity and status

Vultures are some of the largest flying, long lived and famously obligate scavenging avian species. They have been geographically grouped to Old and New World vultures- those species in the Americas are called New World vultures; while those species in Africa, Asia and Europe are known as Old World vultures. Around the world 23 vulture species are distributed in the continental Africa, Asia, Europe, North America and South America (Table 2). Sixteen of 23 species are listed in the highly threatened category of the IUCN Redlist (IUCN 2016). Eight of the 9 most critically endangered vultures occur in the African continent and the Indian sub-continent.
Vultures are pushed towards extinction by different anthropocentric factors such as indiscriminate poisoning, poaching and mortality induced by NSAIDs (nonsteroidal anti-inflammatory drugs) used in livestock husbandry practices around the world. All Gyps species succumb to visceral gouts and kidney failures upon eating livestock carcasses administered with NSAIDs. Diclofenac has been notoriously lethal to vultures and nimesulide has also proven to affect survival (Swan et al. 2006; Das et al. 2011). Retaliatory poisoning of carcasses depredated by wolves, foxes and snow leopards with rodent pesticides have been also contributing to vultures’ death in the Asian highlands (Ming et al. 2015).

The Indian sub-continent has 9 vulture species. Until the 1970s, Asian vulture populations, especially in India, were in the tens of millions. However, beginning in the 1980s and into the 1990s, vulture populations of all the species declined by 98%.

Figure 1. Geographical distribution of Himalayan Vulture (Gyps himalayensis). Polygon filled with light pink is the current distribution adapted from the Birdlife International and polygon with pale orange is the movement range from this study of the annual movements. The study reveals an apparent north-south and east-west extension of the distribution.
(Cuthbert et al. 2007). Except for the Griffon Vulture (*Gyps fulvus*) and the Himalayan Vulture (*Gyps himalayensis*), all other species are threatened. The crash of these particular vulture populations is also attributed to the use of diclofenac in livestock rearing. Even today, despite decades of conservation management initiatives, vulture populations of the four critically endangered species in the mainland India are very low. The Griffon Vulture and Himalayan Vulture were spared from population declines by being geographically isolated highland species, mostly living in the Asian Himalayas and the various highland plateaus. Today, even the Himalayan Vulture is enlisted as near-threatened species based upon expected population declines in the next three generations (IUCN, 2016).

**Table 1**: Global checklist of vultures and its global status in IUCN RedList and Birdlife International 2016

<table>
<thead>
<tr>
<th>English Name</th>
<th>Species</th>
<th>Continent</th>
<th>Status (Birdlife/IUCN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andean Condor</td>
<td><em>Vultur gryphus</em></td>
<td>S. America</td>
<td>Vulnerable (VU)</td>
</tr>
<tr>
<td>Black Vulture</td>
<td><em>Coragyps atratus</em></td>
<td>Americas</td>
<td>Least concerned (LC)</td>
</tr>
<tr>
<td>California Condor</td>
<td><em>Gymnogyps californianus</em></td>
<td>N. America</td>
<td>Critically endangered (CR)</td>
</tr>
<tr>
<td>Cape Vulture</td>
<td><em>Gyps coprotheres</em></td>
<td>Africa</td>
<td>Endangered</td>
</tr>
<tr>
<td>Cinereous Vulture</td>
<td><em>Aegypius monachus</em></td>
<td>Afro-Eurasia</td>
<td>Near-threatened (NT)</td>
</tr>
<tr>
<td>Egyptian Vulture</td>
<td><em>Neophron percnopterus</em></td>
<td></td>
<td>Endangered</td>
</tr>
<tr>
<td>Greater Yellow-headed Vulture</td>
<td><em>Cathartes melambrotus</em></td>
<td>S. America</td>
<td>Least concerned</td>
</tr>
<tr>
<td>Griffon Vulture</td>
<td><em>Gyps fulvus</em></td>
<td>Afro-Eurasia</td>
<td>Least concerned</td>
</tr>
<tr>
<td>Himalayan Vulture</td>
<td><em>Gyps himalayensis</em></td>
<td>India</td>
<td>Vulnerable</td>
</tr>
<tr>
<td>Hooded Vulture</td>
<td><em>Necrosyrtes monachus</em></td>
<td>Africa</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>Indian Vulture</td>
<td><em>Gyps indicus</em></td>
<td>India</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>King Vulture</td>
<td><em>Sarcoramphus papa</em></td>
<td>Americas</td>
<td>Least concerned</td>
</tr>
<tr>
<td>Bearded Vulture</td>
<td><em>Gypaetus barbatus</em></td>
<td>Africa-Eurasia</td>
<td>Near-threatened</td>
</tr>
<tr>
<td>Lappet-faced Vulture</td>
<td><em>Torgos tracheliotus</em></td>
<td>Africa</td>
<td>Endangered</td>
</tr>
<tr>
<td>Lesser Yellow-headed Vulture</td>
<td><em>Cathartes burrovianus</em></td>
<td>Americas</td>
<td>Least concerned</td>
</tr>
<tr>
<td>Palm-Nut Vulture</td>
<td><em>Gypohierax angolensis</em></td>
<td>Africa</td>
<td>Least concerned</td>
</tr>
<tr>
<td>Red-headed Vulture</td>
<td><em>Sarcogyps calvus</em></td>
<td>India</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>Rüppell's Vulture</td>
<td><em>Gyps rueppelli</em></td>
<td>Africa</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>Slender-billed Vulture</td>
<td><em>Gyps tenuirostris</em></td>
<td>India</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>Turkey Vulture</td>
<td><em>Cathartes aura</em></td>
<td>Americas</td>
<td>Least concerned</td>
</tr>
<tr>
<td>White-backed Vulture</td>
<td><em>Gyps africanus</em></td>
<td>Africa</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>White-headed Vulture</td>
<td><em>Trigonoceps occipitalis</em></td>
<td>Africa</td>
<td>Critically endangered</td>
</tr>
<tr>
<td>White-rumped Vulture</td>
<td><em>Gyps bengalensis</em></td>
<td>India</td>
<td>Critically endangered</td>
</tr>
</tbody>
</table>
1.6 Choice of focal species and questions

The Himalayan Vulture is the heaviest (6-12kg) flying bird in Asia. It has long (M = 2.5 m) and broad (0.55-0.60 m) wing dimensions that enable its seamless flight in their area of occupancy. It is known to occur and range throughout the rugged mountains in the Asian countries (Kazakhstan, Kyrgyzstan, Uzbekistan, Tajikistan, Afghanistan, Pakistan, India, Nepal, China, Bhutan and Myanmar) covering an area of about 2,680,000 km² (Birdlife International, 2016). The population is estimated to 66,000-334,000 mature individuals (Birdlife International, 2106) with an expected decline in the next three generations qualifying it to the near-threatened status (Proffitt and Bagla 2004; IUCN 2016).

It is not only a migratory species but an obligate scavenger which demands enormous flight movements for survival. Its food sources range from large-bodied carrions of wild ungulates and livestock succumbed to natural death or depredation, and human corpses offered to vultures on the sky burials mostly in the treeless alpine and cold arid zones in the regions where Buddhist culture prevails. It has a long and prehensile neck with razor-sharp mandibles well adapted to forage from inside and beneath skin of dead large-bodied mammals. Himalayan Vultures have no choice than to feed on food (carrasses) of livestock treated with NSAIDs (non-steroidal anti-inflammatory drugs) proven lethal to their survival (Virani et al. 2011). Vultures are anatomically equipped with large elastic pouches or crops which can store about 1.5 -2 kg of meat in one feeding bout, besides the internal digestive tract. Storing food which is about 20% of its body weight, may prove advantageous for its depredation by mammalian canids and felids. However, after a feeding bout, usually vultures choose a vantage and a raised position to become easily airborne in the event of predation risks or disturbances. If it were on a flat terrain after foraging, and a sudden predation risk arises, it regurgitates meat from the crop that serves as depredation deterrence while at the same time reduces its body weight which enables an escape flight.

Being migrants, vultures perform biannual migratory movements from their summer areas of Mongolia, Inner Mongolia, Qinghai and Tibetan regions of China to their winter areas in the northern plains of India, and Himalayan countries of Nepal and Bhutan. However, some individuals chose to winter in parts of China. Vultures are soaring raptors popularly known to harvest wind energies, such as thermals and orographic uplifts as well as tail winds for energy conserving movements. During
migration vultures have to cross over the tallest peaks of the Himalayas into thin air. Vultures have to navigate and fly over various land features and landmarks, through atmospheric spaces with varying environmental factors which may positively or negatively influence movements or migration.

All the above biological, morphological and habitual characteristics favour the Himalayan Vulture as a subject species for annual movement studies. For this doctoral thesis, answers to three questions have been attempted. (1). What are the environmental factors causing mortality in Himalayan Vultures? An assessment on this question is performed with various environmental parameters especially for their spring migration as compared to their annual movements. (2). What are the flight characteristic responses to various geophysical, atmospheric and environmental variables? What constitutes the optimal environmental conditions for flight in Himalayan Vultures? Why are Himalayan Vultures visiting the specific places across their range? (3) How do Himalayan Vultures seamlessly fly over the tallest land features on earth with lowest air density? This chapter concentrates on the behavioural adaptations vultures engage to perform their flight movements. Indeed, it deals with flight mechanisms employed by the vultures.

1.7 Overview of Chapter 2
Like many other animals on earth, large and long living vertebrates are seriously threatened towards extinction. Wildlife populations are affected by anthropogenic activities and global climate change. Vulture populations have dangerously declined from induced death (poisoning & use of NSAIDs- for example diclofenac), direct killing (poaching with various means) and collision with tall infrastructures (electric transmission line & wind turbine). In this chapter, our research assessment is concentrated onto 18 non-breeding adults in annual movements and survival of Himalayan Vultures in relation to impacts and influence of environmental parameters. This chapter assembles how initial departure flight distance from winter areas en route to summer areas affects mortality; what environmental factors favour survival as opposed to causing mortality; whether vultures choose optimal environmental conditions and how individual flight experiences and space use ensure better likelihood of survival. The chapter shows that en route migration mortality in Himalayan
Vultures is about 27% (Proffitt and Bagla 2004). We show that those dead individuals during migration flew north directly against the north-south meridional head winds, were less able to find and use thermal uplifts, and also remained in high density human settlement areas with high humidity and high temperatures. In contrast, those individuals that survived were able to find thermal uplifts, maintained optimal flight height above the grounds, chose to stay away from high density human settlement and remained in higher altitude locations with low temperatures, and their initial flight departure distance was > 1500km. This work also confirms that Himalayan Vultures are truly a migratory species.

1.8 Overview of Chapter 3
The living biodiversity is in constant interaction with abiotic components which are composed of the terrestrial landmass, atmospheric layers with weather phenomena, water, and solar energy from the sun. A living organism shows a form of movement over space and time which culminates in completing life history processes. Such a movement may entail seasonal migratory movements and daily movements in both summer and winter areas. Here, abiotic components are referred to as environmental factors. Chapter 3 provides a descriptive investigation of flight characteristics of annual movements and annual navigation pathways of the Himalayan Vulture in Asia. The chapter attempts to look into how flight characteristics in the annual movements of the Himalayan Vultures are affected by 13 environmental parameters based on the question how vultures occupy space throughout the annual cycle. Our investigations in this section detail how vultures migrate, and how they choose to live in warmer climes in winter, at altitudes below 3800m, and summer in areas at of altitudes above 4000m. In the winter, vultures move from lower NDVI to higher NDVI areas. In the summer range, vultures are exposed to stronger thermal and orographic uplifts, higher surrounding temperature with drier atmospheric humidity and lower precipitation. The chapter also shows that flight height above the ground in winter is half of the flight height during the summer. This section of the annual movement study shows the north-south and east-west movement range extension by the Himalayan Vultures in Asia.
1.9 Overview of Chapter 4

Chapter 4 presents first answers to the core quantitative research question - how Himalayan Vultures seamlessly fly at high altitudes coupled with thin air in the Himalayas and the Tibetan highlands. Of many wonders of natural phenomena on earth, migration of wildlife, especially of migrating birds is one. Soaring raptors can fly at high altitudes of up to 9000 meters. People’s quest to unravel how birds fly long journeys during their migration are still a scientific challenge. While quite a number of studies have been conducted to understand the physiological adaptations of flight mechanisms, the specific mechanisms underlying the behavioural adjustments to high-altitude flights are largely unknown. This chapter details the thermalling flights of Himalayan Vultures from 50-6500 meters above sea level, a 2-fold range of air densities, using high resolution GPS data. To create the necessary lift to support the same weight and maintain soaring flight in thin air birds might modify lift coefficient by biophysical changes, such as wing posture and increasing the power expenditure. Alternatively they can change their flight characteristics. We show that vultures use the latter and increase circle radius by 35% and airspeed by 21% over their flight altitude range. These simple behavioural adjustments enable vultures to move seamlessly during their annual migrations over the Himalaya without increasing energy output to flight in high elevations.

1.10 General Discussion

Chapter 5 presents a summary of the findings of each chapter and highlights the importance for continued research and conservation management of the focal species. It also discusses how already collected movement data sets can be analysed comparatively to better understand annual movement characteristics, migration and navigation, landscape level energetics, daily activity pattern, as well as time and energy budgets. Given that this vulture species is widely distributed, it calls for cooperation among all the Himalayan Vulture range countries for the conservation management of the species. It also advises how these movement data can be used proactively for infrastructure development and installation (high tension transmission power lines, wind turbines, air ports and other development activities). In this chapter I also recommend immediate future research to understand the Himalayan Vulture foraging behaviour and herding movement. Having learned that vultures feed on
human corpses in sky burials in the Buddhist communities in the Tibetan Plateau of China and Parsee communities in parts of Asia, sky burial practice for human corpse disposal is encouraged with caution of the use of NSAIDs. Attention is also drawn on how bio-loggers with high resolution and multi-sensor capabilities on birds will serve as an independent real-time mobile weather buoy which will also serve as sentinels to various weather fronts. Similarly, real time analysis of behavioural (ACC) data may eventually be used to predict natural disasters like earthquake, floods or torrential rains.
Chapter 2

Bio-Logging – New Technologies to study conservation physiology on the move: a case study on annual survival of Himalayan Vultures

2.1. Abstract
Bio-logging, the on-animal deployment of miniaturized electronic data recorders, allows for the study of location, body position and physiology of individuals throughout their ontogeny. For terrestrial animals, 1Hz-GPS-position, 3D-body-acceleration and ambient temperature provide standard data to link to the physiology of life histories. Environmental context is added at ever finer scales using remote sensing earth observation data. Here we showcase the use of such bio-logging approaches in a conservation physiology study on endangered Himalayan Vultures (Gyps himalayensis). We determine environmental, behavioural and physiological causes of survival in immature birds that roam from wintering sites in India, Bhutan and Nepal towards summer areas in Tibet and Mongolia. Five of 18 immature griffons died during one year. Individuals that died had failed to migrate sufficiently far northward (>1500km) in spring. Individuals likely died if they flew against headwinds from the north or were less able to find thermal updrafts. Surviving individuals migrated into cold and dry areas with low population density. We highlight flight experience, long distance movements and remote places with low human population as factors critical for the survival of Himalayan Vultures. High-resolution bio-logging studies can advance conservation management by pinpointing where and why migratory animals have problems and die.

Key words: Conservation physiology, migration, annual movement, survival, environmental parameters

2.2. Introduction
Physiological investigations of animals can now increasingly ´go wild´ with the rapid advancement of ever smaller electronic bio-logging units (Wilson et al. 2014a; Wilson et al. 2015; Ropert-Coudert and Wilson 2005; Bridge et al. 2011; Wilson et al. 2008; Block 2005). Such investigations into the exact details and physiological mechanisms underlying life history or population processes are increasingly important today in light of widespread, global population declines of many animal species (Wikelski and Cooke 2006; Cooke et al. 2014; Lennox et al. 2016; Morales et al. 2010). Researchers in the bio-logging field deploy animal-attached micro-electronic units (´tags´) that
record behaviour, movement, physiology and environment while an individual is conducting its day to day activities, potentially leading to a golden age in ecology and physiological ecology (Wilmers et al. 2015; Kays et al. 2015).

State-of-the-art bio-logging tags include many different sensors and record from them with a sufficiently high sampling rate to allow for a near-complete reconstruction of an individual’s 3D-path through its environment, its movement characteristics, behavioural changes as well as a dynamic assessment of its internal physiological state (Bishop et al. 2015; Hawkes et al. 2013; Scott et al. 2015). Usually, the on-board power supply is too weak and the memory capacity of the bio-logging tag too small to record high-definition data continuously, thus timed sub-sampling is used to gain a statistically valid picture of an individual life (Holland et al. 2009; Shamoun-Baranes et al. 2012). Commonly used sensors report GPS position, 3D-accelerometry, light-level information, conductivity, salinity, external as well as body temperature, heart rate or neuro-state (Rattenborg et al. 2008a; Nathan et al. 2012b). As these sensors have different power requirements, not all of them can be recording at the same rate. The most power hungry sensor, GPS positioning, is often scheduled either by using a ‘behavioural’ 3D-acceleration trigger, i.e., only starts when the animals becomes very active or when it starts beating its wings (LaPoint et al. 2013; Brown et al. 2012). Alternatively, GPS sensing is scheduled whenever the battery power is sufficiently high to allow for high-definition reporting, usually at 1Hz intervals (Flack et al. 2016b), but reaching up to 10Hz (Bouten et al. 2013).

One of the most powerful and simple sensors for conservation physiologists, 3D-acceleration, has not yet reached its full analytical potential (Gleiss et al. 2011; Nathan et al. 2012b; Wilson et al. 2006; Shepard et al. 2008). 3D-acceleration sensors can easily be attached externally, e.g., in a leg band or an ear tag, and can be calibrated against behaviour either on a population or (ideally) individual level (Brown et al. 2013; Nathan et al. 2012a). Combined with the location context from GPS logging, the body acceleration can provide unprecedented details about the physiological and health state of an individual. Wilson and colleagues (Wilson et al. 2014a) showed that even the past medical history of people can be detected via the fine-scale reporting of 3D-acceleration vibrations (Sands et al. 2015; Wilson et al. 2014b). Similarly, the sickness behaviour of animals – perhaps one of the best remote measurements of health in
wildlife – can be inferred from 3D-acceleration loggers (Wilson et al. 2014b). Even more so, stressful situations generally change the way bodies are moving, which again is easily detected using 3D-acceleration sensors. Ideally, other sensors that help to fine-position a body in space such as gyroscopic, magnetic and pressure sensors can be combined with 3D-acceleration sensing to achieve a near-perfect reconstruction of the spatial state of an individual at critical times during its life (Wilson et al. 2014b; Williams et al. 2017). Such IMU (inertial measurement unit) technology is already highly developed in commercial fields such as drone flight and is now adapted to physiological wildlife studies (Floreano and Wood 2015). 3D-acceleration logging also allows a first glimpse into the energetics of an individual via the calculation of ODBA, the overall dynamic body acceleration (Wilson et al. 2006; Halsey et al. 2011). Although it is only a crude first estimate of the detailed energy expenditure of an individual, ODBA is very helpful in understanding long-term differences in energy use between species, populations and individuals, as well as in individuals over time and space. As a very helpful tool in conservation physiology, it is now possible to construct ´energetic landscapes´ to understand which locations within the movement range of an individual demand more power from the animal than others (Scharf et al. 2016).

The internal state of an individual is perhaps best approximated from body temperature and heart rate logging (Butler et al. 2004; Butler et al. 2002). Based on Fick´s equation, heart rate can provide a good proxy for true energy expenditure of an individual if the stroke volume is constant or known, and if the oxygenation of the blood does not change much (Halsey et al. 2008). Combined with ODBA measurements, the quantification of heart rate provides a rather comprehensive assessment of instantaneous energy expenditure, stress and movement energetics (Halsey et al. 2009; Clark et al. 2010; Duriez et al. 2014). The concurrent quantification of body temperature adds an important component of thermoregulation (potential heat and cold stress), but –depending on context – may also indicate a disease or an immune response (Adelman et al. 2010; Adelman et al. 2014).

In the future, bio-logging tags that possess all above mentioned sensors will become commonplace and be miniaturized massively (Bridge et al. 2011; Wikelski et al. 2007). Additional features in tags will include on-board cameras that are triggered by pre-set (previously observed and internally programmed) behavioural changes to also allow
researchers to study the social context of individuals, both within conspecific groups as well as during interspecific interactions (Hays 2015; Kane and Zamani 2014; Watanabe and Takahashi 2013). Understanding the collective behaviour of individuals in the wild is of great importance as we appreciate more and more that physiological changes during the life history of individuals are strongly influenced by biological interactions (Chikersal et al. 2017). Another aspect of the movement physiology of animals that can soon be quantified better is the relative positioning of limbs or other body parts relative to each other. Body area networks of sensors that communicate with each other through Bluetooth-like radio connections may help better understand the forces exerted and received by individuals (Ullah et al. 2012). What is still in its infancy are data loggers reporting olfactory information produced or received by free-roaming animals (Gagliardo et al. 2013; Wikelski et al. 2015; Reynolds et al. 2015). Nevertheless, some progress is being made in the atmospheric chemistry field to miniaturize such sensors into autonomous data loggers that could eventually be used to study olfactory components of the life of individuals. In the future, sound and video could also be recorded by loggers to better apprehend the environmental context around the focal animal to better explain its behaviour.

Although we can use the sensing system mentioned above to infer the internal physiological state of individuals in many cases, there is still a major lack of technological developments applying the existing physiological sensors to work autonomously in free-roaming animals (Ponganis 2007; Ropert-Coudert and Wilson 2005; Cooke et al. 2014). In human and veterinary medicine many sensors already exist that could potentially be combined with bio-logging devices, however there is still little concrete progress in this field, but with some notable exceptions (Schobel et al. 2013). Such sensors could detect glucocorticoid or other hormonal breakdown products, blood sugar, or blood oxygenation and stroke volume (Chen and Chatterjee 2013; Turner 2013). Nevertheless, physiological ecologists will always carefully consider if a correlate of a physiological state is sufficient to provide the answer to an eco-physiological question, particularly in the context of conservation physiology (Cooke et al. 2014; Lennox et al. 2016; Wilson et al. 2015).

Great progress has also been made in terms of neuro-logging devices (Kang et al. 2016) that report the state of an animals’ brain or neuronal systems while the animal
goes about it’s daily business. Starting from homing pigeons, the brain activity during complex navigational tasks has been addressed (Latanov et al. 2005; Vyssotski et al. 2009). The study of sleep in wild animals is also progressing rapidly (Rattenborg et al. 2008b; Voirin et al. 2014), with sometimes spectacular insights into the physiological functioning of individuals in their natural context (Rattenborg et al. 2016).

Compared to the internal physiological or neurological state, it is now rather straightforward to annotate the environmental context along the path of an individual in space and time (Shamoun-Baranes et al. 2010). As the satellite and in-situ remote sensing systems have become public and much more generally available recently (Turner et al. 2015), there even exist automated environmental annotation facilities such as the Env-Data Module in Movebank (Dodge et al. 2013; Kranstauber et al. 2011). Using these annotation systems it now easy and straightforward to determine dozens of environmental factors potentially influencing the behaviour and physiology of wild animals on the move. Here we provide an example of such an analysis for the annual movement of Himalayan Vultures. Moreover, as the remote sensing system can also provide the information of environmental factors in the close and far vicinity of the individual, we cannot determine which environments the individual could have moved through, but did not visit. Knowing what environmental factors an individual avoids can be even more informative than knowing those that it uses (Kranstauber et al. 2015; Safi et al. 2013). In addition, we also start to learn – by the apparent mistakes in environmental selection an individual makes - what individuals know about their environment, and what they may not know (Cagnacci et al. 2010).

**Case study: Himalayan Vultures**

Himalayan Vultures are the heaviest flying vertebrate scavenger in Asia. Here we showcase the use of such bio-logging devices to study the conservation physiology of Himalayan Vultures (*Gyps himalayensis*), which share their conservation fate with many large and long-lived vertebrate species around the world that are in serious decline or on the brink of extinction (for vultures, see: (Ogada et al. 2012; Buechley and Şekercioğlu 2016). Vultures, are particularly threatened: of the world’s 23 vulture species, 12 are critically endangered or almost extinct (Dodge et al. 2014; Mandel et
Survival threats to global vulture populations are from poaching, indiscriminate poisoning, notably by the use of non-steroidal anti-inflammatory drugs (NSAIDs) in veterinary practices of livestock farming (Proffitt and Bagla 2004). In the Hindu state, livestock corpses (cows and oxen) are left for wildlife- predatory birds and mammals and scavengers for consumption. At the general surprise, after having been considered as the most numerous raptors in the world, vulture populations in India were decimated, with 98% population decline relative to 1980s (Virani et al. 2011). The mortality in vultures in India was caused from renal failure and visceral gout, as a result of feeding on livestock corpses administered with diclofenac (Swan et al. 2006). Despite prohibition of some NSAIDs use in livestock, vulture populations slowly recover but remain at extremely low levels (Galligan et al. 2014; Prakash et al. 2012), with an exception of the three highland species (Bearded Vulture, Griffon Vulture and Himalayan Vulture) which apparently still enjoy relatively stable populations, but may face similarly serious declines within the next three generations. Diclofenac is banned from use in livestock in India, Nepal, Bangladesh and Pakistan, and the use of ketoprofen in Bangladesh prohibited. Gyps species are captive bred and raised to be released in “Vulture Save Areas” starting at the end of 2017 or during 2018, as an effort towards vulture population recovery and stabilization. Emergence of new threats from the use of nimesulide- a NSAID substitute for diclofenac is also known to cause mortality in all Gyps species (Cuthbert et al. 2007). Recently, Himalayan Vulture is listed as “near-threatened by IUCN but a recent study proposed to update as “vulnerable” with the prospect of population decline in the next three generations (Paudel et al. 2015). Beside their diet, two aspects of their life history make vultures particularly vulnerable to human threats: their slow life cycle (a low reproductive rate, delayed maturity and long life-span make vulture demography highly sensitive to any increase in adult mortality, (Ricklefs and Wikelski 2002), and their movement ecology. Most vulture species perform long distance movements during their daily foraging routine, and many species are migratory or erratic at some stage of their life cycle (Dodge et al. 2014). These large scale movements complicate the conservation actions usually applied at small scale (e.g., in a reserve or a national park) and justifies the need to study their movements using bio-logging devices to understand the
reasons of their movements and plan adequate conservation actions at the appropriate scale (Wilcove and Wikelski 2008).

In our study we try to find the specific, individual causes of mortality of some Himalayan vultures using bio-loggers with special emphasis on their annual movement strategies and the environmental conditions encountered by the birds during the course of their movements. We concentrate on immature and juvenile birds because young and naïve birds are also generally engaged in erratic movements, potentially leading them to dangerous areas (López-López et al. 2013; Phipps et al. 2013).

2.3. Materials and Methods

2.3.1. Bird capture and data recording
18 non-breeding Himalayan Vultures were captured in Bhutan between November 2014 and February 2015 using wire mesh-mesh cage traps, weighed and measured. All birds included in the study were immature individuals at an estimated age of 1-2 years. Individuals were equipped with high resolution GPS data loggers (45 g, cell phone link, e-Obs GmBH), using an approximately 30 g Teflon-nylon harness. Birds were then filmed before release to calibrate their behaviour against 3D-acceleration data that were collected by the tags (see below). Daily between 02.00 - 20.00 hours UTC, loggers were set to periodically collect 1 Hz GPS fixes for 10 min, whenever solar charge allowed. Whenever there was low sunlight charge of the tag, the GPS fix rate was lowered to 30 minutes. We collected a total of 2.923.736 GPS fixes between February 1, 2015 until January 31, 2016. The tags were also set to collect 3D-acceleration data at 15Hz per axis for a duration of 4 seconds at 2 minute intervals throughout the day. These data were also transmitted through the GPRS connection of the tags. Data are available through the Movebank archive (https://www.movebank.org/node/15294).

2.3.2. Seasonal home range, initial movement distance and migration direction
We determined the home ranges of individuals for the winter period (November-April) and summer period (June-September). We used three kernel density estimates (50%, 95% and 99%) and show the 95% estimated home range in our maps. Home range
area statistics were computed only for the stationary phases of the annual cycle, using Hawthtools with ArcGIS10.0 fixed-kernel estimators at fix interval >10 min, to avoid strong autocorrelation of positions. When the birds moved away from their winter ranges, we determined the initial movement distance as great circle distance from the centroid of the winter range towards the centroid of their first staging area, i.e., an area where they spent more than a week. We then determined the migration direction as the compass direction between these two points.

2.3.3. Environmental Data Annotation

In our analysis we focused on non-breeding individuals (N = 18) as they all face the same life history constraints, i.e., the survival analysis is not confounded by the potentially differing demands of reproduction. GPS tracks and ACC data transmitted from bio-loggers on Himalayan Vultures in the field are stored in the Movebank online database (Fiedler and Davidson 2012). We annotated 13 environmental factors (SRTM elevation, ECMWF Interim Full Daily Pressure Level Pressure Vertical Velocity, ECMWF Interim Full Daily Pressure Level Relative Humidity, ECMWF Interim Full Daily Sunshine Duration, ECMWF Interim Full Daily Total Precipitation, Globe Cover 2009 Land Cover Classification, Movebank Orographic Uplift from ASTER DEM and ECMWF, ECMWF Interim Full Daily Pressure Level V Velocity, ECMWF Interim Full Daily Pressure Level U Velocity, ECMWF Interim Full Daily Pressure Level Temperature, SEDAC GRUMP v1 2000 Population Density Adjusted, MODIS Land Terra Vegetation Indices 05deg Monthly NDVI, Movebank Thermal Uplift from ECMWF) to our GPS data using an automated Env-DATA System available in Movebank (Dodge et al. 2013).

These environmental data were annotated in space and time and interpolated as needed to the GPS data.

We used the 3D-acceleration data to determine the behaviour of the birds throughout their annual cycle. For this we plotted the data using the Movebank acceleration-viewer annotation extension (https://www.movebank.org/node/5920) and visually annotated them from our observation and photograph-calibrated 3D-acceleration data, prior to the release of the birds in a wire mesh cage trap where they were feeding, preening, sitting and interacting with other vultures (for similar methods, see also (Resheff et al. 2014). Combined with the GPS data that gave the spatial and
movement (speed, height and directional heading) context, we used the behavioural classes resting, flying (further distinguishing between flapping flight and gliding flight) and forage to characterize the birds’ actions throughout the year. For the 5 birds that died during the observation year, we detailed the location and acceleration information within the last two weeks of their disappearances. We also sent field teams to three of the carcasses to confirm the most likely cause of death.

2.3.4. Statistical Analysis
We used statistical package SPSS 22 for analysis. We included one entire year of data, starting on February 1, 2015, for all birds except for the five birds that died. For the dead birds we did not include the last two weeks before death into our analyses to ensure that we do not bias the mortality analysis by factors that preceded death (e.g., if birds that sit on the ground continuously are more likely to be poisoned or killed by hunters). For each bird we calculated, for its entire lifetime (minus the last two weeks), or for a maximum of one year, average values for their behavioural parameters (such as flight altitude above the surface, % time resting, % time thermalling, etc.) and the associated environmental parameters (such as NDVI, temperature, humidity, etc.), at each GPS position at a minimal time interval of 10 minutes. Whenever we calculated percentage data, we arc-sin transformed them for the statistical analysis. For the analyses of environmental or behavioural data, we included all parameters that were not correlated stronger than ±0.2. To come up with hypotheses as to which behavioural or environmental factors were potentially influencing the survival of individuals, we conducted several Independent sample T-tests. We are aware that the overall low sample size of our data set does not allow for robust statistical analyses with regard to the multitude of factors, as well as their interactions, that may affect survival. However, as a first approach to determine factors that might affect survival in Himalayan vultures, these analyses may be valid.

2.4. Results
Seasonal home range, initial movement distance and migration direction:
The observed birds migrated extensively both latitudinally as well as altitudinally, moving from the highest altitudes of the Himalayas to low altitude range lands in India.
Figure 1. Annual movement characteristics of Himalayan Vulture (N = 18) (a). Seasonal home ranges: Pale yellow polygons (95% convex) with red polygons (50% convex) in the centre represents the extent of the winter home range, covering India, Nepal and Tibetan Autonomous Region (China). Green polygons (95% polygons) with red polygons (50% polygons) in the centre denote the extent of the summer home range, covering Mongolia, Inner Mongolia and China, in Asian landscape (b). Initial movement distance: Each line symbolises a departure direction and distance from the wintering areas (India, Nepal and Bhutan), northward to the first staging area during migration to the summering areas. The red lines are of Himalayan Vultures that died during their first observation year, blue lines indicate birds that survived their first year of observation.
In the winter, they descended to lower areas in the northern plains of India, the Himalayas of Nepal and Bhutan, and the Himalayan Plateau and south eastern part of China (Figure 1a). The mean winter home range covered 13973 km² ± 6507 (N = 18, 95% CI = 1220 - 26727 km²). In the summer, Himalayan Vultures ascended to the highlands of the Himalayan Plateau, Inner Mongolia and Mongolia. The mean summer home range (61130 km² ± 20062, 95% CI = 21809 - 100452 km²) was approximately four times larger than the winter home range (Figure 1a).

Migrant Himalayan Vultures crossed the Himalayan mountain range biannually during their north and south bound migrations. During the migration, they made stopovers at favourable staging areas. Here, we measured the initial movement distance between the centres of their first major staging areas and their wintering areas for the first northward migration of the year (Figure 1b). The mean initial movement distance was 1086 km (± 119SE, 95% CI = 892 - 1319 km), covered in a maximum of two weeks. The departure direction of Himalayan Vultures were predominantly north-easterly (Figure 1b), with a median departure direction of 52.5 º (95% CI = 34.58 º – 98.88º) during their winter-to-summer migration.

Ultimate causes of Mortality:

During one year, 13 of 18 birds survived while 5 died during their migration movements from the winter areas to the summer areas. Birds that died used as first stopover a site located at a twice lower distance that birds that survived (Independent samples T-test, F = 0.08, t = -3.1, df = 16, p = 0.007; Figure 2a). However, the birds’ survival did not depend on the total distances they moved (Independent samples T-test, F = 0.55, t = -0.8, df = 16, p = 0.43; Figure 2b). These data suggest that surviving birds had a more straight path towards the summer areas in comparison to birds that died, who had a more sinusoidal path and stopped several times before reaching the summer grounds. Thus we conclude that the initial straight-line distance from the wintering sites to the first staging areas mattered for the survival.
Figure 2. (a) The initial travel distance (from the wintering area and the first stopover site) was shorter in individuals that died during their first observation year. (b) The cumulative travel distance did not differ between individuals that died or that survived. Data show means±95% confidence interval, p-values from T-test.

To assess the environmental and behavioural parameters that could affect individual mortality, we selected 7 individual performance variables of the vultures: flight altitude
above the surface, absolute flight height, proportion of sitting on the ground versus flying, proportion of flight in a straight line versus thermalling (circling) flight, and the strength of the thermal uplift or of orographic uplift (as calculated from the Movebank data models). We also included 7 environmental variables: sunshine duration, precipitation, NDVI, ambient temperature, relative humidity, northerly winds versus easterly or westerly winds, as well as one anthropogenic parameter (population density) in the analysis.

Fig. 3a

Winds from north

![Graph showing winds from north](image)

Fig. 3b

Winds from West

![Graph showing winds from west](image)

Figure 3. (a) Animals that died had on average stronger headwinds from the north (meridional winds) during their first migratory bout. (b) The winds from westerly or easterly directions (zonal winds) had no effect on survival fate. Data show means±95% confidence interval, p-values from T-test.
Vultures that often flew against headwinds from the north did not survive their first year (Independent samples T-test, $F = 0.27$, $t = 3.4$, $df = 16$, $p < 0.001$; Figure 3a). In contrast, how individuals used winds coming from easterly or westerly directions did not matter (Independent samples T-test, $F = 0.39$, $t = 0.26$, $df = 16$, $p = 0.79$; Figure 3b).

Figure 4. (a) Vultures that survived selected areas with stronger thermal uplifts compared to individuals that died. (b) The flights in orographic uplifts did not differ between individuals that died or those that survived. Data show means±95% confidence interval, $p$-values from T-test.
Vultures which were less able to find thermal updrafts were more likely to die, while individuals which were able to find and harvest thermal updrafts survived. (Independent samples T-test, $F = 0.66$, $t = -2.0$, $df = 16$, $p = 0.04$; Figure 4a).

In contrast, the influence of orographic uplift on survival was not significant (Independent samples T-test, $F = 0.23$, $t = 0.95$, $df = 16$, $p = 0.34$; Figure 4b). Himalayan Vultures that stayed most of the year in relatively cold places were more likely to survive (Independent samples T-test, $F = 2.9$, $t = 2.77$, $df = 16$, $p = 0.007$; Figure 5a).
At the same time, individuals that stayed in drier areas were more likely to survive (Independent samples T-test, $F = 0.07$, $t = 2.7$, $df = 16$, $p = 0.008$; Figure 5b). Birds that throughout the year spent most of their time in areas with high human population density were more likely to die (Independent samples T-test, $F = 17.9$, $t = 2.38$, $df = 16$, $p = 0.02$; Figure 6a). However, NDVI was not a decisive factor in the survival of
Himalayan vultures (Independent samples T-test, $F = 0.4$, $t = -1.14$, $df = 16$, $p = 0.26$), indicating that individuals survived better if they chose areas with high plant productivity (high NDVI) that at the same time had low population densities. Such areas can be found in the inaccessible highlands of Inner Mongolia and parts of Tibet, but also Mongolia. However, the percentage of the time focal individuals sat on the ground (resting) significantly influenced their survival: vultures that spend more time on the ground (excluding the two weeks before individuals died), instead of flying, were more likely to die (transformed data: Independent samples T-test, $F = 9.7$, $t = 2.01$, $df = 16$, $p = 0.04$; Figure 6b). Thus, it is apparently beneficial for the survival of vultures to spend as much time in the air as possible.
Figure 6. (a) Vultures that survived selected areas with much lower population density compared to individuals that died. (b) Surviving vultures sat much less on the ground compared to vultures that died. Data show means±95% confidence interval, p-values from T-test.

Environmental factors that we also considered to potentially affect survival, but that apparently did not influence the survival of Himalayan Vultures were: flight altitude above the surface ($p = 0.09$), absolute flight height ($p = 0.41$), sunshine duration ($p = 0.08$), precipitation ($p = 0.17$), or the proportion of time flying via thermalling ($p = 0.18$) or via straight-line flight ($p = 0.31$).
**Proximate causes of mortality:**

The five birds that died in the first year of observation were Palya, Dorje, MaaJoen, JigDor and Baen (see data in DOI to be provided upon publication). Using the high-definition data loggers, we could identify the most likely immediate causes of death in these 5 individuals. Palya presumably died from poisoning because along with it there were 7 other dead bodies of vultures. The tag was found on the ground and retrieved (Yachang Cheng, pers. obs.). Dorje, MaaJoen and Baen disappeared in areas with human population and their demise was presumably linked to human causes. Baen’s acceleration record showed it may have died from sickness: the acceleration showed highly irregular activity towards the days of her death. JigDor’s death in Nepal was possibly linked to the ingestion of diclofenac. Nepal is a Hindu state where dead cows are not consumed. Apparently JigDor had fed by the riverbed next to an agricultural field and had flown far away from the feeding site to a place where it soon died.

**2.5. Discussion**

High-definition bio-logging of the annual movements of a cohort of immature Himalayan griffons highlighted the environmental and individual factors responsible for their survival. Although only a subset of parameters that in principle can be recorded electronically was in fact monitored in these individuals, the high-definition location data in relation to remote sensing data from earth observation satellites allowed us to pinpoint areas of success or failure in these individuals. Such data can be highly relevant for conservation as they show exactly what the cause of death is in a group of animals that is globally endangered. Similar studies have successfully been done in other raptor species during their migration (Klaassen et al. 2014). We also want to caution that our analysis is still using long-term averages of environmental parameters to allow for an overall comparison between individuals. In future analyses using a larger sample size of individuals and ideally a lifetime tracking approach, it will be important to determine seasonal and regional differences in how both behavioural and environmental parameters influence survival.
The factors that turned out to be very important were long range movements away from their wintering quarters, especially in areas in India and Nepal that have high human population densities. Himalayan vultures survived particularly well in areas that were not dominated by humans but still have enough vegetation (or high NDVI) and thus provide carcasses of vertebrates that supply food for the vultures. Apparently, vultures mostly feed on livestock and not wildlife carrion. Thus, desert areas are not providing good food supplies, whereas areas with intermediate NDVI appear to be better. We suggest that villages with rural communities could be the most appropriate location to find dead livestock carcasses (if they can find them before farmers, or at sites with sacred cows, not eaten by men), and sky burials sites.

We did not yet include the birds’ time spent in protected areas in the analysis, but future studies will address this aspect.

Our data also highlighted individual experience as a decisive factor for survival. Immature vultures that were finding thermals at a better rate and were better able to exploit tailwinds had a higher survival probability. We would like to emphasize that the calculation of thermal and orographic updrafts is obviously complicated within mountainous regions such as the Himalayas, thus our analysis can only provide a suggestion into a possible relationship between updraft components and survival. In the future, such relationships will be entirely testable with more refined environmental data. In Eurasian griffon vultures, it was shown that young birds behaved less efficiently in thermals under strong winds compared to experienced adults (Harel et al. 2016). This is similar to what has recently been found in young storks (Rotics et al. 2016; Flack et al. 2016a) and shows how important the ontogeny and ontogenetic experience is for the survival of juvenile birds. It should also be noted that many of the foraging areas of the Himalaya vultures are linked to human habitation directly, namely to the sky burial sites. We estimated that approximately 20% of their foraging activities in China (Tibet, Inner Mongolia) were at traditional sky burial sites. This is consistent with estimates just based on population numbers by Ming (pers. comm.).

The specific causes of death included starvation and poisoning, which was confirmed on the ground in two of the five cases. The use of acceleration data combined with GPS tracks collected in the two weeks before death was useful to give cues about the likely cause of death. Thus even for the Himalaya vultures that are much less exposed
to diclofenac poisoning, the apparent poisoning of mammalian carcasses may turn out detrimental for the survival of these birds (Das et al. 2011; Acharya et al. 2009).

With the rapid technological advancement and miniaturization of devices in animal tracking as well as the inclusion of multiple sensors (such as high resolution GPS and ACC, pitot pressure, gyroscope, magnetometer) we can now track annual movements and soon the entire life history of an animal in high definition. In the future, animals outfitted with new generation tags may become sentinels of weather and climate as well as prevailing environmental conditions at the finest spatial and temporal granularity (Kays et al. 2015). Tagged animals will collect and relay real time information of environmental conditions, surrounding tracked animals or record ephemeral environmental conditions quite precisely. Once such systems are implemented, our interpretations of animal behaviour as well as the challenges faced by animals in the wild in relation to environmental factors (weather, habitat and land use) may become even easier. As a result, we may be able to intervene in the species conservation management in real time at the very location where animals face survival challenges (Cooke et al. 2014; Wikelski and Cooke 2006). Such detailed devices combining GPS and ACC data transmitted by GSM could help finding and rescuing several vultures (G. barbatus, A. monachus, N. percnopterus) from reintroduction or rehabilitation programs in France (O. Duriez, unpublished results).

Remote sensing environmental data (weather, habitat and human land use) can now be commonly used in animal tracking. For example, the global data repository Movebank (Fiedler and Davidson 2012) offers open access environmental data that be easily be annotated to GPS data with the Env-DATA system (Dodge et al. 2013). In our analysis, 13 environmental variables were used in the survival model. While most environmental parameters significantly explained the survival and death of Himalayan Vultures, NDVI parameters failed to provide evidence of significance. While it is intuitive that areas with high NDVI mean greater biodiversity, it may not necessarily mean high ungulate populations, which Himalayan Griffons are dependent upon for survival. Survival of vultures around the globe are vehemently threatened by poisoning, poaching and use of NSAIDs in husbandry practises of livestock farming (Ogada et al. 2012). Advanced bio-logging may help to conserve them and at the same time provide a new way to study the physiology of life histories in the wild (Wikelski and Ricklefs 2001; Block 2005).
Ethics. Ministry of Agriculture and Forests, Bhutan approved this study (UWICE/ADM/20/201-12/998). Royal Civil Service Commission, Bhutan, letter of award (RCSC/HRD(8.00)2014/975, LTA-38935).

Data accessibility. Data are deposited in the Movebank Data Repository (7) http://dx.doi.org/10.5441/001/1.143v2p2k.
Chapter 3

Flight characteristics of Himalayan Vultures during their annual movements across Asia
3.1. Abstract

Migration is a challenge to any migrating animal. During migratory journeys, birds traverse long distances to arrive to an intended goal area. Migrating birds may be unaware or may have to endure and overcome geophysical, climatic and atmospheric challenges in their commute space. Migratory movements are thus influenced by geophysical, climatic and atmospheric conditions. Physical fitness may fundamentally determine the individuals’ annual migration distances and spatial extent of movements. The migrants may also wilfully explore into new boundaries off their existing movement range in pursuit of a suitable living space. In the Asian landscape, challenges to migrating birds are enormous and formidable, coupled by thin air and high altitude. We observed free ranging wild Himalayan Vultures to understand how their annual movements are affected by various environmental factors at geophysical, climatic and atmospheric layers. Himalayan Vultures range at mean altitudes > 4000msl in summer areas, and in winter quarters, they range < 3800msl. We show environmental factors selected by vultures during the course of their annual movements. In the winter, vultures move from lower to higher NDVI landscapes. We describe flight type characteristics, and investigate conditions vultures require to switch from one to another flight type, in a given locomotion space. We also assess how flight and foraging movements in vultures are affected by environmental parameters. We document for the first time, north-south and west-east extensions of movement ranges by Himalayan Vulture. The annual cumulative distance travelled by an avian scavenger like Himalayan Vulture is large. We show that survival of Himalayan Vultures will require large areas with good ungulate populations and proportional population of predators including sky burial cremation practices.

3.2. Introduction

Every individual wildlife species, both on land and in water exhibit some form of movement, to either complete or continue annual life history processes. Animal migration and movement patterns, and their navigational skills continue to intrigue human intelligence and understanding (Berthold 2001). Phenomenal migrations by monarch butterfly (Danaus plexippus) from Mexico to North America, humpback whale (Megaptera novaeangliae) in Pacific and Atlantic oceans, loggerhead turtle (Caretta
**Carettata** from islands of Japan to Mexico, and arctic tern (**Sterna paradisaea**) migration from Arctic to Antarctic are fascinating migration fits (Wiener et al. 2011).

Wildlife perform movements with a purposeful intent to arrive at a goal area which may be predetermined or selected with experience of occupancy. For long distance experienced seasonal migrants, their goal of migration may be to hit their summering or wintering areas, using true navigation, showing immense cognitive site fidelity, while for first year juveniles, unaccompanied by parents or adults during migration use vector navigation mechanism to reach to winter areas innately predetermined. However, our understanding of the global migration and navigation mechanisms are still poor (Bingman and Cheng 2005).

Migrating birds travel long distances over heterogeneous land cover and geomorphic land features, through various gradients of atmospheric environmental conditions, to arrive to a goal area. For a migrating bird, its goal area during spring migration may be a summer home range, and a winter home range in its autumn migration, however their daily movement goals may vary. Migrating birds may be unaware of the challenges which will emerge along their migration route (Alerstam and Christie 1993; Akesson et al. 2012). Migrating birds may have to select appropriate spatial corridors with right temporal environmental conditions, which facilitates migration, taking environmental ques from their current commute space. Their movements are positively or negatively influenced by the landscape physical features, prevailing atmospheric and environmental conditions. Their physical fitness and survival may fundamentally determine the individuals’ annual migration distances and extent of spatial coverage (Butler 2010).

From the recent past, animal movement research have been greatly enhanced by the advent of miniaturized solar-powered GPS tags with multiple sensors, data transfers via global mobile network and satellite communication systems to online web-based data storage and automated data management systems (movebank). In our observations, we used miniaturized solar-powered GPS bio-loggers with 3D acceleration sensors (eOBS GmBH, Munich, Germany), and conducted movement studies to collate data at annual temporal and spatial scales. These tags are enabled
to collect movement with additional remote control versatility to collect high resolution GPS and ACC data (Wilson et al. 2006; 2015).

In the Asian landscape, challenges to migrating birds are enormous and formidable, coupled by thin air and high altitude land features of the Himalayan mountain ranges (Nepal & Bhutan) and plateaus (Autonomous Region of Tibet) (Bishop et al. 2015). In this study, we back-pack tagged Himalayan Vultures (N=22) to document and understand the challenges endured during their annuals movements. We define annual movements as episodes of two movement types: spring and autumn migration and ranging movements in winter and summer quarters. We aimed to understand how their annual navigation and movements are affected by various environmental parameters at geophysical, climatic and atmospheric strata. We also characterize flight types (glide & circle) and assess under what environmental conditions vultures adapt and engage two primary flight types- glide and circle. Then we look at how flight and foraging movements are affected by multiple environmental parameters.

3.3. Materials and Methods

3.3.1. Bird capture and data recording
22 birds were captured in Bhutan between May 2014 and February 2015 using wire mesh-mesh cage trap and equipped with high resolution GPS data loggers (45 g, cell phone link, e-Obs GmBH), using an approximately 30 g Teflon-nylon harness. Daily (02.00 -20.00 GMT), loggers were set to periodically collect 1 Hz GPS fixes for 10 min, whenever solar charge allowed. We collected GPS fixes between 25th November 2014 until 24th November 2015. Data are available through the Movebank archive.

3.3.2. Annual movements
Annual movements in Himalayan Vultures are defined by two movement episodes, namely, first- the movements in seasonal summer and winter ranging areas, and second- the biannual migratory movements of the spring and autumn. Vultures make their northward migration in April-June, with peak vulture movement in May, and by July vultures are apparently settled in their summer range (July-October). In summer,
vultures are in Mongolia, Inner Mongolia, and Tibetan Plateau of China. The southward migratory movement occurs from October-November, and most vultures move south in mid-October to November, and by end of November, vultures are in their winter areas (Nov-April). The wintering movement range include India, Nepal, Bhutan and parts of China (Tibetan Plateau and Yunnan). Flight characteristics of the annual movements are described at three broad environmental layers (Dodge et al. 2015): (a). Geophysical parameters, (b). Atmospheric factors, and (c). Climatic variables. Environmental parameters defines in geophysical factors include altitudes, flight height above the ground, NDVI, land cover, population density, and precipitation. The climatic variables are comprised of temperature, humidity and sunshine duration. The atmospheric layer is composed of thermal uplift, orographic uplift, pressure level north-south head winds (v velocity), and pressure level east-west lateral winds (u velocity).

3.3.3. Annual movement and movement trajectory
The annual track of individual vultures were downloaded (data range of exactly one year from the capture release day, and until the last traverse GPS point of dead ones) from the online Movebank database. Data files were converted to shapefiles in ArcGIS10.0 (ref). We used the 95% Kernel Density Estimate trajectory in our studies. Annual track lengths were computed in ArcGIS.

3.3.4. Flight parameters from high resolution GPS
We used high resolution GPS points (1Hz) to determine the flight styles that each individual vulture adopted in a given space during the course of its flight. Flight styles (circle and glide) were determined by the difference in 10 second turning angle. Circle (thermalling) flight style was assigned to aggregates of GPS points characterized by 10-second turning angles of >90º, and glide flight style by turning angles of <45 º. In other words, the circle flight followed a flight trajectory which was non-linear or circular that generally led a bird to gain height, influenced by orographic or thermal uplifts. Whereas, the glide flight followed a straight line or meandering flight trajectory which generally led to loosing height in the air (Figures 1, 2).
Figure 1. Glide flight style. (a) High resolution GPS (1Hz) points showing different types of glide tracks. (b) 3D glide flight tracks on Google Earth Image.

Figure 2. Circle flight style. (a) High resolution GPS (1Hz) points showing different types of circle or thermalling tracks. (b) 3D circle tracks overlaid on Google Earth image.
3.3.5. Flight parameters from behavioural annotation of ACC data

We used the Acceleration Viewer (ACCViewer), a freeware java program developed by Movebank. The viewer can be obtained from www.movebank.org/ node/26108. The 3D (xyz trixial) acceleration (ACC) data were downloaded from the online Movebank database using the ACCViewer. Calibration of behavioural categories were based on the observations (direct sighting, video and photographic evidences) of tagged birds in capture a cage prior to release, and observations in the wild. These field evidences were matched with the timestamped 3D (xyz) responses of ACC data visualized on ACCViewer. Further, we constrained annotated ACC behaviour patterns with attributes of the GPS data (especially with that of timestamp and ground speed) visually in ArcGIS10.0. We annotated with 6 major behavioural categories: such fly (with nested behaviours like, flap-takeoff, flap flight and flap-land), rest (stand alert, stand sleep, belly rest or incubation pose), restless (perched and alert, neck movement and slow walk), WHR (walk, hop & run) - a land commotion, feed, manicurial (preen, sun bask and ruffle) activities and others or unknown.

3.3.6. Environmental data annotation

GPS tracks and ACC data transmitted from biologgers on Himalayan Vultures in the field are stored at the Movebank online database. We annotated 13 environmental factors (see also Table 1, Chapter I) to our GPS data using an automated Env-DATA System available in Movebank, Dodge et al. 2015)

3.3.7. Flight distance

Point (GPS) to point spherical flight distance and time difference were calculated using simple arithmetic formulas. In the actual analysis, 5 minute interval point distances were used to determine their annual movement distances.

Latitude (a1) and longitude (a2) points were converted to radial location with formulae (1-5).

\[
\text{radian} = \frac{\pi}{180^\circ} \tag{1}
\]

\[
a1 = \text{lat}_1 \times \text{radian} \tag{2}
\]

\[
a2 = \text{long}_1 \times \text{radian} \tag{3}
\]

\[
b1 = \text{lat}_2 \times \text{radian} \tag{4}
\]
\[ b2 = \text{long2} \times \text{radian} \]  \hspace{1cm} (5)

Difference between radial locations of longitude and latitude were computed with formulae (6) and (7) respectively

\[ d\text{long} = b2 - a2 \] \hspace{1cm} (6)
\[ d\text{lat} = b1 - a1 \] \hspace{1cm} (7)

The arc distance \((a)\) was determined with formula (8) and calculated circumference between two points with formula (9);

\[ a = (\sin(\frac{\Delta\text{lat}}{2}))^2 + \cos(a1) \times \cos(b1) \times (\sin(\frac{\Delta\text{long}}{2}))^2 \] \hspace{1cm} (8)
\[ c = 2 \times \text{atan2}(\sqrt{a}, \sqrt{1 - a}) \] \hspace{1cm} (9)

We used a constant \(R = 6378137\) to calculate the great circle distance between two GPS point locations with formula (10).

\[ \text{Distance (m)} = R \times c \] \hspace{1cm} (10)

3.3.8. Rate of ascent and descent

We used latitude, longitude, altitude and timestamp data collected by biologgers attached to the Himalayan Vultures in their annual movements to calculate ascent rate or descent rates. Ascent rate was calculated with formula (11) while descent rate was calculated with formula (2).

\[ \text{Ascent Rate} = \frac{\text{New altitude} - \text{Old altitude}}{\text{New time} - \text{old time}} = \frac{\Delta\text{Altitude}}{\Delta\text{Time}} \] \hspace{1cm} (11)
\[ \text{Descent Rate} = \frac{\text{New altitude} - \text{Old altitude}}{\text{New time} - \text{old time}} = \frac{-(\Delta\text{Altitude})}{\Delta\text{Time}} \] \hspace{1cm} (12)

3.3.9. Energetics

We used ODBA (overall dynamic body acceleration) to determine energy expenditures. The calibrated ACC average values of tags deployed on White Storks
were used since tags put on Himalayan Vultures were of the same series for tag orientation and postural correction. Raw burst acceleration data from eObs tag were used to calculate ODBA. We followed methodical steps as suggested at www.3dyne.com, and used the formula (13).

\[ ODBA = \sum(|x(i) - xmean|) + \sum(|y(i) - ymean|) + \sum(|z(i) - zmean|) \]

3.3.10. Statistical analysis

SPSS 24 for Windows was used to analyse annual movements in the Himalayan Vultures. One-way analysis of variance (ANOVA) and Tukey’s post hoc test were performed on 13 dependent environmental parameters against 4 fixed factors (annual timescale-12 months, flight styles and behaviours). We considered individual vultures as a random subsample of the larger Himalayan Vulture population and treated them accordingly in the statistical analysis. One-way ANOVA and Tukey’s post hoc test were conducted to determine energetics on aforementioned independent variables with dependent overall dynamic body acceleration (ODBA). As with flight distance and speed, we used 5 minute time intervals between sampling points to ensure that the movement data as well as the environmental annotation parameters were sufficiently separated in time to allow for an independent statistical assessment. A Himalayan Vulture can travel up to 8 km straight line distance during this time, or change in flight altitude by 3000 meters (assuming a conservative 10 meters vertical speed per second), suggesting that environmental parameters potentially changed dramatically within a 5 minute interval. In the graphs, we show average data +- standard error except in those cases when it is visually preferred to show seasonal or annual trends. In these cases, the error bars are omitted for graphical clarity.

3.4. Results and Discussion

Because there are many potentially inter-correlated factors affecting the movement behaviour of Himalayan vultures, we first report these data in sequence. We concurrently discuss each factor at a low level of overall integration and subsequently offer on overall discussion, bringing all factors together in a synoptic view. Please note
that this style deliberately deviates in part from the usual separation of reporting results and subsequently discussing them. However, we felt that the complexity of single environmental factors make such a procedure valuable and allows the reader to get a deeper understanding of the movement ecology of Himalayan Vultures.

3.4.1. Flight characteristics of annual movement of the Himalayan Vulture
Annual movements in Himalayan Vultures were defined by two movement episodes, first- the movements in summer (July – September) and winter (December – April) ranging areas, and second- the biannual migratory movements of the spring and autumn. Vultures make their northward migration in May-June, with peak vulture migratory movement in June, and by July vultures are apparently settled in their summer range. In summer, vultures are found in Mongolia, Inner Mongolia, and Tibetan Plateau of China. The southward migration occurs from October-November, and most vultures move south in mid-October to November, and by end of November, vultures are in their winter areas (Nov-April). In the winter vultures ranges include northern India, Nepal, Bhutan and parts of China (Tibetan Plateau and Yunnan).

**Migratory movement corridors:** During the south and north bound migrations, Himalayan Vultures used certain river valleys to cross the higher Himalayan mountain ranges, however, they did not follow the same corridors in the two migration events (2015; Figure 3).
River valleys provided the shortest geophysical corridors and also supported flight with gentle ascent in altitudes that eased the crossover. In India, vultures used river valleys of Gangotri in Uttarakhand crossing mountain ranges over 5400m near to Nelang. In Nepal, tagged vultures used four flyway corridors at 5700m west of Mugu, and the river valley of Kali Gandaki at 4900m. In the higher Himalayas of Tibetan Plateau, vultures migrate over Gang Bemchhen at 6500m and Lapche Kang II at 6000m. The tri-junction valley of Amochu, (between Bhutan, China and India-Sikkim) was also used as migration corridor. In the Bhutan Himalayas, almost all river valleys were used as exit and entry during the summer and winter migratory movements. In the upstreams of Wangchu, vultures crossed over the Jhomolhari (6700m) and Jichu Drake (6700m) west of Lingzhi. Along the Mochu valley around Laya, vultures embraced to fly over Ganchen Tag (6600m) and Masang Kang (6500m). In the river system of Phochu, GPS tagged vultures flew over the mountain ranges of Lunana at around 6300m. At the water sources of Mangdechu and Chamkharchu, the Himalayan
Vultures crossed over the mountain ranges of Gangkar Phuensum (7000m). The eastern Bhutan, river valleys of Kurichu, Kholongchu and Gongri were used as migration flyways.

**Range extension:** Immature and juvenile birds perform exploratory movements as a process for dispersal, however, Himalayan Vultures or avian scavengers in general were subjected to compulsive exploratory movements, especially in search of food—primarily composed of dying livestock or wildlife and carrions.

Figure 4. Geographical distribution of Himalayan Vulture (Gyps himalayensis). Polygon filled with light pink is the current distribution adapted from the Birdlife International and polygon with pale orange is the movement range from this study of the annual movements. The study reveals an apparent north-south and east-west extension of the distribution.
The current annual movements study in the Himalayan Vultures, documented the first evidence of distributional range extensions in the north (Mongolia and Inner Mongolia), south (southern and eastern parts of Bhutan, and the northern plains in India Assam and Uttar Pradesh) and in the central Tibetan Plateau (Figure 4, see also introduction chapter).

Two Himalayan Vultures that spent the summer (2015) vastly outside the currently known range were Tooh (4188) and Palya (4009). Tooh spent its summer in the central Mongolia which covered parts of the Mongolian Plateau, while Palya occupied south-eastern parts of Mongolia and Inner Mongolia which covered parts of Gobi desert.

**Annual distance travelled:** An obligate avian scavenger and a biannual migrant, Himalayan Vultures travelled long distances and covered large geographic areas. They were on the move in search of food resources that were ephemeral. In the one-way analysis of variance (ANOVA), there was a statistically significant difference between months with $F (11, 2553901) = 1734.50$, $M = 0.11$, $SD = 0.99$, $p < 0.001$, $R^2 <0.01$, $N = 2553913$; Figure 5a). Vultures flew the highest daily distances in January ($0.60 \pm 2.21$ km) and February ($0.48 \pm 1.78$ km). During the months of July ($0.05 \pm 0.57$ km) and August ($0.07 \pm 0.73$ km), vultures generally preferred to stay stationary presumably from monsoon rains, poor visibility from heavy mist and cloud and high relative humidity.
A Tukey post hoc test determined statistically significant differences between months at 0.05 alpha level. However, there was statistically insignificant difference within groups (March (0.16 ± 0.79 km) and May (0.15 ± 0.93 km), p = 0.14), March and December (0.15 ± 216.79 km), p = 0.99), April (0.14 ± 0.85 km) and May (0.15 ± 0.93 km), p = 0.43), April and November (0.13 ± 1.36 km), p = 0.99), May (0.15 ± 0.93 km) and December (0.16 ± 0.79 km), p = 0.83), (0.13 ± 0.91 km) and October (0.13 ± 1.04 km), p = 1), June and November (0.13 ± 1.36 km, p = 0.70), July (0.05 ± 0.57 km), and August (0.05 ± 0.58 km), p = 0.53). Vultures traversed longest distances during the northward migration.

**Ground speed:** Himalayan Vultures flew at lowest ground speed during the winter months of January (8.13 ± 7.39 m/sec) and February (7.79 ± 71.13 m/sec). In a one-way ANOVA, there was a statistically significant difference between months with F
Figure 5b. Graph showing mean ground speeds reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

Vultures flew at the highest ground speed (16.88 ± 5.74 m/sec) during the southbound migration in November, however, the maximum ground speed for an individual vulture (40.96 m/sec or 147km/h) was recorded during the northward migration (May). During the biannual migrations, high ground speeds indicated vultures used tailed wind support. The difference in means within groups (months) at 0.05 alpha level was statistically significant as revealed by Tukey post hoc test.

**Rate of Ascent:** Rate of ascent were lower in winter months and the lowest was in February (0.58 ± 0.74 m/sec), however, the highest rate of ascent was in December.
In March (3.85 ± 3.46 m/sec), rate of ascent increased by 56%. There was a statistically significant difference between months as determined by one-way ANOVA with $F(11, 1014277) = 3854.61$, $M = 3.08$, $SD = 3.45$, $p < 0.001$, $R^2 = 0.04$, $N = 1014289$; Figure 5c). Rate of ascents were higher during the migration periods.

![Graph showing the mean ascent rates reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.](5c)

Figure 5c. Graph showing the mean ascent rates reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

A Tukey post hoc test showed statistically significant difference within months at 0.05 alpha level. However, rate of ascent were statistically insignificant between March (3.85 ± 3.46 m/sec) and May (3.85 ± 3.71 m/sec, $p = 1$), April (3.29 ± 3.39 m/sec) and September (3.85 ± 3.71 m/sec, $p = 0.11$), June (2.57 ± 3.08 m/sec) and August (2.60 ± 3.17 m/sec, $p = 0.50$), and November (4.39 ± 4.23 m/sec) and December (4.45 ± 4.156 m/sec, $p = 0.15$).
**Rate of descent:** Rates of ascent and descent were directly proportional to each other. The highest rate of descents were during the winter months and biannual migration periods. One-way ANOVA showed a statistically significant difference between months at 0.05 alpha level with $F(11, 1008374) = 3924.58$, $M = -3.05$, $SD = 3.50$, $p < 0.001$, $R^2 = 0.041$, $N = 1008386$; Figure 5d). In the winter months (December to April) mean rate of descents were between -0.61 to -4.58 m/sec, while in their summer grounds (July-September) difference in mean rate of descents were much lower (-2.48 to -3.29 m/sec).

![Figure 5d](image)

Figure 5d. Graph showing the mean descent rates reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

A Tukey post hoc test showed statistically significant difference within months at 0.05 alpha level. However, rate of descents were statistically insignificant between April (-3.27 ± 3.44 m/sec) and September (3.28 ± 3.68 m/sec, $p = 1$), June (-2.50 ± 3.08...
m/sec) and July (-2.48 ± 1.81 m/sec, p < 0.94), and statistical significance in June (-2.50 ± 3.08 m/sec) and August (-2.55 ± 3.21 m/sec, p < 0.04) was lower.

**Altitude (MSL):** Migrating species live at lower altitudes in winter and at higher elevations in summer. In the one-way ANOVA between months and height above sea level, there was a statistically significant difference at .05 level with $F(11, 2042253) = 27008.06$, $M = 4033.98$, $SD = 1133.08$, $SE = 0.79$, $p < 0.001$, $R^2 < 0.13$, $N = 2042265$; Figure 5e) indicating Himalayan Vultures occupy or live at different altitudes every month. Himalayan Vultures in summer ranged between altitudes of 3840 ± 1372 m to 4420 ± 924 m in Tibetan Plateau and Qinghai regions of China.

![Graph](5e)

Figure 5e. Graph showing mean altitude levels moved about by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

However, some of the GPS-tagged vultures also spent their summer in the lowlands of the Inner Mongolia and Mongolia at altitudes as low as 1500m. In their winter
quarters, vultures over winter at elevations of $2975 \pm 1314$ m, in the northern plains and Himalayas of India, Nepal, Bhutan and Yunnan. A few of the GPS back-packed birds were found to winter at elevations of 40m.

The maximum mean height ($N=22$) gained by vultures during northward migration was in June ($4298 \pm 1163$ m) and in southward migration in November ($4664 \pm 568$ m). The mean difference was statistically significant at the 0.05 alpha level within months as revealed by Tukey post hoc test. However, mean differences within months were statistically insignificant in January ($2998 \pm 1405$ m) and February ($2982 \pm 1196$ m, $p = 0.99$), in January and April ($2975 \pm 1314$ m, $p = 0.74$), and in February and April ($p = 1$).

**Flight Height above Ground (HaG):** Air borne birds have the choice to either fly as high above the ground into depths of the sky or remain as low to the ground surface, depending on prevailing atmospheric and weather conditions. There was a statistically significant difference between groups at 0.05 alpha level, as determined by one-way ANOVA with $F (11, 2042253) = 8125.56$, $M = 415$, $SD = 365$, $SE = 0.26$, $p < 0.001$, $R^2 < 0.01$, $N = 2042265$; Figure 5f).

In the summer months (July- September), vultures flew at HaG level from $381.03 \pm 322.68$ m to $492.05 \pm 411.23$ m, nearly two folds greater than flight HaG level in winter (December- April) areas at $160 \pm 434.41$ m to $298.14$ m.
Figure 5f. Graph showing the means heights above ground reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

The flight HaG were lowest in February (160 ± 434.41 m) and January (161.18 ± 246.49 m), whereas the highest HaG level were in the months of June (502.08 ± 467.03 m), July (459.19 ± 353.49 m) and August (492.04 ± 411.23 m), because of northward migratory movement, longer sunshine duration and greater thermal radiations created by solar insolation over the land surface. A Tukey post hoc test revealed statistically significant difference within groups at 0.05 level. But, there was statistically insignificant difference within groups in January (161.18 ± 246.49 m) and February (161.18 ± 246.49 m, $p = 0.1$), in April (378.81 ± 386.05 m) and September (381.03 ± 322.68 m, $p = 0.88$), in April and October (377.02 ± 274.65 m, $p = 0.99$), and in September and October ($p < 0.06$).

**Normalized difference vegetation Index (NDVI):** The MODIS Land Terra Vegetation Indices.05deg Monthly NDVI was used to assess its influence in the movements of
Vultures. The one-way ANOVA at .05 level between months and NDVI was statistically significant difference between months with \( F(11, 2556597) = 38077.67, M = 0.48, SD = 0.21, SE = 0.00, p < 0.001, R^2 = 0.14, N = 2556609; \) Figure 5g). Vultures occupied landscapes with higher NDVI in winter (0.72 ± 0.18 to 0.57 ± 0.11) months than in the summer (0.44 ± 0.17 to 0.59 ± 0.24) months. In the summer range, mean NDVI were low because, Himalayan Vultures roamed in grasslands and meadows in Tibetan Plateau and steppe grasslands in Mongolia, however, the highest mean NDVI (0.59± 0.24) was in July during the highest turnover in plant productivity in the northern latitudes.

Figure 5g. Graph showing the mean NDVI (normalized vegetation index, the ‘greenness of the landscape’) Himalayan Vultures selected throughout the year. Points represent population means, error bars are omitted for graphical clarity.

The lowest mean NDVI (0.31 ± 0.13) was in November as vultures moved over the highlands of Tibetan Plateau and the peaks of the Himalayas with dying and dead
ground vegetation or without ground cover. Whereas, high mean NDVI in winter ranges were attributed to forest landscapes with tall vegetation in the Himalayas and Indian plains. The mean difference within months was statistically significant at 0.05 level as indicated by Tukey post hoc test. However, there was a statistically insignificant difference in NDVI in the areas occupied in April (0.52 ± 0.13) and December (0.52 ± 0.18, \( p = 0.56 \)).

**Population density:** Himalayan Vultures used various land use and land cover types, and their interaction with human landscapes could not be avoided within the ranges of their occurrence in Asia.

![Graph showing the mean population densities experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.](image)

Figure 5h. Graph showing the mean population densities experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

In a one-way ANOVA, there was a statistically significant difference between months with \( F (11, 2555904) = 51346.18, M = 20.69, SD = 62.22, SE = 0.04, p < 0.001, R^2 = \)
0.18, \( N = 2555916 \), Figure 5h) showed vultures used human landscapes with variable population densities. In the summer, vultures occupied landscapes with lower mean human population density of 5.39 ± 6.92 to 8.02 ± 5.89 persons per KM\(^2\), and on the contrary, in the winter quarters, they used landscapes with higher mean human population densities of 38.74 ± 76.71 to 103.52 ± 155.51 persons per KM\(^2\).

During the migratory movements, vultures flew over landscape corridors with lower mean population densities. In their northward migration, vultures traversed migratory corridors with mean population densities between 5.39 ± 6.92 to 27.30 ± 63.57 persons per KM\(^2\), whereas, in their south-bound migration, vultures used landscape corridors with mean population density of 4.85 ± 2.14 to 9.47 ± 15.53 persons per KM\(^2\). Indeed, vultures used landscapes with least human settlements during the peak spring (5.4 persons per KM\(^2\)) and autumn (4.8 persons per KM\(^2\)) migrations, indicated their passage over higher Tibetan and the Himalayas. At 0.05 alpha level, a Tukey post hoc test showed that the vultures occupied landscapes with statistically significant population density. However, there was statistically insignificant difference within months of June (5.39 ± 6.9 persons per KM\(^2\)) and October (4.85 ± 2.14 persons per KM\(^2\), \( p = 0.96 \)) during the peak northward and southward migration months.

**Sunshine duration:** Sunshine duration was directly proportional to day length given the absence of cloud overcast. In the summer, day length in northern latitudes increase by about 7 hours, because of the inclination of the earth’s axis of rotation. In the northern latitudes, vultures in summer benefited from longer sunshine duration. There was a statistically significant difference sunshine duration lengths between months as showed by one-way ANOVA at 0.05 level with \( F (11, 2556597) = 14008.19 \), \( M = 19.23 \), \( SD = 8.78 \), \( SE = 0.005 \), \( p < 0.001 \), \( R^2 = 0.05 \), \( N = 2556609 \); Figure 5i).
Figure 5i. Graph showing the mean sunshine duration experienced by Himalayan Vultures throughout the year. Please note that data are deliberately not corrected for seasonally varying day lengths. Points represent population means, error bars are omitted for graphical clarity.

Himalayan Vultures were disposed to the lowest mean sunshine duration in their winter areas in January (11.77 ± 11.00 kWh/m² day) and February (11.51 ± 11.69 kWh/m² day). The mean monthly sunshine duration in summer months (July – September) from 19.27 ± 7.3 to 21.20 ± 8.9 kWh/m² day. Vultures experienced the longest sunshine duration in July (21.20 ± 8.9 kWh/m² day). Overall, mean monthly sunshine duration exponentially increased from February (11.51 kWh/m² day) until May (20.04 kWh/m² day) and asymptote from June (20.98 kWh/m² day) into July (21.20 kWh/m² day), and gradually decreased from August into September. The mean sunshine duration in November (18.72 kWh/m² day) increased because the vultures were at lower latitudes on their southward migratory movement, while it dipped in December (17.26 kWh/m² day). For an obligate scavenger like Himalayan Vulture,
sunshine duration is critical for their daily movement, forage and overall fitness. The mean difference within groups was statistically significant at 0.05 level as indicated by Tukey post hoc test.

**Total precipitation:** The ECMWF model-based total precipitation data (rainfall and snowfall) was used to determine its effects on vultures’ annual movements. There was a statistically significant difference between months in total precipitation at .05 level, as by one-way ANOVA with \( F(11, 2556597) = 27087.51, M = 0.85, SD = 1.56, SE = 0.00, p < 0.001, R^2 = 0.10, N = 2556609; \) Figure 5j).

Figure 5j. Graph showing the mean monthly precipitation totals experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

Himalayan Vultures were disposed to higher total precipitation during the northward migration movement as summer moon weather conditions picked up. In December,
vultures experienced the driest month with mean total precipitation of $0.21 \pm 1.06$ mm and wettest months in April ($1.93 \pm 2.19$ mm), otherwise they chose to remain in drier landscapes. A Tukey post hoc test showed that there was a statistically significant difference within months in total precipitation experienced by vultures in the landscapes of their annual range at 0.05 level.

But, there was statistically insignificant difference within August ($0.68 \pm 1.29$ mm) and September ($0.67 \pm 0.91$ mm, $p = 0.97$) and October ($0.53 \pm 0.99$ mm) and November ($0.51 \pm 1.22$ mm, $p = 0.08$). In general, vultures chose to summer in much drier areas despite of monsoon weather in the Asian landscapes. Maximum total precipitation was in August (74 mm). High total precipitation in April ($1.93 \pm 2.19$ mm) may be one of the cues which triggers northward migration. As monsoon weather conditions start in May and June in the Indian Plains and the Himalayas, vultures migrate to higher latitudes and altitudes in the Tibetan Plateau to escape from monsoon downpours.

**Thermal uplift:** Any moving object in a space move through another moving medium. The earth’s atmosphere is such a medium with thermal and orographic uplifts, and north-south meridional and east-west lateral winds, with atmospheric humidity which affect movements. For any soaring species that hardly engage in powered-flight it is important to harvest thermal updrafts (rising column of hot air from the heated land surface) in their daily and migratory movements.

Thermals serves as natural energy that assist soaring species gain height and ease flight energy expenditure. In the one-way ANOVA between months and thermal uplift, there was a statistically significant difference between months, at 0.05 level with $F(11, 2556561) = 24637$. $M = 1.42$, $SD = 0.63$, $SE = 0.00$, $p < 0.001$, $R^2 = 0.09$, $N = 2556573$; Figure 5k).
Himalayan Vultures were disposed to the weakest mean thermal uplifts in the months of January ($0.69 \pm 0.78 \text{ m/sec}$) and February ($0.62 \pm 0.73 \text{ m/sec}$). Thermal updraft abruptly increased in March ($1.19 \pm 0.69 \text{ m/sec}$), and gradually increased during the migration (May & June). Vultures may use thermal uplift increment in March and April ($1.24 \pm 0.60 \text{ m/sec}$), as a cue to trigger northward migration, while a decrease in mean thermal uplift occurred in September ($1.39 \pm 0.45 \text{ m/sec}$), possibly as a cue to trigger southward migration. In summer, vultures were in areas with strong thermal updrafts of ($1.39 \pm 0.45$ to $1.68 \pm 0.64 \text{ m/sec}$) which were coupled with longer day length and sunshine duration, whereas, in the winter areas, they were disposed to weak thermal uplifts ($0.62$ – $1.25 \text{ m/sec}$) affected by shorter day length and shorter sunshine duration. Maximum thermal uplifts were in the months of May ($4.10 \text{ m/sec}$) and June ($4.31 \text{ m/sec}$) which coincided with northward migration. However, vultures were
exposed to the highest thermal uplifts in August (1.68 ± 0.64 m/sec) when the sun’s position enabled maximum insolation over the northern hemisphere. The mean difference within months was statistically significant at 0.05 level as compared by Tukey post hoc test. However, there was statistically insignificant difference in May (1.35 ± 0.77 m/sec) and June (1.35 ± 0.66 m/sec, $p = 0.89$), in May and November (1.35 ± 0.43, $p = 1$), and June and November ($p = 0.56$).

**Orographic uplift:** The forced rising of lowland air mass to a higher altitude upon hitting higher altitude land surface producing a weather phenomenon or an orographic uplift- primarily a land surface wind. Orographic uplifts in the Asian landscapes and the Himalayas were strong and heterogeneous given its high land surface variation and orientation.

![Graph showing the means of orographic uplifts experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.](image)

Figure 5l. Graph showing the means of orographic uplifts experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.
The difference in mean between months at 0.05 level, was statistically significant as revealed by one-way ANOVA with $F(11, 2556597) = 2736.66$, $M = 0.29$, $SD = 0.46$, $SE = 0.00$, $p < 0.001$, $R^2 = 0.01$, $N = 2556609$; Figure 5l). Vultures were experienced highly variable annual orographic uplifts across 12 months. Mean orographic uplift increased by 31% in April ($0.34 \pm 0.50$ m/sec) as compared to March ($0.26 \pm 0.38$ m/sec). This increased orographic uplift in April may be a cue to trigger northward migration. Orogenic uplift spiked in September ($0.37 \pm 0.55$ m/sec), and decreased in October ($0.29 \pm 0.46$ m/sec). The dip in orographic lift in October may a cue that trigger southward migration. The mean orographic uplift was highest in November ($0.39 \pm 0.53$ m/sec) because of active westerly winds in the Tibetan Plateau and vultures migratory movement over the Himalayas. The maximum orographic uplift was in June ($5.59$ m/sec) during the peak northward migration. Vultures experienced greater orographic uplift in December as they were exposed to winds in the southern slopes of the Himalayas. A Tukey post hoc test indicated statistically significant difference within months at 0.05 level. But, there was statistically insignificant difference in orographic uplifts experienced by vultures within months of January ($0.28 \pm 0.44$ m/sec) and June ($0.28 \pm 0.45$ m/sec), $p = 0.99$), February ($0.25 \pm 0.39$ m/sec) and March ($0.26 \pm 0.37$, $p = 0.08$), February and July ($0.25 \pm 0.42$ m/sec, $p = 0.98$), February and August ($0.25 \pm 0.40$ m/sec), $p = 0.99$), May ($0.34 \pm 0.54$ m/sec) and December ($0.35 \pm 0.47$ m/sec), $p = 0.98$), July and August ($p = 0.99$).

**Pressure Level Pressure Vertical Velocity:**

The pressure vertical velocity was lowest in April ($-0.28 \pm 0.24$ Pa/sec) which may be a cue to trigger northward migration. The strongest pressure vertical velocity was in January ($-0.06 \pm 0.26$ Pa/sec).
Figure 5m. Graph showing the means of ground speeds reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

There was a statistically significant difference between months at 0.05 level as computed by one-way ANOVA with $F(11, 2552358) = 54147.69$, $M = -0.09$, $SD = 0.16$, $SE = 0.00$, $p < 0.001$, $R^2 = 0.19$, $N = 2552370$; Figure 5m). In summer, vultures were in landscapes with fairly stable pressure vertical velocity atmospheric conditions. The pressure vertical velocity dipped in December ($-0.17 \pm 0.20$ Pa/sec) when the birds were in southern slopes of the Himalayas. The mean difference was statistically significant at 0.05 level within months. However, there was statistically insignificant difference in pressure vertical velocity as determined by Tukey post hoc test in January ($-0.06 \pm 0.26$ Pa/sec) and June ($-0.06 \pm 0.09$ Pa/sec), $p = 68$), February ($-0.08 \pm 0.23$ Pa/sec) and November ($-0.08 \pm 0.18$ Pa/sec), $p = 0.79$), July ($-0.04 \pm 0.08$ Pa/sec) and August ($-0.04 \pm 0.09$ Pa/sec), $p = 1$).
Meridional winds: Meridional winds are directional north-south or south-north winds that have influence in vultures’ daily and biannual migratory movements. In a one-way ANOVA between months and meridional winds, the difference in means at .05 level was statistically significant with $F(11, 2552380) = 76354.23$, $M = 0.15$, $SD = 2.85$, $SE = 0.00$, $p < 0.001$, $R^2 = 0.25$, $N = 2552392$; Figure 5n) indicated that vultures experienced different strengths of meridional winds every month. In the winter areas, Himalayan Vultures preferred to occupy areas with low speed southern or avoided northern meridional winds presumably to keep themselves warm from cold winter temperatures.

![Graph showing the means of meridional winds experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.](image)

Figure 5n. Graph showing the means of meridional winds experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

Whereas, vultures in their summer range they were more likely to occupy areas with high strength northern winds presumably to cool themselves from summer heat and as well occupied north facing slopes. During the northward migration in May, vultures
took advantage of southern winds (1.54 ± 1.99 m/sec). In July, vultures were exposed to lowest meridional winds (-2.03 ± 2.61 m/sec) which also indicated that strengths of south-north and north-south winds were almost equal. Vultures were exposed to the highest strength southern winds in January (0.14 ± 1.69 m/sec) when presumably they maximally occupied south facing slopes. A Tukey post hoc test revealed that vultures occupied areas of different meridional winds within months was statistically significant at 0.05 level. However, vultures were exposed to similar meridional wind conditions in April (1.03 ± 1.73 m/sec) and November (1.01 ± 2.09 m/sec), \( p = 0.72 \).

**Zonal winds:** Zonal winds are characteristic of east-west and west-east winds along local parallel of latitude. The atmospheric conditions of zonal winds definitely affect movement activities in animals, and especially so in flying animals.

![Figure 5o](image)

**Figure 5o.** Graph showing the means of zonal winds experienced by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.
In the one-way ANOVA between months and zonal winds, the difference in means at
0.05 level, there was a statistically significant with $F(11, 2552380) = 47410.90$, $M = 1.08$, $SD = 2.86$, $SE = 0.00$, $p < 0.001$, $R^2 = 0.17$, $N = 2552392$; Figure 5o) showed vultures experienced variable zonal winds at the annual scale. Compared to mean meridional winds (-2.03 ± 2.61 – 2.22 ± 2.34 m/sec), Himalayan Vultures were exposed to stronger mean zonal winds (-0.51 ± 2.69 – 3.78 ± 3.24 m/sec). Vultures experienced the strongest zonal winds (west-east or westerly winds) in November (3.78 ± 3.2 m/sec) during the southbound migration and this was because vultures migrated in the southwest direction. Vultures preferred to remain on eastern slopes during summer appreciating easterly zonal winds. Vultures in winter months used areas disposed to strong westerly zonal winds (17.72 – 37.27 m/sec), as west facing slopes were warmer with longer sunshine duration than east and north facing slopes. In the winter months, vultures occupied south-west facing slopes which was corroborated by their decision to use terrains exposed to stronger southern meridional and westerly zonal winds in their winter areas. And in summer, vultures presumably occupied northeast facing slopes to thermoregulate and guard their body temperatures from the extremely high summer temperatures in the Asian semi-deserts. A Tukey post hoc test revealed that there was statistically significant difference within months at 0.05 level. But, there was statistically insignificant difference in exposure of vultures to zonal winds in February (1.55 ± 1.53 m/sec) and September (1.54 ± 2.44 m/sec), $p = 0.99$.

**ECMWF Pressure Level Temperature:** ECMWF temperature was a model based pressure level temperature of the surrounding environment. The ECMWF temperature was not the precise temperature measured at the GPS locations of vultures with biologgers, but the regional temperature from a meteorological model. In the one-way ANOVA between months and pressure level temperature, there was a statistically significant difference at 0.05 level with $F(11, 2552380) = 86679.04$, $M = 6.45$, $SD = 6.82$, $SE = 0.00$, $p < 0.001$, $R^2 = 0.27$, $N = 2552392$; Figure 5p). In the winter range (November – April) vultures occurred in areas within mean ECMWF temperature (environmental temperature) range of 0.89 ± 7.5 to 9.95 ± 9.12 °C. Vultures experienced the lowest (-1.89 ± 3.90 °C) and highest (9.95 ± 9.12 °C) mean environmental temperatures in November and April respectively.
Figure 5p. Graph showing the environmental temperatures Himalayan vultures were exposed to throughout the year. Points represent population means, error bars are omitted for graphical clarity.

During summer months, vultures ranged in areas within environmental temperature range of 6.56 ± 4.24 to 9.87 ± 5.99 °C. Vultures were exposed to the highest environmental temperature (9.87 ± 5.99 °C) in August. In April (9.95 ± 9.12 °C), the mean environmental temperature increased by 92%, which presumably triggered northward migration. In October (1.56 ± 4.12 °C), the mean environmental temperature dropped by 76% which presumably triggered southward migration. The decreased mean temperature in May was attributed to vultures having reached to high altitude areas, in the course of northward migration, and the increased temperatures from June onwards were from the summer’s rising temperature. Similarly, lowest temperature in November was because of vultures’ southward migration over the highlands of Tibetan Plateau and higher ranges of the Himalayas. There was s statistically significant difference within months in exposure of vultures to surrounding temperatures at 0.05
level. But, there was statistically insignificant difference in January (1.51 ± 7.27 °C) and October (1.56 ± 4.12 °C), $p = 0.96$.

**eObs Temperature:** eObs temperature represents the on-animal temperature recorded by biologgers of an immediate surrounding or of a GPS location of a tagged bird.

![Graph showing the means of on-animal temperatures reported by the bio-logger throughout the year. Points represent population means, error bars are omitted for graphical clarity.](5q)

Figure 5q. Graph showing the means of on-animal temperatures reported by the bio-logger throughout the year. Points represent population means, error bars are omitted for graphical clarity.

The eObs temperature presumably represented true temperature of the birds' location, but could be influenced to some small degree by the birds own body temperature. In the one-way ANOVA between months and eObs temperature, there was a statistically significant difference at 0.05 level with $F (11, 2556752) = 40972.31$, $M = 8.99$, $SD = 11.29$, $SE = 0.01$ $p < 0.001$, $R^2 = 0.15$, $N = 2556764$; Figure 5q).
Himalayan Vultures in summer range occupied areas with eObs temperature range of (10.73 ± 9.32 – 11.34 ± 8.64 ºC), and August (11.34 ± 9.32 ºC) was the hottest month. In the winter areas, vultures appreciated a wider range of mean eObs temperature from -3.29 ± 13.60 – 15.28 ± 12.17 ºC), and December (-3.29 ± 13.60 ºC) was the coldest month. In October (3.81 ± 9.5 ºC), mean temperature dropped by 66% from September (11.13 ± 10.10 ºC), and this dip in temperature presumably triggered southward migration. Among the winter months, eObs temperature was highest in February (15.26 ± 12.17 ºC) attributed to vultures occupy lowlands and southwest facing slopes. In the spring, mean eObs temperature spiked by 23% in April (13.01 ± 13.79 ºC) and this increased temperature may be a cue to trigger northward migration. Low eObs temperature in May (7.83 ± 12.71 ºC) and November (0.27 ± 9.73 ºC) were because of northward and southward migratory movement over highest altitudes of the Tibetan Plateau and the higher Himalayas. A Tukey post hoc test supported that there was a statistically significant difference within months in vultures experience of eObs temperatures at 0.05 level. But, there was statistically insignificant difference within January (10.85 ± 14.65 ºC) and March (10.64 ± 11.59 ºC), p = 0.06), January and June (10.78 ± 8.19 ºC), p = 0.99), January and July (10.73 ± 9.32 ºC), p = 0.75), March and July (p = 0.07), June and July (p = 0.78).

**Relative humidity:** Himalayan Vultures lived in areas with monthly relative humidity range of 50.03 ± 25.62 – 77.81 ± 21.79 %. There was a statistically significant difference between months as determined by one-way ANOVA at 0.05 level with F (11, 2552380) = 43342.73, M = 64.19, SD = 21.29, SE = 0.01, p < 0.001, R² = 0.16, N = 2552392; Figure 5r).
Vultures experienced driest air in the months of November (50.03 ± 25.62 %) and December (53.27 ± 19.34 %), however, vultures lived in more humid air during the other winter months (January - April) with relative humidity range of 62.79 ± 22.65 – 77.81 ± 21.79 %. April (77.81 ± 21.79 %) had the highest air moisture in the entire year. In the summer, vultures occupied areas with lower air moisture, but they were exposed to the highest summer mean moisture in September (73.74 ± 12.91 %). During northward and southward migratory movements, vultures were disposed to higher atmospheric humidity. The mean difference within months was statistically significant as revealed by Tukey post hoc test at 0.05 level. However, there was statistically insignificant difference in vulture exposure to air moisture in February (70.49 ± 18.21 %) and May (70.69 ± 19.84 %), \( p = 0.86 \).
3.4.2. **Annual movements and characteristics of flight styles**

Two flight styles (glide and circle) were described based on the flight track characteristics of 1Hz GPS data sample (see methods above). Determined by the situations of various biotic and environmental factors, vultures adapted their flight styles to powered flight mode or non-powered flight mode. Large soaring birds generally engage non-powered flight for their locomotion to reduce energy expenditure. In pursuit of their flight movements, Himalayan Vultures engaged two tactful flight styles- glide and circle flights.

**Altitude (MSL):** Himalayan Vultures engaged circle flight at lower altitudes \((M = 4022m)\) and glide flight at higher elevations \((M = 4106m)\). In a T-test the difference in means was significant at 0.05 level with \(t = 2375, p = 0.00, R^2 = 0.001, N = 182139\); Figure 6a).

![Graph showing the means and 95% confidence intervals of mean heights above mean sea level (absolute height) reached by Himalayan Vultures in relation to their flight style, i.e. either during](image)
gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum circle flight heights were 131m and 6673m respectively with 95% confidence interval for mean (CIM) = 4020 – 4025m. While the minimum and maximum glide flight heights were 133m and 6877m respectively with CIM = 4104 – 4108m.

**Height above ground level:** Circle flights were used closer to the ground level ($M = 358m$), with 95% CIM = 357 – 358m) whereas, glide flight was preferred at greater heights above the ground level ($M = 480m$), with 95% CIM = 478 – 480m). In a T-test the difference in means was significant at 0.05 level with $t = 5016$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6b).
Regardless of where vultures were in an Asian landscape, they adapted circle flight at lower height above the ground to gain height for a glide flight, which enabled vultures to cover longer distance for their movement.

**Ground speed:** Himalayan Vultures flew with greater ground speed in glide mode ($M = 18$ m/sec) than in circle flight mode ($M = 13$ m/sec). In a T-test the difference in means was significant at 0.05 level with $t = 562516$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6c).

![Figure 6c](image)

Figure 6c. Graph showing the means and 95% confidence intervals of ground speeds reached by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide ground speeds were 0.16m and 43.5m respectively with 95% CIM = 18.02 – 18.04m. However the minimum and maximum circle flight ground speeds were 0.41m/sec and 33.68m/sec respectively with 95% CIM = 13.01 – 13.03m/sec.
Distance: In glide flight mode, vultures covered longer distances per hour \( (M = 9136.52 \text{ m}) \) than in circle flight \( (M = 7042.40 \text{ m}) \). In a T-test the difference in means was significant at 0.05 level with \( t = 8525, p = 0.00, R^2 = 0.001, N = 182139 \); Figure 6d).

![Graph showing the means of ground distances reached per hour by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars are omitted for graphical clarity.](image)

The minimum and maximum glide flight distance were 7.57m and 31.36m respectively with 95% CIM = 8878.27 – 9394.76 m Whereas the minimum and maximum circle flight distance were 21.82m and 24225.49 m respectively with 95% CIM = 6673.19 – 7411.62m.

eObs Temperature: This measured temperature of the immediate environment at locations of GPS back-packed birds. Vultures preferred circle flight \( (M = 9.1^\circ \text{C}) \) over glide flight \( (M = 6.65^\circ \text{C}) \) at higher temperatures. In a T-test the difference in means
was significant at 0.05 level with $t = 26259$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6e).

![Graph showing the means and 95% confidence intervals of mean on-animal bio-logged temperatures reached by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (thermalling). Points represent population means, error bars show 95% confidence intervals.](image)

The minimum and maximum glide eObs temperatures were $-19$ °C and $54$ °C respectively, with 95% CIM = $6.63 - 6.67$°C. While the minimum and maximum circle flight eObs temperatures were $-19$°C and $48$°C respectively, with CIM = $9.07 - 9.12$°C.

**ECMWF Pressure Level Temperature:** The ECMWF PL temperature was a model based landscape temperature layers. Himalayan Vultures preferred to glide when surrounding temperatures were low ($M = 5.81$°C), while they switched to circle flight when PL temperatures were high ($M = 6.86$°C). In a T-test the difference in means was significant at 0.05 level with $t = 10491$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6f).
Figure 6f. Graph showing the means and 95% confidence intervals of mean environmental temperatures experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight ("thermalling"). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide ECMWF PL temperatures were -17.40 °C and 36.09°C respectively, with 95% CIM = 5.79 – 5.82°C. While the minimum and maximum circle flight ECMWF PL temperatures were -17.36°C and 34.79°C respectively, with CIM = 6.84 – 6.87°C.

Orographic uplift: The orographic uplifts did not affect the decision in vultures to choose their flight styles. In orographic winds, vultures engaged both flight styles equally without a preference over the other or chose not to fly. In a T-test the difference in means was not significant with $t = 0.29$, $p = 0.97$, $N = 182139$; Figure 6g).
Figure 6g. Graph showing the means and 95% confidence intervals of mean orographic uplifts reached by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermauling’). Points represent population means, error bars show 95% confidence intervals.

**Thermal uplift:** During strong thermals, Himalayan Vultures chose to glide ($M = 1.57$m/sec) over circle ($M = 1.47$m/sec) or thermalling flight. In a T-test the difference in means was significant at 0.05 level with $t = 13301$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6h).
Figure 6h. Graph showing the means and 95% confidence intervals of mean thermal uplifts experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight ('thermalling'). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide thermal uplifts were 0.00m/sec and 3.81m/sec respectively, with 95% CIM = 1.570 – 1.573m/sec. While the minimum and maximum circle flight thermal uplifts were 0.00m/sec and 3.80m/sec respectively, with CIM = 1.473 – 1.475m/sec. It is concluded that Himalayan Vultures engaged more of glide flight than circle or thermalling flight in strong thermal.

**Sunshine duration:** During the longer sunshine durations, Himalayan Vultures performed more glide ($M = 19.85\, kWh/(m^2\, day)$) than circle ($M = 18.83\, kWh/(m^2\, day)$) flights. In a T-test the difference in means was significant at 0.05 level with $t = 19$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6i).
Figure 6i. Graph showing the means and 95% confidence intervals of mean sunshine durations reached by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight ('thermalling'). Points represent population means, error bars are omitted for graphical clarity. Please note that these data do not include potential differences in day length.

The minimum and maximum glide sunshine durations were 1.20 kWh/(m² day) and 42.11 kWh/(m² day) respectively, with 95% CIM = 19.57 – 20.13 kWh/(m² day). While the minimum and maximum circle flight sunshine durations were 1.19 kWh/(m² day) and 42.95 kWh/(m² day) respectively, with CIM = 18.36 – 19.29 kWh/(m² day).

**Meridional winds:** In the strong north-south winds, vultures adapted glide flight mode \( M = 0.189 \text{m/sec} \) over circle flight \( M = 0.176 \text{m/sec} \) by around 7.6%. In a T-test the difference in means was significant at 0.05 level with \( t = 9.01, p = 0.03, R^2 = 0.001, N = 182139 \); Figure 6j).
Figure 6j. Graph showing the means and 95% confidence intervals of mean meridional winds experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide meridional winds were -11.09 m/sec and 11.11 m/sec respectively, with 95% CIM = 0.184 – 0.196 m/sec. While the minimum and maximum circle flight meridional winds were -9.64 m/sec and 11.19 m/sec respectively, with CIM = 0.169 – 0.183 m/sec.

**Zonal winds:** Vultures decided to glide (M = 1.383 m/sec) over circle (M = 0.898 m/sec) flights in strong east-west lateral winds. In a T-test the difference in means was significant at 0.05 level with $t = 9461$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6k).
Figure 6k. Graph showing the means and 95% confidence intervals of mean zonal winds experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide zonal winds were -9.88 m/sec and 14.98 m/sec respectively, with 95% CIM = 1.377 – 1.389 m/sec. While the minimum and maximum circle flight zonal winds were –9.84 m/sec and 18.13 m/sec respectively, with CIM = 0.892 – 0.905 m/sec. Vultures preferred to occupy areas with stronger east-west winds than north-south winds.

**Population density:** Himalayan Vultures decided to perform circle flight in areas with high human population densities ($M = 18.15$ persons/km$^2$), and engaged glide flight in low population ($M = 15.77$ persons/km$^2$) landscapes. In a T-test the difference in means was significant at 0.05 level with $t = 896$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6l).
Figure 6l. Graph showing the means and 95% confidence intervals of mean population densities experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide flight population densities were 0.21 persons/km$^2$ and 1340.68 persons/km$^2$ respectively, with 95% CIM = 15.67 – 15.87 persons/km$^2$. While the minimum and maximum circle flight population densities were 0.21 persons/km$^2$ and 911.84 persons/km$^2$ respectively, with CIM = 18.03 – 18.27 persons/km$^2$. The vultures performed circle flight in densely populated areas presumably of thermals radiated by human made structures and also high probability of finding food or carrions.

**Normalized difference vegetation index (NDVI):** In areas with high NDVI, vultures preferred circle flight ($M = 0.48$) over glide style ($M = 0.44$). In a T-test the difference in means was significant at 0.05 level with $t = 16563$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6m).
Figure 6m. Graph showing the means and 95% confidence intervals of mean NDVI experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide flight NDVI were –0.03 and 0.82 respectively, with 95% CIM = 0.439 – 0.440. While the minimum and maximum circle flight NDVI were –0.03 and 0.82 respectively, with CIM = 0.482 – 0.483. Vulture engaged circle flight in high NDVI areas possibly to carefully scan for carrions, and presumably a priori roost or day rest flights. It may also be a priori departure warm up flight around a roost sites.

**Total precipitation:** Circle flight was chosen over glide ($M = 0.81$mm) during rain and snow ($M = 0.77$mm). In a T-test the difference in means was significant at 0.05 level with $t = 12451$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6n).
Figure 6n. Graph showing the means and 95% confidence intervals of mean total precipitation experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide flight total precipitation were 0.00mm and 12.39mm respectively, with 95% CIM = 0.764 – 0.769mm. While the minimum and maximum circle flight total precipitation were 0.00mm and 10.72mm respectively, with CIM = 0.807 – 0.814 mm. Vultures may not prefer to fly during very heavy rain or snow, however, during light showers, they possibly engaged circle flight around the locations of their rest or roost perches.

**Relative humidity:** Similar to the decisions made by vultures during rain and snow fall, circle flight ($M = 65\%$) was chosen over glide flight ($M = 63\%$) at higher relative humidity. In a T-test the difference in means was significant at 0.05 level with $t = 2577$, $p = 0.00$, $R^2 = 0.001$, $N = 182139$; Figure 6o).
Figure 6o. Graph showing the means and 95% confidence intervals of mean relative humidity experienced by Himalayan Vultures in relation to their flight style, i.e. either during gliding flight or circling flight (‘thermalling’). Points represent population means, error bars show 95% confidence intervals.

The minimum and maximum glide flight relative humidity were 4% and 100% respectively, with 95% CIM = 63.24 – 63.32. While the minimum and maximum circle flight relative humidity were 2.68% and 99.96% respectively, with CIM = 64.84 – 64.93%. High relative humidity mean moist and wet air, which deterred long distance glide flights, thus vultures performed short stunts of circle flights around roost or rest site. Spaces between barbules in feathers can hold moistures from wet air possibly make birds heavier to fly making energetically expensive.

3.4.3. Comparison of behaviours during flying and feeding
The Himalayan Vulture is an obligate scavenger. With such a foraging habit, Himalayan Vultures depend on predatory kills or left overs, ungulate corpses from
natural death or rejects from human consumption and unwanted wastes produced at butcheries. In the Tibetan Plateau or in the treeless Buddhist landscapes and country sides, sky burial sites provisions an alternative ephemeral food source. However, in the extreme cases of starvation, vultures have been known to feed on grubs from under livestock dungs and vegetation foliage, visit garbage dump sites. Vultures ought to fly in any kind of local environmental conditions, when a scarce, ephemeral and randomly distributed food resource is available. Feeding was a rare behavioural activity, thus vultures remained afloat in atmospheric conditions (such as thermal and orographic uplifts, and zonal and meridional winds) that supported flight which in turn increased the probability of finding food.

**Altitude (MSL):** Himalayan Vultures fed at lower altitudes in valleys with statistically significant difference between behavioural groups at 0.05 alpha level, as populated by a T-test. The difference in means was significant at 0.05 level with \( t = 3116, p = 0.001, R^2 = 0.001, N = 182139 \); Figure 7a). Vultures fed at altitudes of 3175 ± 1296 m and flew at altitudes of 3610 ± 1266 m.
Figure 7a. Graph showing the means of flight heights above ground reached by Himalayan Vultures in relation to their behaviour separated into ‘flying’ (Fly) or ‘feeding’ (Feed). Points represent population means, error bars are omitted for graphical clarity.

**eObs Temperature:** There was a statistically significant difference between behavioural groups. Vultures fed at localities with temperatures of $18.5 \pm 10.09 \, ^\circ\text{C}$ and flew at temperatures of $7.17 \pm 11.43 \, ^\circ\text{C}$. In a T-test the difference in means was significant at 0.05 level with $t = 15, p = 0.001, R^2 = 0.001, N = 182139$; Figure 7b).

Figure 7b. Graph showing the means of on-board bio-logged temperatures experienced by Himalayan Vultures in relation to their behaviour separated into ‘flying’ (Fly) or ‘feeding’ (Feed). Points represent population means, error bars are omitted for graphical clarity.
**Total Precipitation:** The rain or snow did not prohibit Himalayan Vultures from feeding, although they preferred to fly less. In a T-test the difference in means was significant at 0.05 level with $t = 2160, p = 0.01, R^2 = 0.001, N = 182139$; Figure 7c). Vultures did not bother to feed in heavy down pours ($1.4 \pm 2.55$ mm) and they tolerated to fly at some levels of total precipitation ($0.75 \pm 1.51$ mm). We observed the Himalayan Vultures feeding on a carrion of a calf in a running stream, confirming these overall observations.

![Graph showing the means of total precipitation experienced by Himalayan Vultures in relation to their behaviour separated into 'flying' (Fly) or 'feeding' (Feed). Points represent population means, error bars are omitted for graphical clarity.](image)

**Relative Humidity:** Regardless of very damp atmospheric conditions, vultures were not intimidated to feed but they chose to fly less. In a T-test the difference in means was significant at 0.05 level with $t = 71, p = 0.001, R^2 = 0.001, N = 182139$; Figure 7d).
Vultures fed even during high relative humidity (73.97 ± 19.36 %) and they preferred to fly in lower relative humidity (63.51 ± 21.07 %).

Figure 7d. Graph showing the means of relative humidity experienced by Himalayan Vultures in relation to their behaviour separated into ‘flying’ (Fly) or ‘feeding’ (Feed). Points represent population means, error bars are omitted for graphical clarity.

**Population Density:** Wildlife interaction with anthropogenic variables cannot be avoided as all biodiversity shares the only earthly space. Himalayan Vultures fed in areas densely populated by people. In a T-test the difference in means was significant at 0.05 level with \( t = 57, \ p = 0.001, \ R^2 = 0.001, \ N = 182139; \) Figure 7e). Vultures foraged and fed in human landscapes with population density (60.59 ± 119.14 persons/km\(^2\)) and flew in areas with population density (48.85 ± 114.12 persons/km\(^2\)). In the Buddhist states (Tibet & parts of Nepal), vultures visited and fed on human
corpses at the sky burial sites. For the other behavioural activities they generally kept themselves in a sparsely populated or no human landscapes.

Figure 7e. Graph showing the means of population densities experienced by Himalayan Vultures in relation to their behaviour separated into ‘flying’ (Fly) or ‘feeding’ (Feed). Points represent population means, error bars are omitted for graphical clarity.

**Normalized Difference Vegetation Index (NDVI):** Himalayan Vultures found food and fed in areas with high NDVI. In a T-test the difference in means was significant at 0.05 level with $t = 2256$, $p = 0.001$, $R^2 = 0.001$, $N = 182139$; Figure 7f). Vultures fed in areas with NDVI (0.54 ± 0.13) and conducted flights in landscapes with NDVI (0.49 ± 0.18). High NDVI possibly indicated higher total wildlife (ungulate) biomass and greater probability of detecting carrions from death of wildlife.
Orographic Uplift: There was a statistically significant difference between behavioural groups. In a T-test the difference in means was significant at 0.05 level with $t = 172$, $p = 0.001$, $R^2 = 0.001$, $N = 182139$; Figure 7g). Vultures preferred to fly in areas of higher orographic uplifts (0.32 ± 0.48 m/sec) and fed in areas of lower orographic uplifts (0.29 ± 0.45 m/sec). This difference indicated a potential costs of foraging, i.e., birds need to enter areas of low orographic uplift to find food.
Thermal Uplift: When thermal uplifts were available, vulture preferred to fly. The one-way ANOVA, between behaviours and thermal uplift, the difference in means between the groups was statistically significant. In a T-test the difference in means was significant at 0.05 level with $t = 60383$, $p = 0.001$, $R^2 = 0.001$, $N = 182139$; Figure 7h). Himalayan Vultures were on their wings in stronger thermal uplifts (1.48 ± 0.59 m/sec) and during the weaker thermal support (0.57 ± 0.62 m/sec), vultures remained on the ground to feed.
Figure 7h. Graph showing the means of thermal uplifts experienced by Himalayan Vultures in relation to their behaviour separated into ‘flying’ (Fly) or ‘feeding’ (Feed). Points represent population means, error bars are omitted for graphical clarity.

3.4.4. Annual movements and energetics

Overall dynamic body acceleration (ODBA) was used to examine energy expenses in the Himalayan Vultures’ annual movements. We measured energetics at temporal (daily and monthly), spatial (latitude & longitude bins and political boundaries), vertical (altitude gradient) and behavioural (activity and flight styles) scales in individual birds harnessed with biologgers.

Daily Energetics: ODBA pattern assessed over a 24 hours temporal scale showed a normal distribution slightly skewed towards the left (earlier daylight hours). Daily energy expenditure was correlated to daylight hours and supported the diurnal habit of the Himalayan Vultures. In a one-way ANOVA, between 24 hours-time scale and
ODBA, the difference in mean was statistically significant at 0.05 level with $F(23, 347321) = 1518.97$, $M = 25.73$, $SD = 53.06$, $SE = 0.09$, $p < 0.001$, $R^2 = 0.09$, $N = 347345$; Figure 8a).

**Figure 8a.** Graph showing the means of energy expenditure reached by Himalayan Vultures in relation to the hour of the day. Points represent population means, error bars are omitted for graphical clarity.

Vultures went to sleep from 2200 hours (90° E) until 0500 hrs. From 0500 hrs onwards, vultures gradually became active, and the birds increased their movements from 0900 hrs (25.41 ± 56.96) up to 1300 hrs (51.91 ± 73.11). Energy expenditure in vultures gradually decreased from 1400 hrs (50.15 ± 71.62) until the retired to the roost at 1800 hrs (23.76 ± 51.82). A Tukey post hoc test revealed statistically significant difference within hours in energy expenditure at 0.05 alpha level. However, energy expenditure at night from 2200 – 00500 hrs did not show statistically significant difference with $p = 1$. 
Annual Energetics: In a one-way ANOVA between 12 months temporal scale and ODBA, the difference in mean was statistically significant at 0.05 level with $F (11, 347333) = 214.47$, $M = 25.72$, $SD = 53.06$, $SE = 0.09$, $p = 0.00$, $R^2 = 0.007$, $N = 347345$; Figure 8b).

Figure 8b. Graph showing the means of energy expenditure reached by Himalayan Vultures throughout the year. Points represent population means, error bars are omitted for graphical clarity.

Vultures were least active in December with ODBA of $M 13.51 \pm 34.44$, with 52% drop as compared to November ($28.62 \pm 57.35$), possibly a hibernation month. In the rest of winter months (Jan-April), their mean energy expenditure ranged from $22.53 \pm 45.25$ to $24.97 \pm 52.69$. Vultures were slightly inactive in April with ODBA of $24.02 \pm 47.47$ which presumably a preparatory phase for northward migration in May & June. During the northward migration period, ODBA increased by 16% with a maximum in June ($30.21 \pm 57.74$).
The Himalayan Vultures were more active in their summer ranges, presumably provisioned with longer day length and better environmental ambiences. Vultures spent their maximum energy during the peak biannual northward (June) and southward (October) migrations. The mean difference within months was statistically significant at 0.05 alpha level.

But, there was statistically insignificant difference in energy expenditure in January (22.52 ± 45.25) and February (23.87 ± 49.83), \( p = 0.09 \), February and March (24.97 ± 52.69), \( p = 0.19 \), February and April (24.02 ± 47.47), \( p = 1 \), March and April (\( p = 0.36 \)), May (27.79 ± 52.55) and July (27.64 ± 56.15), \( p = 1 \), May and August (28.07 ± 60.12), \( p = 1 \), May and September (29.12 ± 60.79), \( p = 0.14 \), June and September (\( p =0.43 \)), June and October (30.71 ± 60.46), \( p = 0.99 \), July and August (\( p = 0.99 \)), July and September (29.12 ± 60.79), \( p = 0.08 \), July and November (28.61 ± 57.35), \( p = 0.75 \), August and September (\( p = 0.56 \)), August and November (\( p = 0.99 \)), September and October (\( p = 0.10 \)), September and November (\( p = 0.99 \)).

**Energetics in behavioural movements**: There was a statistically significant difference between behavioural groups as determined by one-way ANOVA, at 0.05 level with \( F (8, 347336) = 91043.53 \), \( M = 25.73 \), \( SD = 53.06 \), \( SE = 0.09 \), \( p < 0.001 \), \( R^2 = 0.68 \), \( N = 347345 \); Figure 8c).
Figure 8c. Graph showing the means of energy expenditure by Himalayan Vultures in relation to their behaviours, separated into major behavioural categories. Points represent population means, error bars are omitted for graphical clarity.

Energetically, the cheapest behavioural activity was rest (9.32 ± 8.37), followed by restless (19.65 ± 22.80). A perched and vigilant state of rest was described restless (19.64 ± 22.81), a behaviour that demanded the second lowest energetic cost. Restless behaviours were exhibited during rainy, windy and after feeding activities. Besides rest and restless behaviours, to remain airborne in flight (61.33 ± 35.83) required less energy than any other movement behaviours. The most energy demanding activity was a feeding (541.69 ± 233.66), followed by flap flights (take-off flap flight (368.99 ± 168.63), flap flight (352.81 ± 142.89) and flap land (329.05 ± 151.43) and WHR (204.31 ± 122.47; walk, run and hop) behavioural movements. A
Tukey post hoc test supported that the energy demands within behavioural categories was statistically significant at 0.05 alpha level.

**Energetics and flight styles:** The glide and circle flights were two flight styles determined with 1Hz high resolution data. There was a statistically significant difference between flight styles at alpha 0.05 level with \( F(1, 3858) = 6.48, M = 67.38, SD = 49.58, SE = 0.79, p = 0.01, R^2 = 0.002, N = 168069; \) Figure 8d).

![Figure 8d](image.jpg)

**Figure 8d.** Graph showing the means of energy expenditure experienced by Himalayan Vultures in relation to their behaviour separated into ‘gliding’ (Glide) or ‘thermalling’ (Circle). Points represent population means, error bars are omitted for graphical clarity.

Energy incurred in glide was 68.65 ± 51.69, while in circle flight was 64.15 ± 43.60. For Himalayan Vultures, it was cheaper to circle fly especially when supported with thermal uplifts.
Energetics and altitude (MSL): Although flying is generally energetically the cheapest activity a vulture can engage in, ascending to greater heights even on the wings became expensive to the Himalayan Vultures, as energy requirement also increased. In a one-way ANOVA, between altitude and ODBA, the difference in mean was statistically significant at 0.05 level with $F(8, 166416) = 140.36, M = 31.61, SD = 58.81, SE = 0.14, p < 0.001, R^2 = 0.01, N = 166431$; Figure 8e).

Figure 8e. Graph showing the means of energy expenditure experienced by Himalayan Vultures in relation to their flight height above mean sea level (MSL). Points represent population means, error bars are omitted for graphical clarity.

The energy expenditure exponentially increased with altitude. At altitudes lower than 4000m, ODBA ranged between $25.06 \pm 59.76 - 33.70 \pm 50.71$. To climb from 4000 - 7500 meters, vultures increased energy expenditure by 136 % with ODBA at 4000m of $32.71 \pm 65.58$. Himalayan Vultures spent maximum energy when they crossed over
the higher Himalayas or flying at heights equal to the Himalayas. The increment in energy demand with increased height may be attributed to thin air in air very high altitudes. The mean difference within altitude bins was statistically significant as revealed by Tukey post hoc test, at 0.05 level. However, energy expenses were statistically insignificant.

**Energetics and height above ground (HaG):** In a one-way ANOVA, between height above ground and ODBA, the difference in mean was statistically significant at 0.05 level with $F(24, 166865) = 203.56$, $M = 31.61$, $SD = 58.82$, $SE = 0.14$, $p < 0.001$, $R^2 = 0.03$, $N = 166890$; Figure 8f).

![Graph showing the means of energy expenditure experienced by Himalayan Vultures in relation to their flight height above ground. Points represent population means, error bars are omitted for graphical clarity.](image)

Figure 8f.
Once the vultures reached to a cruise height above ground level (200m) and beyond (>200m), ODBA oscillated between 41.02 ±25.49 and 54.82 ± 32.20. At lower heights above the ground level, vultures steeply increased ODBA presumably engaged powered flight to gain height to reach to cruise height or even to avoid collision on to a terrain surface. A Tukey post hoc test within altitude bins revealed statistically significant difference at 0.05 level. However, energy expenses above 200 meters of height above the ground level was statistically insignificant (p = 1).

**Energetics and latitude:** The GPS back-packed Himalayan Vultures occupied the Asian landscapes between 26 – 46 ºN. In a one-way ANOVA, between latitude (binned at 5° interval) and ODBA, the difference in mean was statistically significant at 0.05 level with $F (4, 168469) = 530.26$, $M = 31.66$, $SD = 58.75$, $SE = 0.14$, $p < 0.001$, $R^2 = 0.01$, $N = 168474$; Figure 8g).
Vultures incurred lowest energy in the latitudes (25 – 30 °N) range of winter quarters with lowest ODBA (27.27 ± 53.72). This was further corroborated by the analysis on monthly energy expenditures at an annual scale. Vultures incurred lowest energy in the Indian plains of Utter Pradesh and Assam. In the latitude range (30 -35 °N), energy demand was with ODBA (41.89 ± 68.54), presumably because of high altitudes and ruggedness of terrain and wind conditions at the higher Himalayas and Tibetan Plateau. In the farther northern latitudes (45 -50 °N), vultures lived in energetically expensive landscapes with ODBA value of 51.23 ± 40.98. This result was also supported by the annual energy expenditures. High energy cost to vultures in northern latitudes could possibly result from their occurrence in high mountains with active zonal winds. However, those vultures that spent their summer in Mongolian steppes expended less energy. The mean difference was statistically significantly different within latitude bins at 0.05 level as revealed by Tukey post hoc test. But, there was a statistically insignificant difference in energy expenses in latitude bins 30 – 35 °N (41.89 ± 68.54) and 40 – 45 °N (39.30 ± 51.15), p = 0.54), 30 – 35 °N and 45 – 50 °N (51.23 ± 40.99), p = 0.63), 35 – 40 °N (38.76 ± 70.11) and 40 – 45 °N (39.30 ± 51.14), p = 0.99), 35 - 40 °N and 45 – 50 °N, p = 0.34), 40 - 45 °N and 45 – 50 °N, p = 0.39).

Energetics and longitude: The longitudinal distribution of tagged vultures was greater than their latitudinal range. Vultures were spread between longitudes of 80 – 112 °E. In a one-way ANOVA, between longitude (binned at 5° interval) and ODBA, the difference in mean was statistically significant at 0.05 level with $F (6, 168467) = 257.76$, $M = 31.66$, $SD = 58.75$, $SE = 0.14$, $p = 0.00$, $R^2 = 0.01$, $N = 168474$; Figure 8h).
Similar to the energetics along latitudinal gradient, vultures incurred less energy in longitude bands where vultures spent their winter, and spent higher energy in longitudes greater than 95°E. ODBA was high at 85-90°E longitude interval was a northward and southward migration corridor in Nepal. Vultures invested maximum energy in longitude bands of 95 - 100°E which encompassed highlands of the Tibetan Plateau, and higher Himalayan mountain ranges between mainland China and Autonomous Region of Tibet.

4. **Summary discussion**
Our observations in this movement study has been on immature vultures (first year old, 2-3 juveniles and sub-adults). The selection of this age group was based on
capture opportunity and our goal of understanding the ontogeny of movement and life history of the Himalayan Vultures. This chapter documents the first year annual movements (2014-2015) only (Flack et al. 2016).

Himalayan Vultures perform their northward spring migration (April - June) and southward autumn migration (mid-Oct to Nov) biannually (Mandel et al. 2008). In the spring, from their winter quarters (<3800msl) of the northern plains and Himalayas of India, Nepal, Bhutan and south and south-eastern China, they migrate to their summer climes (> 4000msl), in uplands of Mongolia, Inner Mongolia, Tibetan Plateau and Qinghai regions China. In summer, vultures roam and range at high altitude landscapes in Asia, where environmental conditions are drier (lower precipitation and humidity) and characterized by open grasslands with low NDVI. There, they experience longer sunshine durations and longer day lengths, lower mean population density and higher thermal updrafts – conditions highly suitable for scavenging vultures. Vultures migrate to lower altitudes in winter where they experience warmers climes and shorter sunshine duration, but also relatively high precipitation, high humidity, stronger thermal uplift and low orographic uplifts (Duriez et al. 2014). Furthermore, they are exposed to forested landscapes with high NDVI and highly variable human population densities. The extent of summer movement range is greater than its winter movements.

Himalayan Vultures summer at altitudes > 4000msl in Mongolia, Inner Mongolia, Tibetan Plateau and Qinghai regions of China, and winter at mean altitude < 3800msl in the northern plains and Himalayas of India, Nepal, Bhutan and Yunnan. Mean flight height above the ground in their summer range (mean range 320-420m) is greater than in winter quarters (mean range 180-340m). During migratory movements, vultures cross at <7500 msl over the Himalayas. In the winters, vultures move from low to high NDVI landscapes in Asia.

Vultures adapt to engage more into circling flight at high altitude landscapes and at greater heights above the ground. They prefer to circle more than glide in landscapes with strong orographic and thermal updrafts. In strong meridional and latitudinal winds, vultures decide to use gliding flight more than circling flight (Harel et al. 2016).
We show vultures feed at locations with high NDVI and human population density, and in the valleys. Vultures prefer to fly on sunny days with long sunshine duration and in strong thermal uplifts. They prefer not to fly during snowy or rainy days and in strong orographic wind conditions.

In summary, during this exploratory first phase of observing the birds’ ontogeny, we now have begun to understand annual movements of immature Himalayan Vultures, enlightening us towards an understanding of the ontogeny of movements in general (Nathan et al. 2008). From this movement study, we have been able to hypothesize about the north-south and east-west extension of movement range of Himalayan Vultures. Our understanding of this movement range extensions may remain partial to immature annual exploratory movements. It is unclear what adult birds tagged for movement studies would do during their annual movements. Given that we have data only from non-breeding adults, it calls for further experiments on full-grown adults (Nathan et al. 2012).

In our movement observations, all the birds are now entering their third year of carrying eObs biologgers, however 5 of the 18 tagged vultures are dead. We have indicated in Chapter 2, the survival is dependent upon the birds’ experiences in exploiting environmental parameters. It now becomes very interesting to observe how adult vultures compare. We will soon be able to contrast how flight experience influence their adult life history and their adult survival strategies (Harel et al. 2016).

In the European continent, immature or sub-adult vultures migrate to the southern latitudes in Africa and come north once mature for breeding. In contrast, in the Asian landscape, juveniles or sub-adult Himalayan Vultures migrate north to higher elevation areas and northern latitudes on an annual basis. Movement patterns of juvenile vultures in two continents appear to be almost opposite (Duriez pers. comm.).

From this study, we infer that the Himalayan Vultures migrate from their summer areas to warmer or low altitude areas during the winter. However, ambiguity in whether only immatures or sub-adults exhibit migration remains a pertinent question. If it were only immatures that make north-south and south-north migratory movements in winter and spring respectively, then another question arises as to how unguided movements occur in vultures. Furthermore, are adults able to survive in the cold winters of the
Tibetan Plateau. Is migration innate, or do vultures learn their migratory movements or annual movements from adults, or just based upon their own exploratory movements (Berthold 2001)?

As indicated by ODBA expenditures, southward migration was strenuous than northward migration, we recommend further experiment or analysis on energetic cost in migration. Migration may be an individual choice, but our analysis on environmental variables indicated that Himalayan Vultures may be using certain environmental (such as temperature, humidity and total precipitation, thermal and orographic uplifts) cues to trigger southward and northward migratory movements.

In general, remote sensing data have been used in the analysis of wildlife research to understand ecology or movement ecology. Similarly, we have used remote sensing data available through EnvDATA in Movebank to document and understand how Himalayan Vultures exploit various environmental factors to achieve seamless flights over high altitude and thin air mountains of the Himalayas and Plateau, perform annual movements and survive in their summer and winter areas (Dodge et al. 2016). Having begun to understand how vultures exploit atmospheric environments, we suggest that our data can contribute exciting new information to the nascent field of aero-ecology (Kunz et al. 2008). Currently wildlife movements on earth are mostly studied as terrestrial and aquatic movements depending on a species life history strategy and habitat use over space and time. We support the notion that there may be a need to further discern movement ecology into terrestrial movement ecology, aquatic movement ecology and aero-ecology or aerial movement ecology. We describe aero-ecology as movement of wildlife in the atmospheric space and their interactions with environmental parameters and other resources after an initial take off form the land or water surfaces and prior to landing back to terrestrial and aquatic substrates.

During the course of their annual movements, wildlife are bound to interact with various environmental factors: terrestrial parameters such as land features, land cover and land use, aquatic parameters like ocean currents, saline and fresh water bodies, and atmospheric parameters like thermal and orographic uplifts, precipitation and humidity, and other factors affecting visibility, and food resources available therein. As in our aero-ecological study, in the studies of movements both on land and sea, it
would be very important to document and understand how atmospheric factors and other resources are exploited to benefit one’s living (Ropert-Coudert et al. 2005).

Most remote sensing data available from Movebank have spatial and temporal scale issues. As of now, we may be over extrapolating environmental data to the needs of the GPS positions collected by moving wildlife with GPS biologgers. We foresee that these data issues can be resolved by incorporating weather data sensors in biologgers or by fine scaling of remote sensing data acquisition, such as in ESA’s Copernicus Program (Kuenzer et al. 2014).

From the vast expanse of geographic areas covered by vultures during their annual movements, conservation management of Himalayan Vultures may not become effective unless a collaborative effort is made among the range countries. While Himalayan Vultures have largely been spared from their population decline as compared to other vulture species in India, threats to their survival still exist and are recognized by IUCN (Cuthbert et al. 2007; Acharya et al. 2009; Ogada et al. 2012; IUCN 2016). In the Asian landscapes of China, vultures succumb to retaliatory pesticide poisoning of poisoned carcasses used against wolves and snow leopards (Ming et al. 2015). While disposition of human corpses in sky burials in the Tibetan Plateau supplements food for vultures, mortality risk from NSAIDs (diclofenac) by a dying person may adversely affect the population. The immature and juvenile population of vultures would be affected as they are easily attracted to feeding. In some extreme cases, vultures are also know to glean from garbage dump sites. Other emerging threats are high tension power transmission lines, wind turbines and tall towers used for telecommunication systems.

Using our emerging knowledge of movement ecology of Himalayan vultures (Prakash et al. 2012), coupled with remote sensing information telling us about their dealings with environmental factors, including human presence (Kuenzer et al. 2014), we will ultimately be able to device conservation measures to protect their populations and ensure their long-term survival (Virani et al. 2011).
Chapter 4

Behavioural adaptations to flight into thin air

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4.1. Abstract
Soaring raptors can fly at high altitudes of up to 9000 meters. The behavioural adjustments to high-altitude flights are largely unknown. We studied thermalling flights of Himalayan vultures (*Gyps himalayensis*) from 50-6500 meters above sea level, a 2-fold range of air densities. To create the necessary lift to support the same weight and maintain soaring flight in thin air birds might modify lift coefficient by biophysical changes, such as wing posture and increasing the power expenditure. Alternatively they can change their flight characteristics. We show that vultures use the latter and increase circle radius by 35% and airspeed by 21% over their flight altitude range. These simple behavioural adjustments enable vultures to move seamlessly during their annual migrations over the Himalaya without increasing energy output to flight in high elevations.

4.2. Introduction
Migrant birds often spend part of their lives at low altitudes and then ascend to altitudes of up to 9000 meters (Altshulter and Dudley 2006). Lift acceleration is proportional to air density, and thus, when keeping all other parameters constant (such as flight speed, lift coefficient, wing area) will decrease with elevation (Eq. 1) whereas the gravitational force is near constant. Birds need to adapt their flight-related biophysical properties and/or flight behaviour to thin air. While the physiological adaptations of flying at extreme altitudes are partially understood, particularly with regard to the oxygen transport capacity of blood haemoglobin (Bishop et al. 2015), the behavioural adaptations of high-flying birds are much less known (Butler 2010).

Bar-headed geese (*Anser indicus*) cross the Himalayan mountains using a “roller-coaster” flapping-flight strategy (Dee et al. 2011). Hummingbird in wind tunnel experiments flap faster with larger amplitude and increase power expenditure to increase their lift coefficient in thin air (Dodge et al. 2014). In contrast, obligate soaring birds, such as vultures, are largely unable to employ a powered flight mode for long durations (Dodge et al. 2013).

Himalayan vultures are among the heaviest flying bird species with large wingspan (7.9 (kg), 2.4 (m) respectively, on average in our study. We assess the birds’ strategies
of thermalling from 50 meters to 6500 meters altitude, while crossing the Himalaya during their natural annual flights.

Generally, a thermalling bird with non-powered flight has two contrasting options to create the lift necessary to maintain upward acceleration in a rising thermal in thinner air: (1) Biophysical - change its wing or feather posture and inclination to increase the lift coefficient; (2) Behavioural - change its flight characteristics, i.e., increase its thermalling radius and/or flight speed. We leverage on a new analysis approach to determine wind speed and consequently, airspeed from high frequency GPS data of thermalling vultures, and provide direct observations to the strategy employed by free-flying wild vultures soaring over the Himalaya.

4.3. Materials and Methods

4.3.1. Bird capture and data recording
21 birds were captured in Bhutan between 5/2014 and 2/2015 using wire-mesh cage trap and fitted with GPS data loggers (45 (g), cellphone link, e-obs GmbH) using a ~30 (g) Teflon-nylon harness. Daily (02:00-20:00 GMT), loggers were set to periodically collect 1 (Hz) GPS fixes for 10 minutes, whenever solar charge allowed. We collected 1,694,828 such GPS fixes between August-1 2014 and July-3 2015. Data are available through the Movebank archive (Duriez et al. 2014).

4.3.2. Background aerodynamic theory
The lift coefficient, $C_L$, is determined by the combined effects of all lift-generating mechanical properties of a gliding bird, such as body shape, size, wing posture, and angle of attack. At balanced flight:

$$C_L = \frac{L}{\frac{1}{2} v^2 \rho S} = 2 \frac{m}{S \rho v^2}$$

(1)

where $\rho$ = air density, $v$ = airspeed, $L$ = lift force, $S$ = wing area, $m$ = bird mass, $m/S$ = wing loading, $l = L/m$ = lift acceleration (lift force per unit mass).

For birds flying in circles, as the vultures do while thermalling, we can write the balance of forces in 2 dimensions: vertical – balancing gravity (eq. 2); and tangential – balancing the centripetal force (eq. 3):
\[ l \cos(\theta) = g \]  \hspace{1cm} (2)

\[ l \sin(\theta) = \frac{v^2}{r} \]  \hspace{1cm} (3)

where \( \theta \) = banking angle, \( r \) = thermalling circle radius. In order to stay aloft during circling flight the bird needs to generate a lift acceleration of

\[ l = \sqrt{g^2 + \frac{v^4}{r^2}} \]  \hspace{1cm} (4)

Each of the terms in Equations (2-4) can be determined from the flight data and annotated environmental information and allows us to determine which of the terms trades off with decreased air density. Realistic estimates of air density during the observed flight were obtained from the ECMWF ERA-Interim weather reanalysis dataset and annotated to the tracks using the Movebank-Env-DATA service (Hawkes et al. 2011; Huey and Eguskitza 2001). Wind speed and direction can be determined from the flight path of the bird during circling flight using the method developed by Weinzierl et al. (unpublished) (see Appendix 1). This method expands the approach by Treep et al (Metzger et al. 2011). It assumes that wind speed causes horizontal displacement during thermal soaring. Assuming that over a short time and space the variation of horizontal wind speed are small, the amount of distortion of each "loop" within a thermalling flight pattern can be used to determine the mean wind speed and direction within the area enclosed by each thermalling loop. The wind speed is then subtracted from the GPS ground-speed measurements to determine the bird's airspeed.

4.3.3. Data analysis

We estimated the bird's mean airspeed, \( v \), for 30 second intervals. Only those sequences where the bird made a full circle within 30 seconds were used. Assuming that within a single thermalling circle the bird made a balanced turn at a constant airspeed, a constant circle radius and a constant bank angle, we calculated the angular rate, \( \omega \)

\[ \omega = \frac{\Delta \theta}{\Delta t}, \]  \hspace{1cm} (5)

where \( \Delta \theta \) is the cumulative angular difference across 31 fixes and \( \Delta t = 30 \) (s), the circle radius, \( r = \frac{v}{\omega} \), where \( v \) is airspeed (m/s), and the lift acceleration, \( l \)
\[ l = \frac{L}{m} = \sqrt{g^2 + v^2 \omega^2}. \] 

We fixed wing loading of \( m/S = 10.54 \pm 0.9 \) (kg/m²), based on our measurements of 26 individuals. Because the birds' mass changes significantly as they feed we use the population mean rather than an individually observed value. We further assume that the horizontal wind speed is small relative to the airspeed of the circling bird, and ignore altitudinal variation in gravity and buoyancy. The lift coefficient associated with each non-overlapping track segment can be determined as:

\[ C_L = 2 \frac{m}{S} \frac{l}{\rho v^2} = 21.08 \frac{l}{\rho v^2} \] 

Track segments for which no ECMWF data could be obtained were dropped, resulting in a final sample size of \( n = 8595 \). Processed wind data per circle, and observed physiological data are provided in Appendix 2.

### 4.4. Results

Air densities varied almost two-fold between 50 and 6500 meters flight altitude. We found that the lift coefficient and lift acceleration remained relatively constant throughout the entire range of elevations (Fig 1a-b). While in theory the wing area could have changed to perfectly offset the effects of the angle of attack on the lift coefficient, a more parsimonious explanation is that body posture remained near constant.
Figure 1. Characteristics of acceleration at increasing elevations. (a) The vultures show small variations (-4% to +7%) in the lift coefficient over the entire flight elevation (air densities) range (red line marks the overall mean); (b) The lift acceleration varied very little with height (<2%); (c) The
vertical soaring speed remained near constant, and even increased above 4500 (m) (air density <0.7 (kg/m³). Boxes show mean (vertical line), quartile (box) and 95% (whiskers) confidence interval, as well as outliers (circles) in 15 elevation bins with equal observation numbers.

For the purpose of analysis and comparison of flight behaviour in low vs high altitudes, we define a sub-sample of high-flying and low-flying groups (5% of observed points, n = 430, at lowest and highest air density, respectively). Mean air density in the low-flying group ($\rho_l$ = 1.099 (kg/m³)) is 70.05% higher than for the high-flying group ($\rho_h$ = 0.646 (kg/m³)). The lift coefficients, however, are very similar between high-flying ($C_L = 1.74$) and low-flying ($C_L = 1.83$) groups, (4.87% difference).

The birds increased their mean circle radius by ca. 12.5% per 1000 meter increase in altitude (Fig 2a). The birds’ airspeed increased strongly as they were ascending into thinner air (Fig 2b). While vultures flying close to sea level flew at speeds of 10.5 m sec⁻¹, they were speeding up to 13.5 m sec⁻¹ at 6500 meters altitude, ~30% increase in airspeed.
Figure 2. Behavioural changes in the flight characteristics of thermalling vultures. (a) Flight circle radius increases in relation to decreasing air density (increasing elevation). (b) Airspeed increases with elevation. Red line represents a linear model fitted to the inverse of the air density and the squared
airspeed (slope=115.7, R²=0.46 p<0.0001). Data show average (vertical line), quartile (box) and 95% confidence interval, as well as outliers (circles) in 15 elevation bins. (c) One flight segment of the vulture Yoezer. Dots mark the reported GPS locations of the vulture during flight over the Himalaya ridge. Land surface and topography obtained from GoogleEarth.

4.5. Discussion

For soaring birds the energetic cost of flying is very low (Nathan et al. 2012). We therefore assume they adjust and optimize their gliding flight to any altitude within their flight space by behavioural means other than increased power output.

We found that the lift coefficient of soaring Himalayan vultures changed very little despite a large change in air density (Fig 1a). The relatively constant lift coefficient provides no evidence to support compensation for thinner air by biophysical changes to wing configuration, and by parsimony, suggests that they adjust for thinner air behaviourally by adjusting their flight characteristics, such as increasing their airspeed and circle radius.

By calculating the theoretical ratio between the corresponding velocities needed for maintaining a lift acceleration that will offset gravity at high and low elevations (using Equation 1) we can determine the airspeed compensation over the vultures' flight elevation range as

$$v_h = \left(\frac{\rho_l}{\rho_h}\right)^{0.5} \times v_l = \left(\frac{1.099}{0.646}\right)^{0.5} \times v_l = 1.304 \times v_l$$

where $\rho_l, \rho_h, v_l, v_h$ are the air densities and airspeeds at low and high altitudes, respectively.

Assuming a fixed wing configuration, as indicated by the relatively constant lift coefficient, the airspeed compensation predicted by Equation (8) will be needed to keep the sink rate constant while flying in a straight line in air thinned from 1.099 to 0.646 (kg/m³). The magnitude of the observed airspeed difference between low and high elevations – roughly one third (Fig 2b) – is in agreement with this expected value (30.4%).
Soaring in a circular flight pattern provides additional constraints as the banking angle diverts some of the lift force from countering gravity to countering the centripetal force. The sink rate of a turning bird, $v_{st}$, can be corrected relative to the straight-line equilibrium sink rate, $v_s$, following (Parrott 1970): $v_{st} = v_s / \sqrt{\cos^3 \theta}$. We found that low-flying birds fly at a shallow banking angle of $\theta = 23 \pm 1.5^\circ$. Therefore, reducing the banking angle, which for a fixed velocity will translate to increasing the circling radius, can at best improve the sink rate (and therefore the vertical soaring speed) by a small amount (~11%). The choice of banking angle at low elevations is thus, driven by the needs of centering the thermal. However, at higher elevations circles of the same size would translate to a steeper banking angle (~42°, Equation 3) because of the faster flight velocity in thinner air, which impacts the sink rate by ~36%. We find that high-flying vultures increase circling radius by 56% (from 28.3 (m) to 44.3 (m) relative to low-flying ones, thus, keeping banking angle as well as lift acceleration roughly constant, throughout the elevation range of their flight.

The above calculations apply to theoretically ideal circling flight in a spatially constant wind field within an area-limited thermal. In reality the circling radius should be driven, to a large degree, by the availability of thermal uplift, the size of the thermals and the distribution of vertical airspeeds within the thermal column. Little is known about the explicit distribution of size and structure of thermals over the Himalaya (or anywhere else) at any given time, though they are generally expected to be stronger near their centre and widen with elevation. Our calculations, supported by our observations, indicate that at high elevations the choice of thermalling circle radius is increasingly constrained by the air density in addition to the regular constraints of centering a thermal. Our finding that vertical soaring speed does not decrease, and in fact, slightly increase, with elevation (Fig 1c) indicates that given the thermal uplift conditions in the Himalaya vultures employ behavioural adjustment to their flight characteristics that allow efficient soaring at high elevations despite the increasing challenges (Fig 2c). In general we expect that most soaring bird species, where individuals experience widely differing air densities, will use similar behavioural adaptations to thermalling flight in thin air (see also (Pennycuick 1972)), namely to keep power output minimal and increase airspeed and circling radius.
Ethics. Ministry of Agriculture and Forests, Bhutan approved this study (UWICE/ADM/20/201-12/998). Royal Civil Service Commission, Bhutan, letter of award (RCSC/TGD(8.00)2014/975, LTA-38935).

Data accessibility. Data are deposited in the Movebank Data Repository http://dx.doi.org/ 10.5441/001/1.143v2p2k.
4.6. Appendix

4.6.1. Appendix 1: Speed estimation method

Provides definitions of the parameters used, and step wise description of formulation methods for estimation of wind speed and air speed from GPS-observed locations and ground speeds.

Definitions:

\( G = [\vec{g}_1', ..., \vec{g}_n'] \) – Set of GPS observed ground-speed vectors (x (latitudinal) and y (longitudinal) components) (m/s).

\( \Delta t \) - Constant sampling rate (s).

\( \vec{w} = (w_x, w_y) \) - Assumed constant horizontal wind vector (m/s) within a single thermal circle (here we defined a single circle over 30 seconds) (Figure 1).

\( \vec{a}_i = (a_{i,x}, a_{i,y}) \equiv (\vec{g}_i' - \vec{w}) \) - The bird’s air-speed vector (m/s).

\( a_i = \|\vec{a}_i\| \) - The apparent air speed, \( a_i \) (m/s), is defined using the vector-distance operator.

Approach:

Within each circle, we model \( a_i \) as a first-order autoregressive process, AR(1), with mean, \( a \), representing the bird’s assumed constant air speed, and unexplained and small-scale variance due to turbulence, \( \sigma_a^2 \), such that \( a_i = (1 - \phi)a + \phi a_{i-1} + N(\sigma_a^2) \), where \( N \) is a mean-zero Gaussian random distribution and \( \phi (0 \leq \phi \leq 1) \), is an autocorrelation coefficient. Substituting the observed ground speed vector into the definition of air speed, we obtain:

\[
\vec{a}_i = \vec{g}_i' - N(\sigma_g^2 I) - \vec{w}
\]  

where and \( I \) is the 2x2 identity matrix.

By reorganizing equation (1) and assuming that the GPS error \( \sigma_g \) is small relative to \( a_i \), we obtain the following approximation for air speed, \( \vec{a}_i \)

\[
a_i = \| (\vec{g}_i' - \vec{w}) - N(\sigma_g^2 I) \| \approx \vec{a}_i + N(\sigma_g^2).
\]

We can derive the negative log likelihood of observing the sequence of GPS groundspeed vectors, \( G \), given wind \( \vec{w} \) as
\[ l(G, \bar{w}) = -\log(P(\bar{a}_1) \prod_{i=2}^{n} P(\bar{a}_i \lor \bar{a}_{i-1})) = \]
\[ \frac{1}{2} \left\{ n \log(\sigma^2) - \log(1 - \phi^2) + \frac{1}{\sigma^2} \left[ (\bar{a}_1 - a)^2 (1 - \phi^2) + \sum_{i=2}^{n} (\bar{a}_i - [(1 - \phi)a + \phi \bar{a}_{i-1}])^2 \right] \right\} \]  
where constant terms were omitted. By setting the derivative of the likelihood function with respect to zero, we obtain the maximum likelihood estimator for mean air speed
\[ \hat{a} = \frac{\bar{a}_1 + (1 - \phi) \sum_{i=2}^{n} \bar{a}_i + \bar{a}_n}{1 + (n - 2)(1 - \phi) + 1} = \frac{\|\bar{g}_1 - \bar{w}\| + (1 - \phi) \sum_{i=2}^{n} \|\bar{g}_i - \bar{w}\| + \|\bar{g}_n - \bar{w}\|}{1 + (n - 2)(1 - \phi) + 1} \]  
Using this estimator and applying Bessel's correction for sample size, i.e. multiplying by \(n/(n - 1)\), and assuming that \(\hat{a} \approx a\), we get an estimator for the variance term:
\[ s^2(G, \bar{w}) \equiv \]
\[ \frac{1}{n - 1} [(\bar{a}_1 - \hat{a})^2 (1 - \phi^2) + \sum_{i=2}^{n} (\bar{a}_i - [(1 - \phi)\hat{a} + \phi \bar{a}_{i-1}])^2] = \]
\[ \frac{1}{n - 1} [(\|\bar{g}_1 - \bar{w}\| - \hat{a})^2 (1 - \phi^2) + \sum_{i=2}^{n} (\|\bar{g}_i - \bar{w}\| - [(1 - \phi)\hat{a} + \phi \|\bar{g}_{i-1} - \bar{w}\|])^2] \]  
and obtain
\[ l(G, \bar{w}) = \frac{1}{2} \left\{ n \log(\sigma^2) - \log(1 - \phi^2) + \frac{n}{\sigma^2} s^2(G, \bar{w}) \right\} \]  
Because the first two terms and the factor \(n/\sigma^2\) are independent of \(\bar{w}\), we can calculate the likelihood estimate for the unknown wind vector by minimizing the unexplained variance in air speed \(s^2(G, \bar{w})\):
\[ \bar{w} = \arg\min_{\bar{w}} [s^2(G, \bar{w})]. \]  
For each track segment, we obtain mean air speed \(\dot{a}\), setting \(\bar{w} = \bar{w}\). Also for each segment, mean vertical speed ground speed around point \(k\), \(g_{z_k}\) is calculated as
\[ g_{z_k} = \frac{(x_{k+m} - x_{k-m})}{(n - 1)\Delta t} \]  
where \(x_k\) is GPS height at point \(k\). Change in heading between two consecutive GPS fixes, \(\Delta \theta_i\), is defined as the angle between the air speed vectors \((\dot{g}_i - \bar{w})\) and \((\dot{g}_{i+1} - \bar{w})\); the cumulative change in heading can then be defined as \(\Delta \theta_{cum} \equiv \sum_{i=k}^{n} \Delta \theta_i\). Assuming that the bird is flying in a perfect circle at constant air speed, we calculate the mean angular rate in radians, \(\dot{\omega}\), the circle radius, \(r\), and the time per full circle, \(\Delta t_c\), are:
\[ \dot{\omega} = \frac{\Delta \theta_{cum}}{\Delta t_{cum}}; \quad r = \frac{\dot{a}}{\omega}; \quad \Delta t_c = \frac{2\pi}{\dot{\omega}} \]  
Using the fact that in a balanced turn the centripetal acceleration is \(\ddot{a}\dot{\omega} = [L/m]\sin(\beta)\) and the gravitational acceleration \(g = [L/m]\cos(\beta)\) where \(L\) is the lift, \(m\) the bird mass, and \(\beta\) the banking angle, we obtain estimates for the banking angle
\[
\beta = \tan^{-1}\left(\frac{\ddot{\omega}}{g}\right)
\]

(10)

and the lift acceleration

\[
\frac{L}{m} = \sqrt{g^2 + \ddot{a}^2\omega^2}
\]

(11)

Figure 2. Track distortion by wind. Consider positions sampled at a fixed rate from a bird which is flying in a perfect circle in windless conditions. The resulting track might look like (a). Now consider (b), which shows the vectors connecting subsequent positions from (a) (in blue). The blue vectors in (b) represent individual movement steps of the bird, e.g. "3m northward and 1m eastward". Now add some sidewind to the picture. The displacement of the bird in each movement step caused by sidewind is represented by the red vectors in (b). By combining blue and red vectors we get the movement steps of a bird flying under the influence of sidewind (c). If we append the vectors from (c) in chronological sequence, then we get the typical ground track of a bird which is displaced by wind while circling.
5. General discussion and personal reflection

Knowledge Base: When I started to strike the letters on the computer keyboard to paraphrase the words in this section, I pondered and mirrored a bit of my knowing of the Himalayan Vultures. The reflection quickly terminated with a clear conclusive phrase, “I did not know anything.” What I had known of the vulture was limited to my own local space, time and experience, and frankly it now appears that I was boasting within such a small space. I knew they were a migrant, but I had put it into the altitudinal migratory bird category which summers in the mountains above 4500 meters and winters in the lowlands below 3500 meters within Bhutan. My geographic limit was my country and my ecoregion, which also reflects how poorly a person I was in knowing about bird migration or animal migration in general.

Bird Capture: Capture of a wildlife and correctly backpacking biologgers on to the living specimen is the start of the movement studies, thus a mention of it is very appropriate in here. About three years before this work on vultures was undertaken (2014), I had captured 14 Black-necked Cranes (Grus nigricollis) in their winter areas in Bhutan. Of course, I had my colleagues to assist me catch cranes. The learning curve to catch the cranes in the wild without the use of anaesthetic drugs was really the best choice for the bird. A load of emerging capture ideas had to be field tested only to gather the folly of failures from rodents sniping snares and inappropriate materials available in the locality. The basis of capture techniques were from the knowledge of the farmers or villagers or from people who practised occasional hunting of galliformes (pheasants and partridges) for protein.

When I was a teenager, I remember I participated in such adventures in the forests around the village I grew up. But for this new capture task, bird had to be caught alive without injury and released upon fitting with biologgers. Capture techniques had to be adapted differently with the behaviour of the cranes using different microhabitat feeding areas (paddy fields, farmlands, dwarf bamboo tussocks, wetland slushes and meadows). This field knowledge base was a useful experience to manoeuvre capture techniques of the Himalayan Vulture. In April 2014, very much delighted to be a student of Professor Dr. Martin Wikelski (Director, MPIO) in vultures, I began to learn and listen to stories of foraging behaviours of vulture to envision and adapt capture methods. One day, Mr.
Rinchen Singye (a colleague at the Ugyen Wangchuck Institute for Conservation and Environment) showed me a crowd of Himalayan Vultures feeding on the carrion of a mule. The picture gave me a sigh of relief because I found the capture method from his picture, and the first trapping idea emerged: a *bait spring-net trap*. Mr. Lungten (another colleague at the Institute) collected a dead bird from a dumpsite site of rejected meat, poisoned with borax, and the second trapping idea was born: a *pit-bait trapping method*. In conversations with herders and farmers, their stories revealed another catching method which is to *dash-catch over fed vulture*, or the *feed-grab method*, while vultures are eating large carrions.

The ultimate best capture technique was a collapsible steel-frame reinforced *wire mesh cage trap* (6 x 6 x 40ft). This cage trap was laid with a whole carrion or body parts with open doors on its sides. When an adequate number of vultures walked into the cage to feed on carrion, the doors were pulled to shut. In order to capture more birds, the cage was partitioned keeping trapped vultures on one side and baited more vultures to walk in on the open opposite side.

Most vultures were captured using the cage trap, however the first vulture (3200m, Pelela, Bhutan) was captured using the *dash-catch* method. The over-fed vulture (JigDor 4003) was chased uphill into the forest and caught by hand. NgangKa (4002) was caught using the familiarization feeding technique. NaZhoen (3922) was rescued upon a fall from a breaking tree branch that it tried to perch on. In case no capture techniques had succeeded, I had the imagination to wear a helmet and lay myself on the ground with a layer of meat spread over my body, and to catch those vultures come to feed by the neck.

**Benefits of using high resolution bio-loggers**

**Initial Findings:** Investigation of this species in its annual movements has been worthy to science. This initial analysis has resolved the non-migratory ambiguity even among veteran vulture experts in Asia who have been involved in biological studies (MaMing, 2016). It is for the first time that the migratory movements are proven beyond doubt.

In the survival analysis with respect to how environmental parameters affects mortality, it is found that individual vultures which may not be able to correctly handle abiotic environmental conditions are more likely to die. This movement study also provides evidence that the north-south and east-west movement range is extending. However, records of vagrants beyond the current result need to be observed in southeast Asia to ascertain our hypothesis.
**Calling for more data and further research:** From September 2014 to February 2015, 22 Himalayan Vultures were back-packed with eOBS GmbH loggers and 11 birds have been alive into their second year of data collection data. The analysis performed to compile this thesis has been very elementary, but this huge volume of data demands further rigorous analysis to document the stories of vultures’ telling to humanity by the way of collecting data on their own. Many more questions can be asked to the same data set.

The data gathered by the vultures have the potential to validate old migration and navigation theories. Based on the high definition flight data, our results can be used for the prediction of thermals in a landscape. We can also show how vultures use landscape cues to find thermals, understand how they find food and communicate to other members of the flock or any other vultures in an area, as well as understand aspects of social interactions and predict when they get hungry after the last feeding bout.

However, in this batch of movement observations, as we have only equipped immature or sub-adult Himalayan Vultures, we strongly recommend to equip breeding adults with state of the art biologgers to likewise understand the annual movements performed by the experienced and older birds. Data accumulated from the current research will currently only enable us to only understand the annual movements with the potential to delve into the ontogeny of movement in the immature or sub-adult age band. We do not have data to compare and contrast movement characteristics of adults to our data from immatures and sub-adults. Depending on survival of tagged vultures and the functionality of solar-powered biologgers on vultures, we may not be able to collect movement data for many years.

**Asia-wide collaborative conservation efforts**

Vultures across the globe are a highly threatened species. 16 of the 23 vulture species are threatened towards extinction. Their scavenging habits have been providing enormous cleaning services in nature by feeding on dead and decaying carcasses which otherwise rot and may lead to the outbreak of diseases. Being a scavenger and a migratory species, vultures are bound to traverse large swaths of land, extending movements over numerous national boundaries. Central to its wide range movements and threats faced by vultures, our results call for a collaboration among the range countries to effectively contribute to the birds’ long-term survival. Securing the Himalayan Vultures’ winter and summer areas
including breeding sites and colonies may not be adequate to safe the species. Instead, conservation management along the migration corridors deserves attention.

Other than wild ungulates, livestock form a major food source for vultures. Therefore, encouragement of livestock rearing with best practise husbandry management will be important for saving vultures. Abandoning the use of mortality-causing NSAIDs (diclofenac and nimesulide) in livestock must be continuously encouraged, and research in producing non-lethal NSAIDs for use in livestock management would be of importance. Livestock rearing and nomadic pastoral livelihoods must be encouraged if vulture conservation were to be successful.

In the countries where sky burial cremation practises are prevalent, such culture must be encouraged and continued as it is the best form of ecological practise. If sky burial practises are continued, human corpses would be the ultimate sustainable food resource for vultures. There may be a need to raise awareness to avoid administering NSAIDs in people nearing to death whose body will be disposed to vultures.

At last

My name is simply Sherub. To publish in international journals, I had to have a given and a family name, so I doubled up my name and I am now known in the literature as ´Sherub Sherub´, abbreviated as: S. Sherub.

6. Permits and animal ethics statement
The Ministry of Agriculture and Forests, Bhutan approved this study (UWICE/ADM/20/201-12/998). Royal Civil Service Commission, Bhutan, letter of award (RCSC/HRD(8.00)2014/975, LTA-38935).

7. General acknowledgements
I am indebted to the space resource in its entirety which allows life and movement to happen.

To the Tsa Wa Sum (the King, Country and People) of Bhutan my sincere gratitude for having taken leadership to maintain resources that our landscape is bestowed with for any Bhutanese to perform a meaningful study with the core intent to develop research
competency. As a citizen, my humble submission to the Constitutional Monarchs (His Majesty the 4th Druk Gyalpo Jigme Singye Wangchuck and the 5th Druk Gyalpo Jigme Khesar Namgyal Wangchuck) for their exemplary conservation leadership.

The Royal Government of Bhutan is acknowledged for permission granted to me of the study opportunity offered by the Max Planck Institute for Ornithology (MPIO), Vogelwarte Radolfzell at the University of Konstanz, Germany. Professor Dr. Martin Wikelski (also the Director), MPIO for having taken me as his fellow student from the remoteness of the Himalayas. Without Martin’s unfailing support in terms of resources and advisory, I would not have learned so much of what I know of the Himalayan Vulture (Gyps himalayensis) today. You have really educated me to say ‘I do not know’ from this simple research I performed with your guidance. I discovered that my knowing of nature had been from little observation, hearsay and extrapolated, not from careful observations and in-depth experiential exposures. To you, Professor Martin, I know that my humble salute and submission of thanks is not adequate. I can only remain to be working with you in wildlife movement research to further document and understand movement phenomena in the Himalayan part of the mother earth’s face.

Professor Gil Bohrer, Ohio State University is recognized for all his guidance and help in atmospheric aerodynamics in flight or moving objects in the air. Similarly, Rolf Weinzierl is appreciated for his advises and lessons in mathematics.

In the Royal Government of Bhutan: Lyonpo Yeshi Dorji, Minister, Ministry of Agriculture and Forests, Dasho Sherub Gyeltshen and Dasho Tenzin Dhendup former Secretaries of the ministry, Dasho Chencho Norbu (then Director General, Department of Forests and Park Services), National Environment Commission, are acknowledged for their valuable support and guidance. Nawang Norbu (PhD), Director, Ugyen Wangchuck Institute for Conservation and Environment Research (UWICER) is highly appreciated for his immense support in any matters related to achieving this studies without any glitches in the field. Without Nawang’s grandeur, this work will not have shine to this level of science. The colleagues at the UWICER: Mr. Ugyen Tenzin is thanked for being my second arm in performing field work in this study effort. Mr Rinchen Singye is appreciated for his assistance in the field work and most importantly showing me a photograph of Himalayan Vulture feeding on the horse carrion. It was his photograph that boosted imagination of how easy is to capture vulture. I am very much obliged to Mr. Tshethub Tshering, Mr Karma Wangdi, Mr. Jigme Dorji, are Mr. Leki Dukpa for bearing the winter cold at Pelela (2014-2015). Mr. Tshering Tempa and all other colleagues at the UWICER are recognized for their occasional field visits at the research
camp and moral support. Mr. Tshewang Dorji is indebted for his timely release of funds for the field works. Dechen Tshomo and her crew of administrative staff are also appreciated for their administrative support. Mr. Ugyen is thanked for sharing information of a dead mule in his village. This mule is appreciated for bringing hundreds of vultures and easing capture for our tracking experiment. My thanks is also expressed to Peurey, whose carcass captured four vultures at the beginning of field work.

At the MPIO, my sincere gratitude are to Wolfgang Fiedler for providing a training on managing the eObs GmBH tags, and Sarah Davidson for her involvement in data preparation. Bart Kranstauber, Andrea Flack, Yachang Chen, Reyes Fernandez, Wolfgang Junkermann for their stimulating discussions. Andrea Flack (Postdoctoral Fellow) and Rafa (a visiting doctoral student from Spain) are thanked for their unending assistance to my R power. Dr. Xiolae (visiting scholar) and Ms Yachang Chen are much appreciated to find sky burial sites within the movement range of the Himalayan Vulture. At the MPIO, Vogelwarte Radolfzell, Jennifer Globol and Elke Henkenhaf receive my humbleness for their kind assistance in any kind of administrative efforts.

My family members are immensely thanked for.
8. Declaration of Author Contributions

Authors’ contributions. Sherub and Martin Wikelski conceived and designed the project, together with input from David Wilcove and Nawang Norbu.

CHAPTER 2. Bio-Logging – New Technologies to study conservation physiology on the move: a case study on annual survival of Himalayan Vultures
Sherub: conceived and designed the study, performed all analyses and wrote the manuscript.
Wolfgang Fiedler: helped with the download of all tag data, contributed to the design of the study and to finalizing the manuscript.
Olivier Duriez: contributed to the design of the study and provided valuable feedback on the manuscript.
Martin Wikelski: helped to design and conceive the study, and contributed to finalizing the manuscript.

CHAPTER 3. Flight characteristics of Himalayan Vulture (Gyps himalayensis) during their annual movements across Asia
Sherub: conceived and designed the study, performed all analyses and wrote the manuscript.
Martin Wikelski: helped to design and conceive the study, and contributed to finalizing the manuscript.

CHAPTER 4. Behavioural adaptations to flight into thin air
Sherub: conceived and designed the study, acquired data, helped with the analyses and drafted the writing of the manuscript, revised and finalized the manuscript.
Rolf Weinzierl: analyzed the data, co-drafted the manuscript, revised and finalized the manuscript.
Martin Wikelski: conceived and designed the study, revised and finalized the manuscript.
Gil Bohrer: analyzed the data, co-drafted the manuscript, revised and finalized the manuscript.
9. References


Alerstam T, Christie DA (1993) Bird migration. Cambridge University Press,


Phipps WL, Wolter K, Michael MD, MacTavish LM, Yarnell RW (2013) Do power lines and protected areas present a catch-22 situation for Cape vultures (Gyps coprotheres)? PloS one 8 (10):e76794


Wilcove DS (2008) No way home: the decline of the world's great animal migrations. Island Press,


10. List of Publications

During the PhD Studies at the University of Konstanz:


Edmund Gittenberger, Sherub S, Björn Stelbrink (2017) Erhaia Davis & Kuo (Gastropoda, Rissooidea, Amnicolidae) also in Bhutan. ZooKeys (13326).

During the time prior to my PhD Studies at the University of Konstanz:

i. Multimedia Birds of Bhutan Wed Application (http://birdsofthehimalayas.herokuapp.com/2015).- **Lead Author.**


xvii. A report on High Altitude Wetlands in Bhutan under the umbrella project of “Saving the Wetlands Sky High” initiative. -- Lead Author
xviii. An audio CD title ‘bird songs of bhutan’ vol II, 10th October 2011. It contained songs from 396 bird species in Bhutan. A dedication publication on the occasion of the Royal Wedding of our 5th Druk Gyalpo. -- Author


xx. An audio CD titled ‘bird songs of bhutan’ vol I, 5th June 2010. It contained songs from 108 bird species. -- Author


xxvii. Ornithological Survey in Bhutan, published in Issue 1, Drukja Yig Sel (Bhutan Bird Newsletter).


xxix. Feasibility Study on Mitigation of Flooding by Mao and Taklai Rivers in Bhutan (Feb-July 2004). This report was presented to the Council of Cabinet Ministers (CCM) at 1400 hours on 1st March 2005. -- Author


11. Curriculum Vitae

1. BIODATA
   i. Name: Sherub Sherub,   ii. Birth Place: Bhutan,   iii. Nationality: Bhutanese

2. FOREIGN COUNTRIES VISITED & INTERNATIONAL PARTICIPATION
   i. Regional Meeting in Black-necked Crane Conservation in Arunachal Pradesh, India (January 2015)
   ii. Regional Meeting in Black-necked Crane Conservation in Xining, China (July 2014)
   iii. Regional Meeting in Black-necked Crane Conservation (23-24 April 2011), New Delhi, India.
   v. Research field visit to Indian states of Assam & West Bengal (Dec. 23 2006 – Jan. 7 2007).
   viii. Autonomous Region of Tibet, People’s Republic of China (July 2000) for *Grus nigricollis* (Black-necked Crane) banding research in the western China at the summer breeding grounds organized by the International Crane Foundation, Baraboo, Wisconsin, United States.
   ix. Malaysia (October 1999) to attend the Birdlife International World Conference at Kuala Lumpur.
   x. Indian states of Madhya Pradesh & Utter Pradesh on study tour on tracking tigers (May-June 1999).

3. MEMBERSHIP OF ENVIRONMENTAL SOCIETIES
   i. International Crane Foundation (2003-till date).

4. EDUCATION
   i. 2014- till date A PhD candidate. Max Planck Institute for Ornithology- University of Konstanz, Gemanay
6. RELEVANT COURSES COMPLETED AS A COMPONENT OF;


b. B.Sc (general).

Applied Entomology, Animal Physiology, Plant Taxonomy and Ecology, Plant Physiology, Chemistry (organic, inorganic and physical), English and Dzongkha.

7. ADDITIONAL TRAINING AND RELEVANT EXPERIENCES

a. Trainings and Seminar

i. Training on Natural Sound Recording and Analysis, 12-18th June 2010, Sierra Nevada-California, USA. Organized by Macaulay Library of Sounds, Cornell Laboratory of Ornithology.


iv. NCBS-NCF Workshop on Laboratory Techniques in Conservation Biology: Conservation Genetics and Carnivore Diet Analysis, organized at National Centre for Biological Sciences, TIFR, Banglore, India from April 9-12, 2007.

v. Power Point presentation on “Ornithological studies in Bhutan and importance of Ornithology in Forestry Institute” at the National Level Stakeholders Consultative Workshop for Ugyen Wangchuck Environmental & Forestry Institute (UWEFI) Program Development, 4-5th July 2006, Royal Banquet Hall, Thimphu, Bhutan. The workshop’s objective was: to identify various training needs at the forest Rangers and forest Guards level in the forestry and environmental sector through close consultation with the relevant stakeholders and institutions.

vi. Attend the Core Working Group Retreat 7-9th July at Natural Resources Training Institute (NRTI), Lobesa for the development of new curriculum for UWEFI based on NRTI’s modules.
vii. 20th International Seminar on Forest and Natural Resources Administration and
Management August 22nd through September 9, 2004. Colorado State University,
College of Natural Resource, Fort Collins, Colorado and The United States
Department of Agriculture, Forest Service International Programs.

viii. Attended a workshop on Migratory Waterbirds in Asia to (i) conclude and endorse
the proposed Central Asian Flyway Action Plan to Conserve Migratory Waterbirds
and their Habitats (10-13 June 2005, New Delhi, India) and (ii)endorse the
proposed Western/Central Asian Site Network for Siberian Cranes (and other
waterbirds) (12 June 2005, New Delhi, India).

b. Surveys and Research (others)
i. Transboundry movement studies of Black-necked Crane (Jan 2010-ongoing), in
collaboration with Max Planck Institute of Ornithology.

ii. Script for an awareness documentary titled “The Wangchuck Centennial Park,
December 2008.”

iii. Currently, I am leading the survey of totally protected species of flora and fauna
enlisted in Schedule I of the Forest and Nature Conservation Act, 1995, funded by
SDS through Biodiversity Conservation Project II. I am also the principal
investigator for listing and delisting bird species in the Schedule I of the FNCA,
1995.

iv. DNA sample collection for Langurs and Macaques with Dr. Aimi and Dr. Yoshi
Kawamoto, Japanese Primatologist, Kyoto.

v. Grus nigricollis (Black-necked Crane) banding research in western China
organized by International Crane Foundation (July 2000).

vi. Bird fauna survey in Bumdeling Wildlife Sanctuary, report submitted to Nature
Conservation Division.

vii. Avifauna survey in Thrumshingla National Park with Tim and Carol Inkipps from
U.K (Feb, 2000).

viii. Tiger & Leopard Depredation Survey in Jigme Dorji National Park (unpublished
report, August 1998).


8. CONTRIBUTION in SIGHTING NEW BIRD RECORDS to the BIRDLIST of BHUTAN

i. Ixobrychus cinnamomeus (Cinnamon Bittern). This new record was observed at
Dubjethang (4200m), Lingshi on 11 July 1999.

ii. Columba rupestris (Hill Pigeon). First time record at Lingshi proper on 13th July 1999.

iii. Sphenocichla humei (Himalayan Wedge-billed Wren Babbler). This secretive bird was
sighted at Chulongbi (650m), Lingmethang, Mongar on 1st January 2000.

iv. Porzana parva (Little Crake). This species was observed at Singye Dzong, Lhuntse
at an altitude of 3000m in September 2001.

v. Aegolius funereus (Boreal Owl). Rodugla, Lhuntse February 2001

vi. Gallirallus striatus (Slaty-breasted Rail). This species was sighted in a small wetland
by the Golf Course at Thimphu in May 2001. Two typeSs of its calls were recorded.
vii. *Esacus recurvirostris* (Great Thick-Knee). A breeding population of 13 birds were observed on 27th Feb. 2004, at Maokhola, Gelephu. Later this species was also sighted at in the riverbeds of Taklai Khola.

viii. *Vanellus malabaricus* (Yellow-wattled Lapwing). A pair was seen at Sheytkhari, Gelephu on 10th April 2004.

ix. *Bubo bengalensis* (Indian Eagle Owl). An electrocuted specimen was brought to me by the Bhutan Power Corporation on 22nd December 2004. Fortunately, this specimen was a new record for Bhutan. Performance of post-mortem confirmed the specimen as a female bird.

x. *Bubo himachala* (Eurasian Eagle Owl). A skin was examined to be identified as this species at Soejanggothang, Paro, on 21st February 2005.

xi. *Rostrula benghalensis* (Greater Painted Snipe). On 20th May 2005, this species was observed in the riverbeds of Taklai Khola.

xii. *Himantopus himantopus* (Black-winged Stilt). A juvenile was photographed at the sewage treatment plant at Babesa, Thimphu, on 13th September 2005. Bronze-winged Jacana was another new record for Bhutan observed in the same area by Peter Spierenburg.

xiii. *Dupetor flavicollis* (Great Bittern). On 20th October 2005, this species was observed along with Ram Bdr. Subba (a forester, currently in Phuntsholing Range).

xiv. *Ixobrychus sinensis* (Yellow Bittern). At Khuruthang, Punakha on 15th November 2005, this species was sighted together with Ram Bdr. Subba.

xv. *Podiceps nigricollis* (Black-breasted Grebe). During a monitoring survey of the White-bellied Heron, this species was identified at Lekithang, Punakha in November 2005.

xvi. *Dicaeum erythrorhynchos* (Pale-billed Flowerpecker). A smallest of the flowerpeckers in Bhutan was identified at Manas Range Campus on 14th May 2006, along with Dorji Wangchuk (RMNP).

xvii. *Prinia socialis* (Ashy Prinia). On 13th April 2006, in grassy woodlands of Kukulung, Royal Manas National Park, this species was a new observation to the birdlist of Bhutan.

xviii. *Pitta cyanea* (Blue Pitta). This magnificent bird was sighted in the southern foothills of Gortey, Royal Manas National Park, on 6th April 2006.

xix. *Pericrocotus cinnamomeus* (Small Minivet): On the 14th April 2006, three to four pairs were sighted on a shrub of phyllanthus in Special Thang, Royal Manas National Park.

xx. *Larus ridibundus* (Black-headed Gull). This species was identified as new record for Bhutan during the first Measuring, Monitoring and Mountain Biodiversity- Birds (M3B) training on 23rd November 2013. The bird flew over Drangme Chu towards Mathuguri from the Bhutan Manas.

xxi. *Gallinula chloropus* (Common Moorhen). Three individuals were observed in the back waters of dam-waters of Kurichu Hydropower station in Gyalpozhong on 23rd January 2015. It was observed during the second National Waterbird counted lead & organized by the UWICE in Bhutan.

xxii. *Lanius cullorioides* (Burmese Shrike). On 3rd April 2015, an individual of this species was mist-netted at Lamai Goempa. This netted bird was taken out of the mist-net by Mr. Ugyen Tenzin, one of the mist-net team member at the UWICE.

xxiii. *Charadrius leschenaultii* (Greater Sand Plover): Photographs of this bird species was taken on 30th June 2012 on the sandbanks of Chamkhar Chu. It is a passage migrant and a winter visitor.
xxiv. *Leucosticte brantii* (Brandt’s Mountain Finch): This species was observed between Rinchen Zoela and Methachutha, Wangchuck Centennial National Park in August 2008 the bird diversity survey in the park.

xxv. *Turdus maximus* (Tibetan Blackbird): In August 2008 a breeding pair with two juveniles were seen at Lunana, Wangchuck Centennial National Park.


xxvii. *Leptoptilos javanicus* (Lesser Adjutant): Chuzagang, Gelephu, Sarpang

xxviii. *Halcón pileata* (Black-capped Kingfisher): Samtang, Bajo, Wangdiphodrang


**Assisted to identify as new record for Bhutan**


ii. *Calcarius lapponicus* Lapland’s Spurwing. Sighted by Mr. Tshering Chophel (BWS) on 21st February 2013


v. *Spinus spinus* Eurasian Siskin. Sighted by Mr. Dorji at Bubja, Trongsa on 4th June 2013.

vi. *Pluvialis fulva* Pacific Golden Plover. Seen by Mr. Rinchen Singye at Khuruthang, Punakha on ----.

vii. *Callacanthis burtonii* Spectacled Finch. Observed by Mr. Heshey Tshering, Bhutan Birding & Heritage at Takti Kothri on ……


ix. *Anastomus oscitans* Asian Openbill. Sighted by Mr. Sangay Dorji at Dawathang, Chuzagang, Gelephu on 8th July 2014.

x. *Pholidus badius* Oriental Bay Owl. Observed by Mr. Tashi Dorji (Zhemgang Territorial Division) in Kikhar Forest Management Unit, Zhemgang on …….. A dead specimen was observed in Lhamoizhingka in September 2015.

xi. *Clamator jacobinus* (Jacobin Cuckoo) Mr. Rinchen Tshewang (Forest Range Office) Lhamoizhingka photographed a juvenile of this species on 15th September 2015.

xii. *Tyto alba* (Barn Owl). Seen by Mr. Kencho Gyeltshen (JDNP) at Zomlingthang, Punakha on …….

xiii. *Aviceda leupotes* Black Baza. Mr Dorji Wangchuk (RMNP) photographed this species in Gelephu on -------.

xiv. *Leptopoecile sophiae* (White-browed Tit Warbler). Observed by Mr. Tshering during a Snowman Trek around Laya, Gasa in ……..

xv. *Gallicrex cinerea* (Watercock). Mr. Tshering (Freelance Guide) sighted this species in small wetlands at Babesa, Thimphu.

xvi. *Halcyon capensis* (Stork-billed Kingfisher). Mr. Phub Dorji (JDNP) photographed this species on 10th November 2014 in Phuntsholing, Chukha.
9. AWARDS RECEIVED

1. JSWoesA 2015-Special Edition
2. India-Bhutan Foundation
3. CEPF
4. Received an International Student Research Award amounting to US $ 2000.00 from the Zoological Society of Milwaukee, Wisconsin to conduct field visit in Bhutan while pursuing M.Sc. at the University of Wisconsin-Madison, USA (May 2002).