Flight in nature II:
How animal flyers land

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ABSTRACT

In this review paper, different landing strategies of diverse species of animal flyers and gliders, both extinct and extant, are analysed. These methods vary depending on the animal group and the sensory system used by the animal to detect its landing site. In almost all species the use of delayed stall during the landing manoeuvre was observed. Sometimes wing flapping was used to aid in deceleration. With respect to guidance and navigation, most insect, bird and mammal gliders use their vision to guide them to landing via optical flow or motion parallax. Bats, which are nocturnal creatures, rely on their auditory system as they use echolocation to find their nesting site. Some butterfly and moth species guide themselves to landing using their olfactory sense as they follow pheromone trails. The information presented here can be used as a source of information for novel bio-inspired unmanned aircraft design.

NOMENCLATURE

τ indicator of time-to-contact (s)

x optical flow variable (m)

x rate of change of optical flow variable (ms^{-1})

1.0 INTRODUCTION

It is known that flight is a very successful form of locomotion in nature. Myriads of animal flyers have evolved to use this ability to gain access to new niches and food sources. Powered flight has evolved in four different animal groups and unpowered flight is seen in almost every group of living species. Because of this, scientists and engineers have studied them to find novel ideas and concepts for aircraft design, especially those involved in Unmanned Aerial Vehicles (UAVs). Some of them have already been discussed in the preceding paper[1]. Many more examples, however, can be given in other areas such as hovering, navigation, formation flight and energy harvesting.

Hovering is a desirable characteristic for UAVs that are used for surveillance and search and rescue operations. Usually they use methods that require high power because they do not exploit the advantages of flapping wings. However, Kurtulus, David, Farcy and Alemdaroglu have studied the aerodynamics of flapping motion during hover, both computationally and experimentally. Using a rectangular wing with a NACA 0012 aerofoil the authors were able to measure the wake of the flapping wing at Reynolds number of 1,000, observing the formation of leading edge, translational and rotational stopping vortices. Even though the computational simulation technique cannot accurately reproduce all vortex formations, accurate aerodynamic predictions could be obtained[2]. Within a different study, the symmetrical figure-of-eight wingtip path of a hovering humming bird has been reproduced and studied. By using a 25Hz electric engine and a cam-follower mechanism, Keshevan and Wereley have implemented a system that allows a diverse range of wingtip paths to be produced. The obtained results are very similar to observed flapping trajectory of the wings of hummingbirds (*Trochilidae* family) that hover. This mechanism presents itself as an option for the design of a hovering UAV[3].

Flying animals have also been used to improve the navigational characteristics of UAVs. One of the explored strategies is optical flow – the apparent displacement of the characteristics of the environment due to the movement of the observer. Optical flow is used by many animals in nature, including most flying insects and birds. Hrabar, Sukhatme, Corke, Usher and Roberts designed a combined optical-flow and stereo-based navigation system, with the objective of implementing it on a UAV capable of flying within canyons[3]. This was also attempted by Wang, Zang, Fan and Zhao, who combined optical flow with GPS, inertial navigation and laser range systems with the idea of improving the UAV's system performance. Results showed that the optical flow system permitted a better vertical positioning of the aircraft which benefits its landing performance[5]. Optical flow has also been adopted by Sanfourche, Delaune, Le Besnerais, De Plinval, Israel, Cornic, Treil, Watanabe and Plyer for environmental modelling and mapping. Using the visual input of a UAV, images are collected and processed to reconstruct the characteristics of the local ground to map the terrain. Additionally, combining the mapping with the flight performance information of the UAV, the system can also be used to know the aircraft's position. This is beneficial for aircraft flying in GPS-locked zones or uncharted territories[6].

Animal migration techniques such as formation flying can be advantageous in UAVs, especially to fly long distances and/or long endurance missions. Yun, Chen, Lum and Lee carried out a research study based on the advantages seen with this technique by designing a control system that permits

unmanned helicopters to follow a co-operative leader/follower flight scheme. Collision avoidance and other safety protocols were implemented to each UAV independently. Initial tests showed how a helicopter could follow a computerised leader without crashing[7]. Bennet and McInnes take formation flight further by developing a guidance algorithm that allows up to nine UAVs to fly in formation. Computational simulations show that all the aircraft can adequately follow different formation patterns in the three-dimensional space by controlling only two variables from the lateral and longitudinal equations of motion[8].

As a final example, energy harvesting will be considered. Current technology has not led to manmade objects capable of eating, and probably will never achieve this due to ethical and moral principles. It is possible, however, to mimic the energy harvesting techniques of flying animals and apply them to UAV design. In a study presented by Langelaan a method for extracting energy from wind gusts by unmanned aircraft is presented. The soaring aircraft is modelled using the complete longitudinal dynamic equations and the problem is solved with trajectory optimisation techniques. It is determined that usable energy is found in vertical wind components and its gradient. Taking this into account, a flight controller is designed such that it can take advantage of these variables. Simulation results show that the presented methodology can generate energy savings of 32% compared to non-soaring UAVs[9]. Based on Langelaan's work, Chakrabarty and Langelaan develop a methodology to plan long distance soaring trajectories that allow energy extraction from a known wind field. The methodology uses a technique called regenerative soaring in which a propeller is used to store the extracted energy by wind-milling. Realistic environments are simulated, which include the presence of ridges and information gathered from wind measurements. The constructed paths show that this method allows the UAV to follow energetically favourable trajectories that let it reach its goal[10].

Similar to what was shown in the preceding paper about animal take-off strategies, the examples mentioned above are applicable to cruising UAVs. It was observed, however, that animal flyer take-off techniques can be a source of innovation for unmanned aircraft design[1]. In this paper, focus will be given to the landing strategies of flying and gliding animals, with the purpose of inspiring bio-inspired solutions to UAV landing. The study will go through pterosaur, insect, bird, bat and gliding mammals. For this case gliding reptiles and gliding marine animals are omitted as information about their landing manoeuvre was not found or was insufficient.

2.0 LANDING IN INSECTS

This study starts with the landing techniques observed in insects. According to Dudley, the way in which the approach is performed usually varies between species, however the actions of the six limbs can be generalised for most flying insects. In approach, the prothoracic legs are extended forwards while the mesothoracic and metathoracic ones are extended backwards. On touchdown, no forward run is carried out, so the legs are responsible for the dissipation of all kinetic energy and absorption of the landing loads[11]. Nachtigall mentions that once contact is made with the ground the legs grip to it by the use of claws, spines and/or sticky paths called pulvilli. This prevents the animal from rolling after touchdown. Dragonflies, from suborder *Anisoptera*, and craneflies, from the *Tipulidae* family, are given as specific examples[12].

The first flying insect to be analysed is the fly. In a study carried out by Borst, the leg movements of the house fly (*Musca domestica*) are studied quantitatively in order to determine their exact landing procedure. On initial approach, the prothoracic and mesothoracic legs are folded below the body, while the metathoracic ones are stretched back. When the animal decides to land, the prothoracic legs start to extend forwards and the mesothoracic ones are lowered. After this, the

landing procedure follows Dudley's and Nachtigall's description. The sequence is depicted in Fig. 1 of Borst's paper[13]. In a similar study by Nachtigall, the procedure taken by an unspecified species of fly in landing on a ceiling – as shown in Fig. 47 of his work[12] – is described. In this case the approach has the same body posture as described by Borst, however in it the fly extends its forelimbs towards the inverted horizontal surface. After contact, the energy is dissipated by the legs which also anchor the animal to the ceiling. The residual momentum is then used to rotate the animal into its final position, in which all limbs are supporting the weight of the animal[12]. But what triggers the fly to land? According to a study by Fernandez and Taddei, who used the house fly as a test subject, landing is provoked by two different stimuli. The first is the expansion of the animal's surroundings as they rely on optical flow. The second is the change in the perceived light flux from the surface immediately in front of them[14]. In further experiments on the house fly, Wagner shows that the animal begins to decelerate when the expansion rate of the image in front of it reaches a specific value. According to his analysis, the deceleration is an indicator of the start of the landing process in the house fly[15]. The same conclusion is reached by van Breugel and Dickinson, by carrying out observations of the fruit fly (*Drosophila melanogaster*)[16]. Tammero and Dickinson, who also study the fruit fly, conclude that leg extension is also a specific characteristic of the animal preparing to land. Although variation in flapping frequency and amplitude is observed during the landing procedure, these actions were not specifically associated to it as they were also present when the insect carried out a collision-avoidance manoeuvre[17].

Now consideration will be given to the honey bee (*Apis mellifera*), a species whose landing manoeuvre is slightly different from the fly's. In an experiment carried out by Evangelista, Kraft, Dacke, Reinhard and Srinivasan, they observed how this bee landed on a surface with different inclinations. Preliminary analysis showed that during the approach they entered into a semi-hovering state, in which the animal decreased its altitude until getting to approximately 10mm to 15mm from the surface. After this, the honey bee began a stable hovering phase that ended when it extended its legs to land. Some differences were noticed when the inclination of the landing surface was varied. For inclinations between 0° and 30°, the hind- and middle legs were the first to make contact with the floor. Then, up to an inclination of 120°, the front legs are also used during touchdown. From here, initial contact is made by the front legs. Figure 1 shows sample pictures of the honey bee landing in horizontal, tilted and inverted positions. An important observation from all landing scenarios is that the insect always touches the surface with their antennae before touchdown, suggesting that they use these to identify its inclination. The research concludes by suggesting the use of optical flow and stereo-vision in order to determine when to enter into the semi-hovering and hovering phases[18]. The use of visual guidance for landing in the honey bee, suggested by Evangelista *et.al*, has been studied by several researchers. According to Ibbotson, flight deceleration in this species is related to visual cues. According to his observations, translational visual-flow fields are used to control flight speed when landing, meaning that the animal uses optical flow[19]. On a separate research project also related to *Apis mellifera*, Srinivasan, Zhang, *chahl*, Barth and Venkatesh study the way in which visual cues are used in altitude control. Their analysis shows that these bees commence landing by descending at steep angles, between 22° and 41°. After this, altitude variation is controlled by having a descent speed that maintains the angular velocity of the ground's image at a constant value, which is consistent with the use of optical flow. Because of this, altitude variation will have an exponential behaviour, which relates to the observations made by Evangelista *et al*. To conclude their study, the authors suggest that the animal knows when to extend its legs by the felt reduction in thrust or by sensing the proximity to the ground[20].
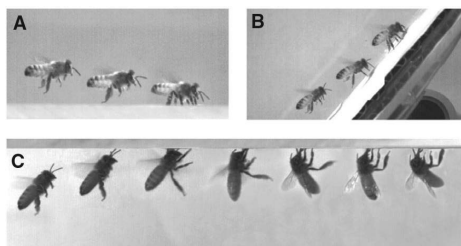
Figure 1. Honey bee landing in surfaces with different inclinations[18] Reprinted from 'The moment before touchdown: landing manoeuvres of the honeybee Apis mellifera', by C. Evangelista, R. Kraft, M. Dacke, J. Reinhard and M.V. Srinivasan, 19/1 Figure 1 Honey bee landing in surfaces with different inclinations[18] Reprinted from 'The moment before touchdown: landing manoeuvres of the honeybee Apis mellifera', by C. Evangelista, R. Kraft, M. Dacke, J. Reinhard and M.V. Srinivasan, 19/10/2009, *Journal of Experimental Biology*, **213**, (2), page 265, Copyright 2009 by the Company of Biologists Ltd. Reprinted with permission. 0/2009, *Journal of Experimental Biology*, **213**, (2), p 265.

Now focus will be given to butterflies and moths, which are also of interest in this study. No specific information on the dynamics of their landing was found, so it is assumed that they follow the general procedure stated earlier. They do present, however, an interesting variation in the way in which landing is triggered in them. In a study made by Foster and Harris on the light brown apple moth (*Epiphyas postvittana*), it was determined that the olfactory system led the animal to its landing site as it followed the pheromone trails produced by plants. When the moth was near the desired landing site, it used visual cues, like geometry and size, to finally decide where to land[21]. This was later confirmed by Rojas and Wyatt with a study of the cabbage moth (*Mamestra brassicae*), which showed that the animal would follow the pheromone trail, but would not land if there was no leaf present[22]. In a different study the Japanese yellow swallowtail butterfly (*Papilio xuthus*) was the test subject and Koshitaka, Arikawa and Kinoshita demonstrated that this species identifies its landing site by the colour contrast of the targeted landing site. In the absence of it, the animal is unable to land[23].

To finalise insect landing, the praying mantis (*Mantis religiosa*) will be explored. Hyden and Kral studied this insect and found it carried out a side-to-side head movement, known a peering, before jumping. Analysis showed that this movement is performed by the insect in order to select its landing site prior to jumping. Variations in the visual field during this movement allow the animal to determine the edge of the landing site and thus know exactly where it wants to go[25]. The use of peering to determine the jump distance is known as motion parallax and its use has also been observed in locusts. Figure 2 gives an example of peering in a praying mantis that jumps towards a static landing site[24].
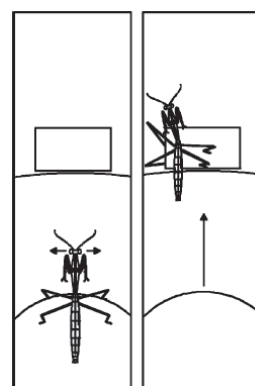
3.0 PTEROSAUR LANDING

Pterosaurs are the only extinct flying animal group that will be taken into account in this study. Because of this, it is important to note that the information presented here is based on theories, fossil evidence and comparison to other extant flying animals. To begin, Bramwell and Whitfield studied fossil evidence of the *Pteranodon ingens* and came

Figure 2. Peering movement of a praying mantis[24]. Reprinted from 'Behavioural-analytical studies of the role of head movements in depth perception in insects, birds and mammals', by K. Kral, 29/08/2003, *Behavioural Processes*, **64**, (1), p 3.

to several conclusions on how they managed to land. Due to its large mass, this animal should have landed into the wind on cliffs. They believe that the legs would not be able to absorb the landing impact, meaning that they should carry out a belly landing. The authors support this theory by saying that, at the time, ferns populated the grounds instead of grass. Also, the *Pteranodon ingens* would have had long fur on its chest. These two elements would be able to absorb the landing impact. Another characteristic of the *Pteranodon ingens* that is analysed is the head crest; its large area could be used as an airbrake, but to use it the animal should have to tilt its head. This action could only be performed a few seconds before touch down, at which point the animal should look forward again to see its landing site[26].

Landing in cliffs would have been common for pterosaurs; however fossil evidence shows that pterosaurs also lived in continental areas away from cliffs[27]. Taking this into account, Fastnacht analyses the fossil findings of a young pterosaur from the *Dsungaripteridae* family found in Oker, Germany; a location with no nearby cliffs. The remains were so well preserved that the three-dimensional characteristics of the leg bones could be studied. Results showed that the bones had the capacity to resist compressive loads, which could imply that the animal actively landed on inland grounds and used its legs to absorb the impact[28].

Chatterjee and Templin are also supporters of the theory that pterosaurs landed using their legs. By modelling the body of an *Anhanguera piscator* and running some simulations with it, they conclude that this and other pterosaurs could have landed with a bipedal stance followed by a short run. The bipedal stance is a result of the need to avoid injury to its wings. During approach, the animal decel-erated by increasing drag. This was accomplished by tilting its wings to a higher Angle-of-Attack (AOA), pitching its body up, deflecting the pteroid bone so it would act as an air brake, spreading its uropatagium and lowering the legs. Larger pterosaurs could have probably used their wings to flap and decelerate, or maybe even require a headwind approach[27]. The use of the pteroid bone has been experimentally demonstrated to work as an airbrake and as a means to maintain the airflow attached to the wing at high AOA[29]. Another study also by Chatterjee and Templin, this time based on fossil remains from the *Tapejara wellnhoferi*, supported their earlier findings. Additionally, after modelling the head crest of this particular species, it was concluded that it gave the animal enhanced control for complex manoeuvres including landing. Also, the identification of webbed feet in the animal provided it with a means for braking in air or landing in water by skidding[30].

Other interesting fossil findings support the theory that pterosaurs landed using a bipedal stance. Mazin, Billon-Bruyat and Padian study a set of pterosaur track-ways found in Crayssac, France, and concluded that the patterns are consistent with a landing site. From the findings it can be seen that the first tracks are elongated; this added to the fact that there are no other impressions behind them indicate that this is the place where the animal touched down. The elongation of the first track suggests the animal did not have a run after touchdown, but the forward speed was not nil. Also, the absence of hand prints indicates that the landing was bipedal. After this, the animal would lower itself to a quadrupedal stance and walk away, giving way to other landing pterosaurs. Figure 2 of Mazin's paper illustrates the proposed landing sequence[31].

4.0 BIRD LANDING

Previous sections describe the landing strategies of the two most complicated types of flying animals – insects which are difficult to study considering their small size and pterosaurs as they are extinct. Interesting results, however, have been observed and theorised. Now, focus will be given to birds, whose advantages in size and variety of living species have led them to be widely studied. Different to take-off[1], landing strategies do not have a significant correlation to animal size. Because of this, it is

not necessary to classify birds into size groups; instead, a general description will be given followed by the specific differences between species. The general landing manoeuvre of a bird is described by Jack as a gliding descent where the tail is lowered and spread fanwise to decelerate, followed by a quick change in flight configuration that leads the animal to stall; the latter is referred to as deep stall. This state is achieved at a flight altitude that allows the bird to drop to the ground without injuring its knees. Sometimes the birds may need the additional assistance of wing flapping to fully stop[32].

A species of bird that has been widely studied is the pigeon (*Columba livia*). In his book about bird flight, Headley describes the complete landing manoeuvre performed by this animal. The author reports that the bird commences landing by descending either by giving its wings an upward slope and slowly floating down or by flexing its wings and inclining its body downwards to rapidly lose altitude. When reaching the landing site, the pigeon will stretch its legs, tilt its body upwards and completely spread its wings so that its entire area is facing the wind. If the bird wants to carry out a sudden stop, wing flapping is also observed. In this case the body is nearly upright, which leads to think that the wings are moving horizontally. The animal reaches the ground by a short drop[33]. Figure 3 illustrates the pigeon's landing process prior to touchdown. In order to review how vision is used by pigeons to guide themselves through landing, Lee, Davies, Green and Van Der Weel study the variation of optical flow variables in them while approaching and alighting. They start by defining the optical flow variable Tau (τ), which is an indirect measurement of the time to contact of the bird with a static object. Equation 1 defines the value of Tau as the ratio between the optical flow variable x and its rate of change with time. Theory says that if the rate of change of Tau with respect to time is constant and between 0·5 and 1·0 the animal will be in a controlled-collision course. After filming pigeons in landing manoeuvre and analysing the behaviour of Tau in them, it was determined that it was held constant during touchdown. It was also found that during approach its rate of change with time was much higher than 0·5, but less than 1·0, meaning that pigeons land in a controlled-collision manner. These results evidence that *Columba livia* use optical flow to control their landings[34].

$$\tau = x/x \qquad \ldots (1)$$

Kral also studied the use of vision in pigeons. According to his findings, these birds also use the concept of motion parallax, mentioned in Section 2. From his observations, it was determined that pigeons bob their heads when approaching their landing site and this action is used to help the animal determine its flight speed[24].

Passing on to a slightly bigger species, Horton-Smith reports very similar behaviour to the pigeon in the Australian silver gull
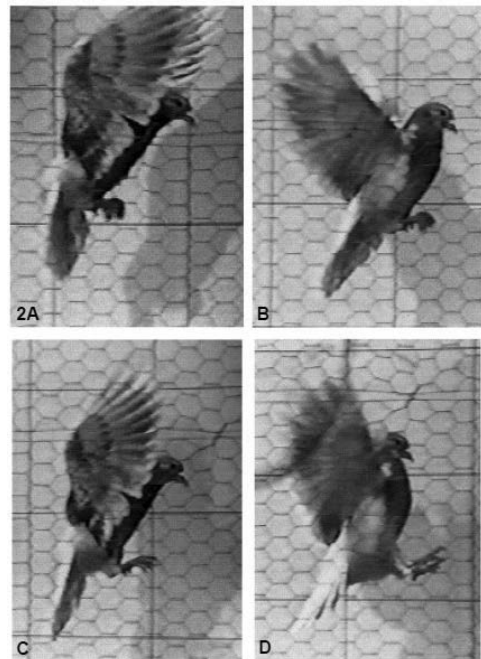
Figure 3. Perching sequence of the pigeon[34]. Reprinted from 'Visual control of velocity of approach by pigeons when landing', by D.N. Lee, M.N.O. Davies, P.R. Green and F.R. Van der Weel, 05/02/1993, *Journal of Experimental Biology*, **180**, (1), p 92.
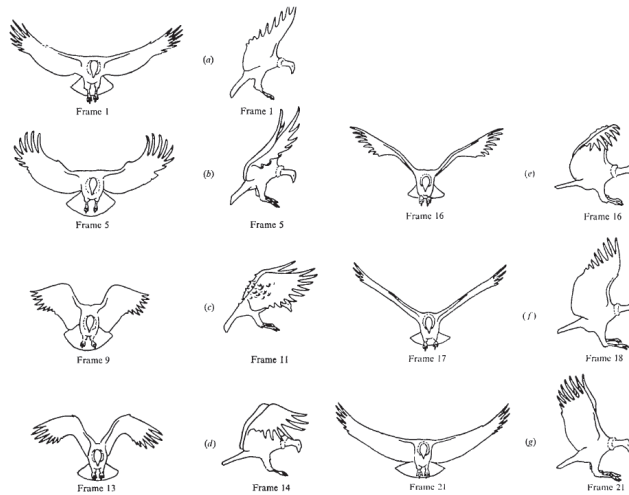
Figure 4. Wing beat cycle for a landing Andean condor[37]. Reprinted from 'Flapping flight of the Andean condor in nature', by J. McGahan, 25/04/1972, *Journal of Experimental Biology,* **58**, (1), p 241.
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(*Chroicocephalus novaehollandiae*) and additionally states that the flapping motion while landing is only performed when the gull overshoots its landing site as it is a corrective manoeuvre. Overshooting usually occurs in calm weather as there is no head wind to aid in deceleration. Other corrective actions seen in gulls include the extension of secondary feathers to increase the wing area. On the other hand, if the weather is gusty, the gulls have been seen to roll over one wing-tip to then sideslip to the ground[35].

Landing studies have also been conducted on larger bird species. One of these was carried out by Hankin, who published a book based on his observations of bird flight, which included their descent and alighting procedures. The first manoeuvre he describes is a leisurely descent; observed in white scavenger vultures (*Neophron gingianus*), common vultures (*Pseudogyps bengalensis*) and black vultures (*Otogyps calvus*); named metacarpal descent. In this scenario, the birds circled downward with reducing speed in a spiral of decreasing diameter. Wings were placed in a flexed position with maximum camber during this period and flexure angle was increased when facing winds. In some occasions the legs could be seen to hang down, presumably to aid in the reduction of speed. When the perch was near, the legs were dropped down (if not extended already), the body was pitched up and then it perched. On occasions the alulae feathers were extended. When the vultures wanted a more rapid descent, they used what Hankin calls carpal descent. In this case, instead of circling down, the bird greatly flexes its wings and descends nearly vertically. Throughout the entire procedure the alulae feathers are in forward position and the descent speed seemed to remain constant. When the animal finally extended its wings, the legs were dropped down and then it perched as in the metacarpal descent. When in carpal descent, sometimes the bird encountered strong winds that made it retire its wings backwards by twisting its shoulder, changing the position of the aerodynamic centre. This specific case is named shoulder descent. Adjutants (*Leptoptilus dubius*) were also observed performing the carpal descent, however they showed wing arching in order to descend instead of wing flexing. The final descent mode observed by Hankin, named stop descent, is basically a carpal descent but this time, immediately before perching, the birds flap their wings horizontally, bringing them to a full stop prior to dropping on to the perch. This manoeuvre is observed in vultures, cheels (*Milvus govinda*) and adjutants[36].
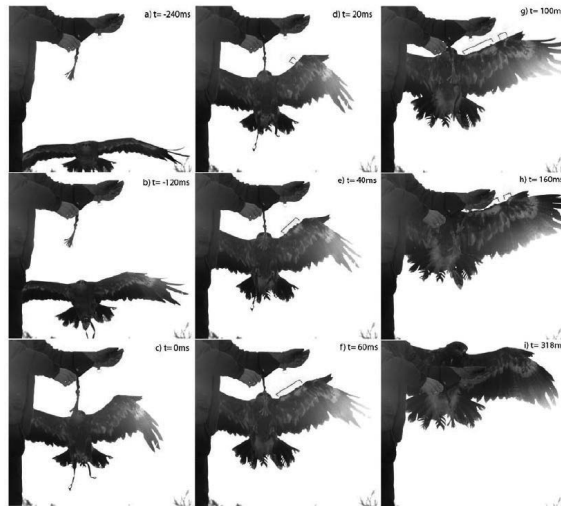
Figure 5. Landing sequence of a steppe eagle[38]. Reprinted from 'Use and function of a leading edge flap on the wings of eagles', by A.C. Carruthers, G.K. Taylor, S.M. Walker and A.L.R. Thomas, 2007, 45th AIAA Aerospace Sciences Meeting and Exhibit, Reno, NV, USA, p 5.

Continuing with the larger species, McGahan carries out a study of the flapping movement employed by the Andean condor (*Vultur gryphus*) in several stages of flight, including landing. From his study it is determined that during landing the wings are always positioned over the body so that they will not interfere with the perch at touchdown. During the upstroke the elbow and wrist flexure are higher. In the downstroke the pitch of the body increases while changing the AOA to increase the lift produced in order to compensate for the reduction in speed. The alulae feathers are also extended to help prevent flow detachment. Body pitch is lowered on the following upstroke and the pattern is repeated. Stall is reached near the perch, where the condor drops. Figure 4 shows a reconstruction of the observations made by the author[37].

Carruthers, Taylor, Walker and Thomas carried out an experiment using a steppe eagle (*Aquila nipalensis*) as a test subject to determine how it used the alulae feathers during unsteady manoeuvres, including landing, by installing video cameras on the animal's body and recording its wings during flight. The landing sequence of the eagle can be seen in Fig. 5. The authors identify three stages in the landing. The first – the approach – consists of a low glide near the ground with the wings fully stretched and possibly using ground effect. The second phase consists of a rapid pitch-up manoeuvre caused by wing and tail flexing as well as leg extension in the forward direction. During this phase the eagle gains some height. The final stage consists of a deep stall, where the tail is fully flexed down and the wings are fully extended and with high AOA. The authors believe that this configuration works more like a parachute than as a lifting device. Video analysis shows that the alulae feathers are used during the end of the second stage and throughout all of the third[38]. In a different study, Carruthers, Thomas and Taylor deepen the analysis made with a similar experimental setting. Here, the authors now report the deflection of the lesser underwing and upperwing covert feathers simultaneously with the deployment of the alulae mentioned earlier. Other observations include the fact that the eagle landed into headwind and when no headwind was available, the animal used wing flapping to aid deceleration. When flapping was used, it was usually seen only during the approach stage. A flapping perching sequence is shown in Fig. 6[39]. In a later paper, Carruthers, Thomas, Walker and Taylor say that

Figure 6. Flapping perching sequence of a steppe eagle[39]. Reprinted from 'Automatic aeroelastic devices in the wings of a steppe eagle Aquila nipalensis', by A.C. Carruthers, A.L.R. Thomas and G.K.Taylor, 11/09/2007, *Journal of Experimental Biology*, **210**, (23), p 4142.

in order to carry out the pitch up manoeuvre, the eagle must morph its wings considerably so they take the form of the letter M. Morphing is also achieved by the deflection of all the control feathers mentioned above[40].

Regarding nocturnal birds like barn owls (*Tyto alba*), it is known that they rely on their auditory sense instead of vision in order to locate their prey. Several studies, like the one from Hausmann, Plachta, Singheiser, Brill and Wagner, show how they use variations in sound waves in order to detect their prey and land over or near it. Although specific techniques are not given, it is said that variations in the sound source can be used to correct the flight path, given that they are perceived within a proper reaction time[41].

Other, less common methods of landing are also presented. For example, Pennycuick has spotted how birds from the *Alcidae* family, which nest on the edges of cliffs, land. He says that they descend following a ballistic trajectory that is levelled out below the cliff edge with excess speed. After this, the bird rapidly pulls up turning kinetic energy into potential energy; that is the bird gains altitude. If the bird makes an accurate judgement of its needs, it should be able to reach just above the cliff edge and safely drop to the ground[42].

Norberg and Norberg describe the landing procedure of the aquatic red-throated loon (*Gavia stellata*). The bird starts to descend with a steep glide, sometimes accompanied by sharp turns that help with the reduction of speed. As it approaches the water the bird levels off so that it remains approximately 0·5m above the surface, point at which the wings are raised and flexed. The body is inclined upwards and tail is flexed downwards to brake. After some time, the bird extends its feet so that they touch the water to further decelerate. This is shortly followed by the tail making contact with the water for the same purpose. As speed decreases, the loon pitches its body forward until it attains a horizontal position in which the lower body is on the water surface[43].

To end this section, the plunging technique of the northern gannet (*Mallotus villosus*) will be described. Although this technique is mostly used for foraging rather than landing on water, it does represent a culmination of the flight stage of the bird. Garthe, Benvenuti and Montevecchi observed that, after plunging vertically from a considerable height, the gannet will carry out either a V-shaped dive or a U-shaped dive. Descent rates suggest that in occasions the bird accelerates to increase its speed before entering the water. The type of dive depends on the fish species that the bird is attempting to catch. V-shaped dives are relatively short, having a mean of 3·5m and lasting no longer than 8s. After reaching the maximum depth, the animal would immediately turn back up toward the water surface. U-shaped dives were longer, with 5·2m mean depth, and usually lasting over 15s. Once underwater, the gannet sometimes flapped in order to reach further down to catch its prey, as well to resurface. In this case the bird decelerates to zero speed at the end of its dive and then turns back up, following a parabolic trajectory[44].
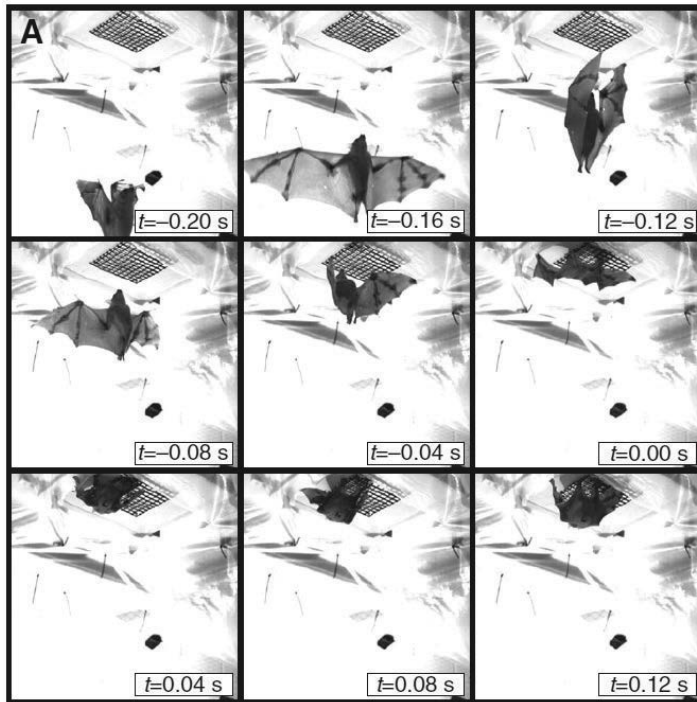
Figure 7. Four-point inverted bat landing.46 Reprinted from 'Bats go head-under-heels: the biomechanics of landing on a ceiling', by D.K. Riskin, J.W. Bahlam, T.Y. Hubel, J.M. Ratcliffe, T.H. Kunz and S.M. Swartz, 17/01/2009, *Journal of Experimental Biology,* **212**, (7), p 948.

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5.0 LANDING IN MAMMALS

To finalise this study, the landing strategies of both flying and gliding mammals will be discussed. Analysis will start with bats, which carry out powered flight, followed by gliding mammals.

Most bats are known for landing in an inverted position. Pennycuick describes this manoeuvre in a general way. He says that it consists of the bat attaching its claws to a ceiling or branch from which it can then rotate into an inverted hanging position. The manner in which the bat approaches the landing site varies between species[42]. Norberg and Rayner complement this by saying that some bats can accommodate their posture by rotating in flight and grabbing their roosting place in an already inverted pose. The bats capable of doing this have rounded wingtips because this geometry allows rolling at low speeds[45].

More specific studies have also been conducted. Riskin, Bahlman, Hubel, Ratcliffe, Kunz and Swartz studied the inverted landing dynamics of three different bat species; the lesser short-nosed fruit bat (*Cynopterus brachyotis*), the Seba short-tailed bat (*Carollia perspicillata*) and the Pallas long-tongue bat (*Glossophaga soricina*). Two different landing manoeuvres were observed. The first one, named four-point landing and depicted in Fig. 7, consists of an approach to the ceiling with the wing partially folded and the limbs extended laterally. When the bat made contact with the surface, claws and thumbs were used to grab themselves with a belly-up posture. The landing terminated when the forelimb thumbs released the webbing and the bat ended in an inverted position. The second type of landing, named two-point landing and shown in Fig. 8, began with
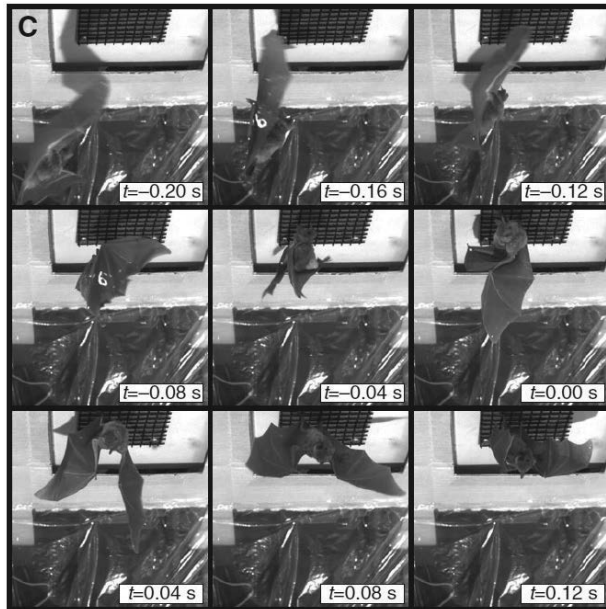
Figure 8. Two-point inverted bat landing.46 Reprinted from 'Bats go head-under-heels: the biomechanics of landing on a ceiling', by D.K. Riskin, J.W. Bahlam, T.Y. Hubel, J.M. Ratcliffe, T.H. Kunz and S.M. Swartz, 17/01/2009, *Journal of Experimental Biology*, **212**, (7), p 948.
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the bat approaching the ceiling with an increase in body pitch. Afterwards it carried out a yaw rotation, either positive or negative, until the legs were above the head. The inertia of the animal led it to the ceiling where it grabbed hold by using its claws[46].

Due to the location of their food sources, some bats are required to land on the ground. This is the case of the vampire bat (*Desmodus rotundus*), which feeds on the blood of large animals living on the ground. After descending in the same way as previously described, the bat enters into a quasi-hovering stage over the place where it wants to land. This is followed by a lowering of its forelimbs so that they are oriented towards the ground. The elbows begin to flex and then the hands make contact with the ground. As the elbows continue to flex, the body starts to rotate downwards until the hindlimbs also reach the ground. This is essentially the reverse of the process utilised during the take-off. If the vampire bat wishes to land on a vertical surface, it first needs to carry out a pitch up manoeuvre after it has completed the approach. Flapping is used to decelerate before making contact with the wall. Elbows will be minimally flexed to improve shock absorption and the four limbs will reach the surface simultaneously. Figure 9 shows the landing sequence of a vampire bat landing on a horizontal surface[47].

Hankin carried out some observations in the landing process of the bat species known as the flying fox (*Pteropus medius*), which must also land on the ground. The bat begins its landing procedure by a gliding descent, in which its wings are configured to have the maximum camber. Even though it is losing altitude there is no increase in speed; in fact it sometimes was observed to decelerate. Before perching, the wings were stretched forward while still maintaining maximum camber. The forward wing movement produces a pitching rotation that increases the angle of incidence. It also results in the feet spreading as they are linked to the wings. Just before landing, the legs are brought together and advanced[36].
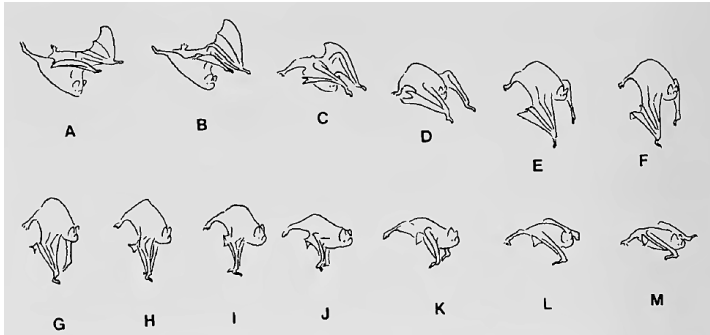
Figure 9. Horizontal landing sequence of a vampire bat[47]. Reprinted from 'Locomotor morphology of the vampire bat Desmodus rotundus', by S. Altenbach, 22/08/1979, The American Society of Mammalogists, Special Publication, (6), p 50.
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The inverted and horizontal landing methods for bats have been explained. Now consideration will be given to the guidance aspects of landing. Bats are mostly nocturnal creatures, so it is possible that they cannot fully rely on their sight to choose an ideal landing location. To study this, Tian and Schnitzler investigated the use of echolocation in the greater horseshoe bat (*Rhinolophus ferrumequinum*) when approaching and landing. It was found that the bats emitted double sound pulses to locate their landing site and this was followed by more pairs of sounds. As the animal reduced its speed, the frequency of the sounds was increased to compensate for Doppler effects. Also, as the animal approached the landing site, the duration of the sound pulses was reduced. These results evidence the use of sound to guide the animal to its landing place[48]. On a similar study, Siemers and Ivanova determined that other species of horseshoe bats also use echolocation to land on the ground and capture moving prey. The species included in this study were the Blasius horseshoe bat (*Rhinolophus blasii*), the Mehely horseshoe bat (*Rhinolophus mehelyi*) and the Mediterranean horseshoe bat (*Rhinolophus euryale*)[49]. Melcón, Denzinger and Schnitzler report a similar behaviour in the Natterer bat (*Myotis nattereri*)[50] and the greater mouse-eared bat (*Myotis myotis*)[51]. Koblitz, Stilz, Pflasterer, Melcón and Schnitzler also prove that the big brown bats (*Eptesicus fuscus*) use echolocation in order to reach their landing site, with the added contribution that the animal only utilises the sonar signal from their target, without being influenced by other sources[52]. Yovel, Geva-Sagiv and Ulanovsky show that the Egyptian fruit bat (*Rousettus aegyptiacus*) also uses echolocation to target its landing site, but uses its tongue to create the sound instead of the larynx. They propose that this is a characteristic of all bats from the *genus Rousettus*. Results show that this tactic is at least equally efficient as *laryngeal echolocation*[53].

Now consideration will be given to gliding mammals. In their work on the evolution of flight, Caple, Balda and Willis describe the general characteristics of the landing procedure of gliding mammals such as flying squirrels and flying lemurs. When the animal is approaching its landing surface it carries out a pitch-up manoeuvre, similar to the deep stall movement observed in birds, in order to reduce speed and lose momentum. After speed is reduced, contact with the surface is achieved, initially with the forelimbs, but closely followed by the hindlimbs after a quick body rotation, making it a quadrupedal landing[54].

Paskins, Bowyer, Megill and Scheibe carried out a study of the landing in the northern flying squirrel (*Glaucomys volans*) and their observations follow exactly the descriptions given by Caple *et al* and Templin. Additionally they mention that the tail is aligned with the body and that the head is tilted backwards immediately prior to landing while the tail was set parallel to the ground. All limbs touch the landing site simultaneously. Figure 10 shows the described landing sequence. In

Figure 10. Landing sequence of a northern flying squirrel[55] Reprinted from 'Take-off and landing forces and the evolution of controlled gliding in northern flying squirrels Glaucomys sabrinus', by K.E. Paskins, A. Bowyer, W.M. Megill and J.S. Scheibe, 12/02/2007, *Journal of Experimental Biology,* **210**, (8), p 1417.
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experiments conducted inside a barn, the squirrel was observed to pitch up less than before, which led the forelimbs to touch the landing surface first. After this, the body rotated until the hindlimbs also made contact with the landing surface[55].

6.0 BIO-INSPIRED LANDING APPLICATIONS

Up to now, several landing techniques of animal flyers and gliders have been studied. As it was mentioned by Jiménez and Smith, this information can be applied to the development of bio-inspired solutions for unmanned aircraft landing mechanisms if a given set of premises are followed[1]. In fact landing using delayed stall is already a common strategy for UAVs; it has been reported for the Aerovironment Raven and Pointer. When the aircraft is descending, it rapidly changes its AOA, such that it enters into stall. To avoid recovery, the UAVs have fixed stabilizer deflections which do not let it roll back to a proper position. As the aircraft is in stall, it will stop producing enough lift to fly, which will cause it to fall. To avoid reaching high speeds, these UASs have wings with large surface areas that will work as parachutes[56].

Other innovative landing strategies have also been implemented. One of them was developed by Ruffier and Franceschini[57]. In their research the authors develop a landing mechanism for a rotorcraft based on optical flow. The controller is configured such that when it is commanded to land, it will initiate a slow nose-up roll, which will reduce the horizontal velocity. Then, the optical flow controller will start reducing the flight altitude as it is set to maintain a constant horizontal-speed-to-altitude ratio. Results show smoother landing when using closed-loop laws. The authors do not specify the technical information of the optical flow sensor.

Optical flow has also been combined with inertial navigation in order to develop new landing strategies for unmanned rotorcraft. Hérissé, Hámel, Mahony and Russotto have developed a control strategy that allows a quadrotor to land safely on static and moving platforms using information obtained by optical flow[58] Inertial measurements are taken with the sole purpose to counteract unwanted rotations that occur on flight. Simulation results showed that correct landing were possible over static, oscillating and stochastically moving platforms. Experimental results

Table 1
Summary of landing techniques of animal flyers and gliders

Animal	Landing Mechanism	Wings	Tail	Legs	Sensory System
Fruit fly	Slow and decelerated descent, followed by short drop. Flapping stops when legs touch the ground	Frequency, amplitude, shape and wing path varied to control speed.	N.A.	Shock absorbers	Visual – Motion parallax
Bumblebee	Hovering descent, followed by short drop. Flapping stops when legs touch the ground	Frequency, amplitude, shape and wing path varied to control speed.	N.A.	Shock absorbers	Visual – Optical flow
Butterfly	Selects landing site, slow approach, short drop and wings shut	Frequency, amplitude, shape and wing path varied to control speed	N.A.	N.A.	Olfactory
Pterosaurs	Delayed stall with flaring, followed by a belly drop / Delayed stall with flaring, followed by a short bipedal drop	High AOA, maximum extension, no flapping and extension of the pteroid bone	N.A.	Retracted / Fully stretched	N.A.
Pigeon	Delayed stall with flaring, followed by a short bipedal drop	High AOA, maximum camber and flapping assistance for braking	Bent down and spread fanwise	Fully stretched	Visual – Optical flow
Eagle	Delayed stall with flaring, followed by a short bipedal drop	High AOA, maximum camber, deflection of alula and covert feathers and flapping assistance for braking	Bent down and spread fanwise	Fully stretched	Visual – Optical flow
Vampire bat	180° mid-air yaw rotation to grab roosting place / Delayed stall with flaring followed by a short quadrupedal drop	Partially folded, forelimbs extended laterally and anteriorly, hindlimbs Maximum camber. Rounded wingtips / Maximum camber. Parachute-like geometry for braking. Pointed wingtips	Stretched patagium	Feet rotated upward to grab roosting place / Pitchdown rotation so forelimbs touch the ground first	Auditory – Echolocation
Flying squirrel	Quadrupedal landing with flaring to slow down	Limbs are pushed forward to form a parachute-like form	Flattened in the direction of motion. Flexed parallel to the ground prior to landing	Forelimbs touchdown first	N.A.
Flying lemur	Quadrupedal landing with flaring to slow down.	Pitches upwards to reorient wing in the flow.	N.A.	Fully stretched. Four limbs touch ground Simultaneously	N.A.

confirmed what was obtained by simulations, as the rotorcraft was able to land over a platform moved manually. An embedded camera with a 70° viewing angle was used as an optical flow sensor using a custom-designed controller.

Other innovative techniques not based in visual cues have also been used for bio-inspired landing strategies. One of them has been developed by Lussier, Ashbeck and Cutkosky in which an unmanned aircraft is capable to perch on a vertical surface by using claws[59]. The designed system in this research work uses an ultrasonic sensor to detect a presence of a wall. When it is 6m away from it, the aircraft starts a pitch-up manoeuvre, until reaching a 90° angle. This new position will generate high drag which reduces the horizontal speed to about $1ms^{-1}$ to $3ms^{-1}$, point at which the UAV will contact the wall and hang on to it with the claws. No specific landing height is aimed for. Successful experiments were obtained when the aircraft had a forward speed of at least $8·5ms^{-1}$ before starting to pitch up and when the wall's surface roughness was high enough for the claws to get hold of it.

As a final example, Siddall and Kovac propose the design principles for a UAV capable of aquatic locomotion. Their considerations lead them to a landing system based on the plunging technique used by gannets, which has been described earlier. This strategy is chosen as it eliminates most of the complications involved in a soft water landing, resulting in a robust design. No models or experiments for it are reported [60].

7.0 CONCLUSION

A wide range of flying animals has been studied and their landing techniques have been identified. Table 1 summarises the landing techniques of the most significant ones. It can be seen that most of them rely on a high AOA configuration that leads to deep stall and a short drop onto its legs. Flapping wings and control surfaces are usually employed in larger animals, especially when weather conditions do not favour deceleration or when flight-path corrections are required. Sensory perception is essential in determining the landing site, visual cues being the most commonly used. Once again, it is observed that nature offers myriads of landing strategies that can be utilised in novel UAV design. In fact, as it has been previously shown, by taking careful consideration on the way lessons from nature are applied several novel technologies have been implemented for UAV landing, being delayed stall the most common strategy in use today. The advantage of this is that it can be implemented relatively easy to present fixed-wing unmanned aircraft. Optical flow is also being used as a landing technique. Its advantages are that there is no need for specific sensors as current cameras can be used with custom developed control hardware, making it a cost-effective option. Once again, nature has been proved to be a useful resource when searching for solutions to engineering problems. It is important, however, to follow the design premises mentioned in the preceding section.

The analysis of landing techniques followed by different flying insects has shown that the dynamics are very similar in between species, as only minor changes can be observed, especially during the approach phase. These variations are usually related to the animal's morphology and the geometry of the landing site. It has been seen, however, that landing is triggered by visual cues, sometimes combined with olfactory cues. Optical flow is a visual strategy that is already becoming popular in UAV design, while olfactory is not as it requires a highly sophisticated system that still needs technological development and that will possibly have limited engineering application.

Pterosaur landing theories seem to follow a similar tendency. Evidence suggests that these animals were able to land in a bipedal stance and that no running was needed afterwards, although that possibility cannot be discarded. Belly landing will not be discarded as well, as it could also

be used when alighting near cliffs. Unfortunately the study of extinct animals will not provide information of the use of senses to guide the landing manoeuvres.

From the review carried out for birds, it can be generalised that their landing procedure, with some exceptions, can be divided into three steps:

● Descent

● Pitch-up manoeuvre

● Stall and drop

Depending on weather conditions or other factors, the birds may use some wing strokes in order to help decelerate prior to landing. The landing process is highly dependent on the visual sense of the animal; optical flow and/or motion parallax variables are used to control the approach and to guide the animal to its landing site. The auditory sense is also engaged by nocturnal animals that need to guide themselves towards their prey. This sensory-dependent landing is similar to that of insects. Bird manoeuvres are the most studied and provide enough information to enable replication for small unmanned aircraft that use fixed or flapping wings.

Bats execute very unique manoeuvres while landing. This is possibly because they usually land on ceilings or other inverted surfaces and because they fly during the night in almost complete darkness. When landing on the ground, manoeuvres also differ to what has been observed in birds and insects, as well as what has been proposed for pterosaurs. These manoeuvres may require complicated mechanisms in order to reproduce them mechanically. The fact that these animals are nocturnal means that their visual sense is not sufficient for guidance to a landing site, thus they have developed an auditory navigation system: echolocation. Sonar technology is similar to echolocation and thus is a possible means to implement bio-inspired guidance to landing.

Gliding mammals like flying squirrels, have a landing technique that is very similar to that observed in birds. Like them, they have an approach phase with constant or reducing speed, followed by a pitch-up manoeuvre and finalising with touchdown. Experimental results show that gliding mammals use aerodynamic forces to reduce the landing force on their legs, when compared to other non-flying mammals, a strategy that can be exploited in aircraft design. No particular study was found on what sensory system is used for guidance, but it was mentioned that these animals usually choose their landing site prior to take-off. This leads to the conclusion that their navigation is highly visual, probably with the use of optic flow or motion parallax.

ACKNOWLEDGEMENTS

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