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Multi-modal locomotion: from animal to application

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Abstract
The majority of robotic vehicles that can be found today are bound to operations within a single media (i.e. land, air or water). This is very rarely the case when considering locomotive capabilities in natural systems. Utility for small robots often reflects the exact same problem domain as small animals, hence providing numerous avenues for biological inspiration. This paper begins to investigate the various modes of locomotion adopted by different genus groups in multiple media as an initial attempt to determine the compromise in ability adopted by the animals when achieving multi-modal locomotion. A review of current biologically inspired multi-modal robots is also presented. The primary aim of this research is to lay the foundation for a generation of vehicles capable of multi-modal locomotion, allowing ambulatory abilities in more than one media, surpassing current capabilities. By identifying and understanding when natural systems use specific locomotion mechanisms, when they opt for disparate mechanisms for each mode of locomotion rather than using a synergized singular mechanism, and how this affects their capability in each medium, similar combinations can be used as inspiration for future multi-modal biologically inspired robotic platforms. (Some figures may appear in colour only in the online journal)

1. Introduction

Looking forward we want to be able to design mobile robots that are adaptable, autonomous and robust and that are optimized for the given tasks and operations. The predominant type of mobile robots currently in active use are vehicles that utilize a more traditional locomotion mechanism such as the tracked terrestrial locomotion used by the PackBot by iRobot or propeller driven underwater vehicles such as the Tethys AUV [1, 2]. Although these systems are proving successful, the additional benefits that more adaptable platforms can bring are also being sought.

Natural systems offer potential solutions to engineering design problems for a number of key reasons. Firstly consider 3 Author to whom any correspondence should be addressed. an insect in nature; what happens if it loses a leg? It does not simply perish, but adapts its gait in order to continue on, optimizing its performance following the loss of limb [3]. This robustness of design and level of autonomy would be highly beneficial if reproduced in future robotic systems.

Additionally, mechanisms that have come about after millions of years of evolution offer highly efficient locomotive strategies, although these are optimized for operations within a specific task-space. It is clear that the predominant use of energy within animals is for locomotion (i.e. travel to feeding grounds, feeding, migration etc) with only the remaining energy being available for growth and reproduction. Therefore the more efficiently the animal moves throughout the various modes, the more energy will be available elsewhere. This increase will help with the raising of infants and lead to more of 1748-3182/14/011001+18$33.00 1 Bioinspir. Biomim. **9** (2014) 011001 Topical Review the animals genes being passed to the next generation, which is the main inherent aim of all animals.

Provided the robotic vehicles that draw inspiration from these animals are required to operate within similar environmental conditions, these highly efficient locomotive strategies can be replicated [4–6]. This fact is also true for multi-modal locomotion. When designing vehicles required to operate in a variety of substrates, replicating mechanisms found within nature should lead to similarly efficient strategies.

For many animals, the primary venue of locomotion tends to be mono-modal; that is the majority of their task-space demands only a singular modality, with minimal need of alternative morphologies for transportation. Some organisms, however, operate at high levels of competence in a range of substrates, potentially providing valuable inspiration for the design of multi-modal robots.

By analysing morphologies of multi-modal locomotion in animals and understanding why specific combinations perform particularly well together, fundamental lessons and paradigms can be elucidated. These can provide a foundation for design analysis in future engineering projects. These characteristics can then be used as inspiration when considering future mobile robotic platforms. As emerging technologies begin to mature, robot platform designs are implementing these methods to push the boundaries of what is capable of a mobile robotic platform. The increasing demand of platforms with multi-modal capabilities is evident thanks to the numerous workshops specific to multi-modal locomotion, which have taken place at numerous IEEE conferences in recent years (IROS 2009, ICRA2011, BIOROB 2012 and IROS 2013). Although many cases of mobile robotics already exist, examples presented and discussed within this research are limited to platforms with an element of biological inspiration.

1.1. Locomotion performance

The fundamental reason for multi-modal animal locomotion is for survival. The need for these multiple modes can arise from different requirements relating to survival including fast escape, fast pursuit, searching for food, breeding, nesting, saving energy and migration. Each mode of locomotion described in this report can be broken down into several key attributes.

The speed at which the animal can travel will greatly affect the animal's success, i.e. either escaping predators or catching prey. However animals do not operate at their maximum speed very often, but rely on it for different key tasks.

Furthermore the animal's acceleration and manoeuvrability plays a key role in its success in the wild. For example predators that have a greater acceleration than the prey, but have a slower top speed, are still capable of catching the prey provided the attack is timed correctly [4]. Greater manoeuvrability is also vital in order to survive. Some types of prey have developed greater manoeuvrability which can be used to evade attacks made by predators with quicker acceleration [4].

The next factor of interest is the animal's level of endurance. As mentioned previously animals do not maintain their top speed for long, however they may need to operate for sustained periods at a rate lower than maximum speed, but at a level that nevertheless causes fatigue. However, the most important element can be considered to be the economy of energy for the particular mode. This is of vital importance as this helps establish the trade-offs made in energy consumption between different multiple modes of locomotion. This can then be directly linked to real engineering problems.

Considering all the attributes of locomotion modes it is clear that no animal will excel at all of these. The animal optimizes trade-offs between the different attributes of the locomotion modes based on its own measures of performance.

The requirement of locomotion optimization can easily be demonstrated by bird flight. The more efficiently the bird flies the less energy is used for locomotion, resulting in more food available for the brood, hence giving the infants a greater chance of survival and subsequently carrying forward the animal genes. By understanding how particular multimodal animals have made this compromise, future engineering projects can adopt similar criteria.

1.2 Modes of locomotion

Modes of locomotion in nature can be decomposed broadly into three categories; terrestrial, aerial and aquatic. There are situations where the lines are blurred such as movement on the surface of water or underground tunnelling, but generally the types of locomotion used by the animals can be categorized into one of these three areas. The modes of locomotion can be broken down into specific types; these can be seen in table 1. Animal types that use that particular method are also presented. References are provided within the table that offer detailed descriptions of each mode. What is important to note is that multi-modal animals can utilize one of two options; firstly, morphology of one type of locomotion can be used in order to operate in different environments, with a level of adjustment made to accommodate the different conditions, or secondly use two completely different techniques in the different environments.

Many different types of locomotion are used across the biological classes, but what has to be remembered is that each has a varying level of competence within the substrate, and as such careful consideration must be given before assuming that mimicking the animal's techniques will provide the most suitable combination for real engineering problems.

1.3. Environmental considerations

For each different substrate there are key elements that help define the way animals can move within them. For land, force is required to overcome gravity and to support and move the body weight of the animal. In the air, gravity is also the major issue, but rather than just having to overcome this force for structural support, animals need to generate lift to counter its effect in order to stay airborne. During aquatic locomotion the effect of gravity is not as apparent and can often be disregarded as the animals have developed mechanisms which effectively make them neutrally buoyant at varying depths. However movement in water comes with additional drawbacks, in that while the density of air is approximately 1.2 kg m^{-3}, in water this value increases to approximately 1000 kg m^{-3} which results in a large increase in the resulting drag forces. Table 2 summarizes the features associated with the various substrates. It is clear that each environment offers its own benefits and drawbacks.

Table 1. Modes of locomotion.

		Birds	Reptiles	Amphibians	Fish	Mammals	Arthropods	Cephalopods	Reference
Terrestrial	Walking	Y	Y	Y		Y	Y		[4, 7]
	Running	Y	Y			Y	Y		[4, 7]
	Hopping	Y		Y			Y		[4, 7]
	Snaking		Y		Y				[4, 7]
	Two anchor principle						Y		[4]
	Peristalsis						Y		[4]
	Rolling						Y		[4]
	Burrowing		Y			Y	Y		[4]
Aerial	Flapping		Y			Y	Y		[4, 7–10]
	Gliding		Y	Y	Y	Y	Y		[4, 7–10]
Aquatic	Flapping appendages	Y	Y	Y	Y				[4, 11, 12]
	Oscillating tail		Y	Y	Y	Y			[4, 11, 12]
	Paddling with feet	Y	Y	Y		Y		Y	[4, 11, 12]
	Jet propulsion							Y	[4, 11, 12]
	Crawling		Y	Y	Y	Y	Y	Y	[4, 11, 12]

Table 2. Environmental considerations and features of various mediums.

	Air	Water surface	Underwater	Land	Underground
Need altitude for support	Y	N	N	Y	N
Resistance to motion	Low	Medium	Medium	Low	High
Coasting possible	Y	Y	Y	N	N
Body passively supported (by pressure)	N	N	Y	N	Y
Range (one day)	High	Low	High	Medium	Very low
Places of refugee (protection)	N	N	Y	Y	Y
Ability to stop/rest	N	Y	N	Y	Y

1.4. Analysis of locomotive literature: aims, method and limitations

Various combinations of multi-modal locomotion have been investigated, with biological systems that exhibit these abilities detailed, in an attempt to determine trends exhibited in nature. For each modal combination cases are found that utilize the same propulsive mechanism in each medium, along with examples using two disparate mechanisms in an attempt to determine which option is preferential for various tasks. In light of the lack of quantitative data for specific multimodal animals, the performance of the animals has been qualitatively determined based on referenced literature in an attempt to elucidate potential trends that could then be used in engineering design, unravelling the compromises they opt for. Where possible, quantitative data has been included to strengthen the arguments.

Tables 3–5 detail all the biological examples discussed within each section, along with some additional cases. It should be noted that this is a relatively arbitrary sampling based on the authors' choice to give an array of natural trade-offs. A brief summary of the locomotion strategies is given along with a performance measure. These are ranked from 0 to 10, ranging from 0 meaning incapable in that medium, to 10 implying a very high level of performance. 'Compromise rank' provides a quantitative value for the level exhibited by specific animals. The authors would like to stress that these values are based on their own observations and findings within literature, taking into consideration factors such as level of mobility and energy efficiency where these are known. The references within the tables refer to the literature upon which this ranking was based, rather than the source that provided the performance ranking.

There are numerous literature sources aimed at understanding the various modes of locomotion utilized in multiple media, as shown in table 1 [4, 7–12]. Within these literature sources, techniques for determining efficiencies and measuring other performance measures, such as cost of transport (COT), can be found relating to a single mode of locomotion. However, making direct comparisons of performance in more than one substrate is not generally detailed. Although these sources provide a solid basis for the understanding of locomotion in general, only rarely is there mention of the compromises that might be met by these animals. This limits their applicability in the understanding of multi-modal compromises, as we are interested in knowing the performance in both modes.

Sources that have begun to quantify the intricacies of multi-modal locomotion do exist. In the following review sections, references have been made to these. However, the manner in which these literature sources have analysed the animals differs from case to case, making direct comparisons of the findings difficult. This highlights the need for further quantitative studies across the range of multi-modal locomotion.

Further to research associated with analysing specific cases of locomotion, certain literature sources investigate unifying models and scalability implications of locomotion along with their associated energy costs [13–16]. The authors in all cases acknowledge that these principles offer only approximations. It would however be interesting in future multi-modal analysis to compare any gathered data to these theories, to see if they species of interest were outliers on these trends or whether the laws still held.

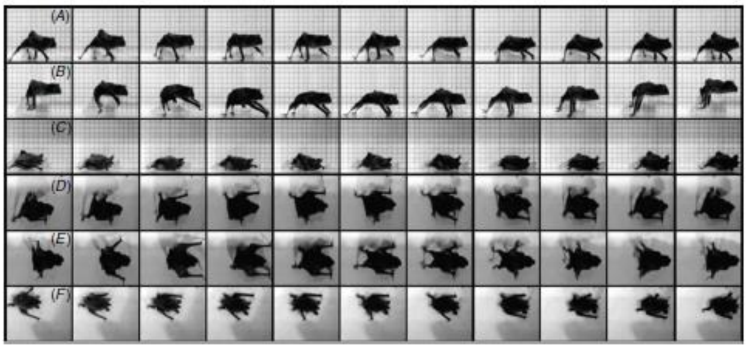

Figure 1. Terrestrial locomotion of *D. rotundas*: (*A*) walking at 0.12 m s^{-1} and (*B*) bounding at 0.60 m s^{-1}; and *M. tuderculata* moving at 0.35 m s^{-1}. (Dorsal views of the same three sequences are shown in (*D*), (*E*) and (*F*), respectively.) Reproduced with permission from [18].

Table 3. Aerial/terrestrial animals' performance matrix (reference relates to literature which ranking was based on, not on source of performance ranking).

Aerial/terrestrial	Class	Species	Aerial ability	Terrestrial ability	Aerial rank	Terr. rank	Overall rank	Compromise rank	Reference
				Same mechanism					
Patagium between limbs	Mammals	Short tailed bat, *Mystacina tuberculata*	Flapping patagium	Quadruped gait (walking only)	9	3	12	0	[18]
	Mammals	Common vampire bat, *Desmodus rotundus*	Flapping patagium	Quadruped gait (walking and novel running like gait)	9	3	12	0	[18]
	Mammals	Mastiff bat, *Molossus currentium*	Flapping patagium	Quadruped gait (walking and running)	9	3	12	0	[19]
	Mammals	Flying squirrels, subfamily *Petauristinae*	Extended limb formation, expanding patagium with tail used for stabilization	Quadruped gait	2	6	8	4	[20]
	Mammals	Flying phalangers, Genera *Acrobates* and *Petaurus*	Extended limb formation, expanding patagium with tail used for stabilization	Quadruped gait	2	6	8	4	[20]
	Mammals	Flying lemurs, genus *Cynocephalus*	Extended limb and digit formation, expanding patagium between all potential areas	Quadrupedal hoping	3	4	7	6	[20]
Passive patagium body mechanism	Reptile	'Flying' Gecko, *Ptychozoon kuhli*	Poor - simple parachuting function	Competent arboreal ability	1	8	9	3	[22]
	Reptile	Tree frogs, *Rhacophorus*	Poor-simple parachuting function	Competent arboreal ability	1	6	7	2	[23]
	Reptile	'Flying' snakes, *Chrysopelea*	Novel body undulation gliding ability	Competent arboreal ability	2	8	10	2	[24]
				Different mechanisms					
Flapping mechanism and bipedal limbs	Birds	Numerous	Flapping lift based mechanism	Competent bipedal gaits	10	4	14	2	NA
Active patagium connected to rib cage and quadrupedal ability	Reptile	*Draco* Lizards	Competent gliding ability	Excellent arboreal ability	4	8	12	0	[72]
Limbs and released furcula	Insect	Springtails, *Collembola*	Limited hopping ability	Competent hexapod gait	1	8	9	2	[73]
	Insect	Dragonfly (mature)	Flapping lift based mechanism	Basic hexapod gait	10	5	15	0	[28]

Table 4. Aerial/aquatic animal performance matrix (reference relates to literature which ranking was based on, not source of performance ranking).

Aerial/aquatic	Class	Species	Aerial ability	Terrestrial ability	Aerial rank	Aquatic rank	Overall rank	Compromise rank	Reference
				Same mechanism					
Flapping mechanism	Birds	Auks, *Alcidae*	Flapping lift based mechanism	Flapping lift based mechanism	9	8	17	2	[30]
	Mammal	Common brown bats, *Myotis sodalist*	Flapping lift based mechanism	Limb propulsion—likely drag based	9	2	11	0	[36]
				Different mechanisms					
Flapping mechanism and foot propulsion	Insect	Diving beetles, *Dystiscidae*	Flapping lift based mechanism	Drag based limb propulsion	8	5	13	0	[74]
	Birds	Eiders, *Somateria*	Flapping lift based mechanism	Lift based foot propulsion	9	6	15	1	[37]
Body undulations (subcarangiform) and deployable wings	Fish	Flying Fish, *Exocoetidae*	Deployable wings allowing gliding ability	Body Undulations	4	9	13	1	[39]
	Fish	Rays, *Batoidea*	Basic gliding	Rajiform median paired fin propulsion	1	9	10	0	[75]

Table 5. Terrestrial/aquatic animal performance matrix (reference relates to literature which ranking was based on, not source of performance ranking).

Terrestrial/aquatic	Class	Species	Aerial ability	Terrestrial ability	Terr. rank	Aquatic rank	Overall rank	Compromise rank	Reference
Same mechanism									
Body undulations	Reptile	Sea-snake, *Laticauda*	Serpentine crawling	Flapping lift based mechanism	6	7	13	3	[47]
Quadruped limbs	Mammal	Water rat, *Hydromys chrysogaster*	Quadrupedal gaits	Drag based quadrupedal propulsion	7	3	10	1	[42]
	Mammal	Californian sea lion, *Zalophus californianus*	Quadrupedal gaits	Drag based quadrupedal propulsion	3	8	11	4	[42]
	Reptile	Green Turtles, *Chelonia mydas*	Forelimb drag based technique	Forelimb lift based propulsion	2	9	11	8	[45]
	Reptile	Fresh water turtles, *Mauremys caspica*	Quadrupedal gaits	Drag based quadrupedal propulsion	6	5	11	3	[44]
Different mechanisms									
Body undulations and quadruped limbs	Mammal	*Lutrinae*	Quadrupedal gaits	Body undulations	7	7	14	1	[43]
	Reptile	*Crocodilia*	Quadrupedal gaits	Body undulations	6	7	13	1	[49]
	Reptile	Californian newt, *Taricha torosa*	Quadrupedal gaits	Anguilliform swimming	6	7	13	1	[50]
Limbs and jet propulsion	Insects	Dragonfly larvae	Hexapod gait	Limbs during slow motion, jet propulsion for rapid acceleration	6	3	9	0	[76]

2. Biological multi-modal locomotion

2.1. Aerial–terrestrial locomotion

In the natural world, active flight (the ability of powered forward flight) has evolved in three lineages; birds, bats and insects. However, the ability to control descent upon leaping into the air has evolved in at least 30 species in mammals, reptiles, amphibians and insects, providing engineers with numerous mechanisms to achieve similar multimodal performances [17]. To aid the understanding of the aerial modes, several authors have extensively analysed the numerous techniques [4, 7–10].

The combination of aerial and terrestrial locomotion in nature has motivations based on very different task-spaces, and these facts greatly influence the level of performance achieved by the different animals. Terrestrial abilities allow animals to perform daily tasks such as sleeping and very often feeding. Terrestrial locomotion is generally more energy efficient over small distances but as this increases, aerial locomotion becomes the mode of choice when wanting to travel larger distances [4]. The bias in the animal's task-space for the requirement to travel longer distances has a large impact on the aerial ability of the animal. As with aerial locomotion, there are several key literature sources that study terrestrial locomotion modes in isolation [4, 7].

2.1.1. Dual use mechanisms. Mammals have achieved competent multi-modal abilities ranging from sustained powered forward flight to simple gliding operations. Two species of bat, the short tailed bat, *Mystacina tuberculata*, and the common vampire bat, *Desmodus rotundus*, are known to be able to fly competently but also have competent terrestrial ability [18]. They both exhibit a quadrupedal gait, similar to that exhibited by other mammals during walking, and the common vampire bat has even achieved a novel gait pattern exhibiting traits similar to the definition of running. These gait patterns are shown in figure 1. According to the literature, the terrestrial ability does not appear to have had a detrimental effect on the aerial ability, as detailed in table 3, although further experimental work would be required to determine this. Investigations by [19] shows that when considering the metabolic rate of the mastiff bat, *Molossus currentium*, another species capable of aerial and terrestrial locomotion, the aerobic metabolic rate during terrestrial locomotion is 3–5 times higher than that of rodents. Furthermore, cost of transport was ten times higher for running than flying, clearly demonstrating the need to choose the correct mode of locomotion for task at hand. The comparison is shown in figure 2. Bats have been included in the section utilizing the same mechanism, as the patagium is directly connected to the limbs on which they walk, hence having a direct impact during both modes of locomotion.

The best known gliders amongst mammals are found in three main groups; the flying squirrels (subfamily *Petauristinae*), the flying phalangers (*Acrobates* and *Petaurus*) and the flying lemurs (*Cynocephalus*) [20]. These animals utilize a deployable membrane, the patagium, connected between the fore and hind limbs on both sides of the body [21]. This mechanism is used to increase the lift producing surface area during aerial locomotion but is held in a fixed position during operations, with only slight adjustments being made in order to aid with steering. Flying squirrels and flying phalangers also utilize relatively large tails for steering and stabilization in flight. The flying lemurs however, the most advanced of the three groups in terms of wing membrane development, do not utilize a tail in this manner but utilize every possible increase in body surface area, including gaps between the fingers and toes.

All the gliding mammals are arboreal in nature, and utilize their gliding ability to travel from tree to tree. With these examples the aerial ability is far simpler than that exhibited by the multi-modal bats, reflecting accordingly when ranking the abilities. Of key interest to note is the fact that as the deployable patagium becomes more expansive, connecting to the extremities of the mammal's body, this comes at a detrimental effect to the terrestrial ability. Whereas the flying squirrels and the flying phalangers remain relatively competent in terrestrial modes of locomotion, the flying lemurs, which have the most evolved patagium, spanning the entire body, resort to a crude hopping mechanism on land.

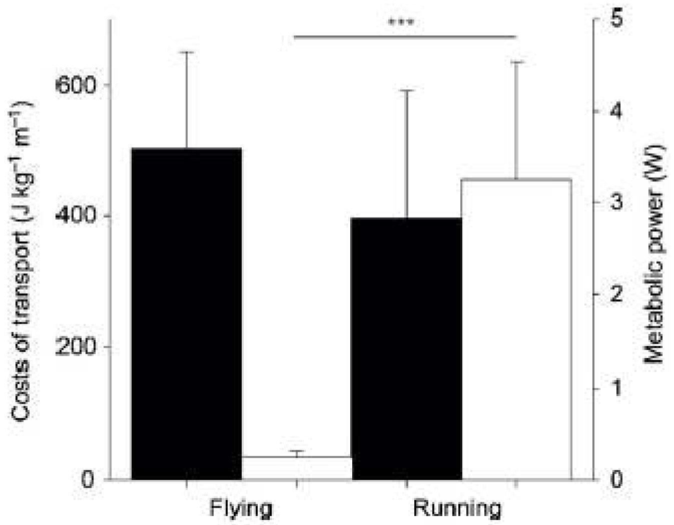

Figure 2. Metabolic power (Watt; filled column) and costs of transport (J kg^{-1} m^{-1}; open column) for running and flying *Molossus currentium*. Reproduced with permission from [19].

This demonstrates the compromises made by the introduction of the patagium for use in aerial locomotion on an originally terrestrial animal. This however is in contrast to the bats, which again use a patagium but in flapping flight, have achieved competent terrestrial abilities. One possible explanation for this is the direction in which the animals have evolved. It is suggested that the terrestrial ability of the bats has been achieved due to individual niches in feeding habits, feeding on prey in the vampire bat and foraging of the short eared bat in the originally predator-less undergrowth of New Zealand [18]. The gliding mammals on the other hand have evolved from arboreal mammals without the extensive patagium and as such only exhibit the crude ability demonstrated within these species.

Reptiles are also known to utilize a patagium attached the body section to aid in aerial locomotion. Similarly to mammals, reptiles utilizing this gliding method are typically arboreal in nature. One such reptile is the 'Flying' Gecko, *Ptychozoon kuhli*, but this mechanism is passive in its nature, in that it automatically deploys upon the reptile launching into the air once sufficient airspeed has been achieved [22]. Webbing is also present between the digits of the gecko. This results in a poorer aerial performance but maintains a more competent terrestrial mode, without such a high level of compromise experienced.

The genus group of frogs, *Rhacophorus*, are a group of tree frogs that have strong webbing located between their digits. This enables the 'flying' frogs to increase their gliding ability upon launch into the air [23]. This once again results in low level aerial performance, but again the mechanism only slightly interferes with the terrestrial mode.

Another reptilian example of gliding is that of the 'flying' snakes belonging to the genus group *Chrysopelea*. This mode of gliding is kinematically distinct from any other forms found in the natural kingdom. Firstly, unlike the other reptilian gliders, prominent body movements are utilized in air rather than simply relying on a fixed wing arrangement. The motion consists of high amplitude body undulations throughout the course of the glide, along a dorsoventrally flattened body. Little is known about the aerodynamics associated with this technique, but it is clear that this technique which transforms the entire body of the snake into an ever changing wing shape is the most dynamic of all vertebrate gliders [24].

All the reptile examples detailed above really only exhibit a very basic aerial ability, with the mechanisms only exhibiting a parachuting aerial mode, reducing the sinking speed of the animal slightly. The added morphology that enables the aerial ability does not appear to have affected the terrestrial ability but the question must be raised as to whether the 'benefits' associated with these examples really provide any useful insights into engineering designs that are not already known. Of the three, the 'flying' snake has the most intriguing mechanism that would benefit from further study.

2.1.2. Multiple locomotion mechanisms. The most documented animal groups with aerial/terrestrial abilities are that of birds and insects. Both groups exhibit excellent abilities in air, capable of sustained powered forward flight, and even hovering in some species, and on land, but these are not necessarily found within a single species. It does however highlight the adaptability that both these species exhibit.
Birds however operate over a greater range of sizes which has obvious implications on the scalability of mechanisms, ranging from approximately 1.5 g to 15 kg [25], which could be of use when considering engineering designs. The terrestrial ability of *Struthioniformes* is excellent, such as with ostriches, but these birds have achieved this at the expense of their aerial ability. Birds are also limited, due to morphological reasons, to bipedal terrestrial locomotion. There are clear advantages to the hexapod gait exhibited by insects, which offers greater stability and adaptability. When considering multi-modal animals using different mechanisms it is clear that as one mechanism becomes more specialized, the importance and hence functionality of the alternative mechanism becomes less prevalent leading to a reduction in performance. It is therefore very difficult to quantify the compromises exhibited unless careful consideration is given to the task-space of the individual animals. This highlights the need for further research in this area.
An interesting study into avian locomotion looking at terrestrial gaits has shown how we should not always treat multi-modal animals with multiple locomotion mechanism with complete separation. Research by [26] has shown that the wings actually help reduce the cost of transport of the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), transitioning from walking gait, then grounded running followed by aerial running. This is shown in figure 3, where the COT can be seen to reduce as the forward speed of the bird increases, transitioning through the aforementioned gaits.

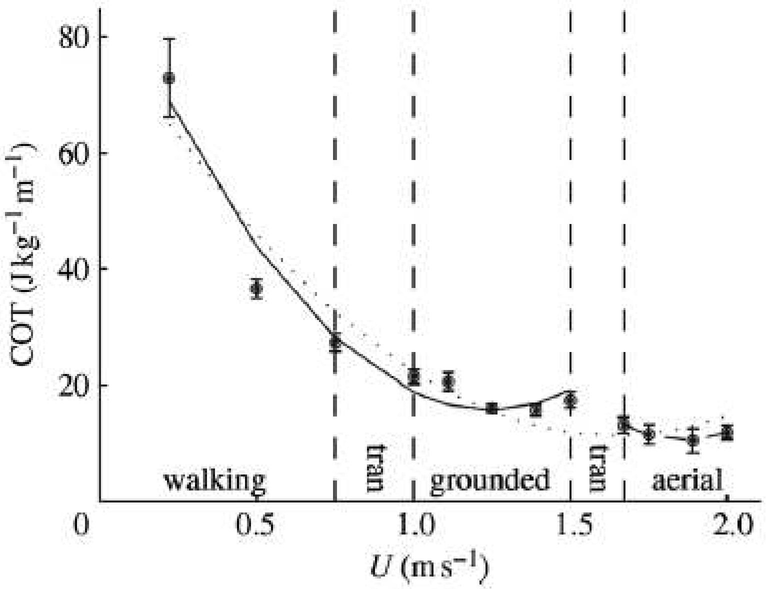

Figure 3. Cost of transport of the Svalbard rock ptarmigan (COT; J kg^{-1} m^{-1}) plotted against forward speed (U; ms^{-1}). Areas between vertical dashed lines (labelled tran) represent the range of speeds where a gait transition occurred. Reproduced with permission from [26].

Although still incapable of sustained powered forward flight reptiles that exhibit a gliding mechanisms independent of its terrestrial mechanism achieved greater performance in both mediums than examples that use a single mechanism. The Draco lizards, part of the *Agamidae* family again uses a deployable patagium that is used to aid in gliding as shown in figure 4 [27]. Unlike the mammal equivalent and that exhibited in the flying gecko and frogs, the membrane is supported by the ribcage. This patagium is actively controlled and enables the Draco lizard to glide large distances in the air whilst maintaining a very agile terrestrial ability. It is the author's belief that this higher level of multi-modal ability compared with the mammals using a deployable patagium is as a result on the two mechanisms acting independently and as such the lizard has not had to compromise on terrestrial ability in place of increased aerial ability.
Additionally, many insects are capable of aerial and terrestrial modes of locomotion. The numerous species of dragonfly exhibit an incredible aerial ability, which operate at fast forward velocities but also controlled slow speed flight and hovering [28]. This ability, remaining independent from the hexapod arrangement of limbs for terrestrial movement, does not experience any level of compromise due to their multi-modal capabilities. This again highlights the benefits of maintaining individual mechanisms for use in both mediums when considering aerial and terrestrial operations.
An overview of the various animals highlighted in this section can be found in table 3. Each animal has been ranked according to the various performance of each mode of locomotion along with the level of compromise experienced by the species.

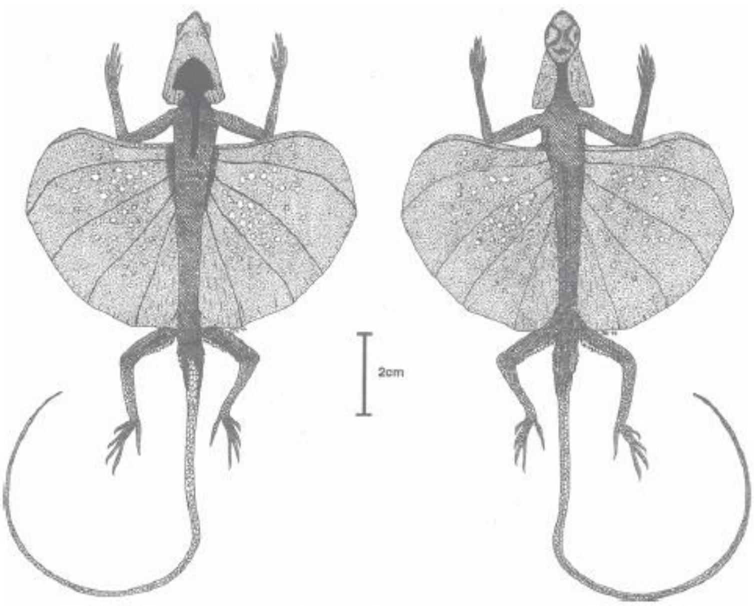

Figure 4. Dorsal and ventral views a *Draco melanpogon* showing outstretched patagium deployed during aerial gliding. Reproduced with permission from [27].

2.2. Aerial–aquatic locomotion

Aerial and aquatic modes of locomotion are similar in nature due to the fact that propulsion mechanisms utilize similar characteristics of aero and hydrodynamics in each medium. The key differences between the two are the increased implications of gravity during aerial operations compared to aquatic operations, and the difference in density of the fluids, being approximately 800 times denser in water than air. These characteristics greatly affect the types of mechanisms used for locomotion. A synopsis of the combination of propulsion mechanisms can be found within table 4.
Aerial and aquatic modes of locomotion have been investigated in isolation by several key authors: Norberg, Pennycuick and Videler for the aerial modes, and Blake, Vogel for the aquatic [8–12].

2.2.1. Dual use mechanisms. Only a limited number of animals are capable of both aerial and aquatic modes of locomotion using the same propulsion mechanism. One such case is the group of birds known as the alcids. This group encompasses species such as the common guillemot, *Uria aalge* (also referred to as a murre), and Atlantic puffin, *Fratercula arctica* [29, 30]. Alcids are capable of competent aerial locomotion using a typical avian flapping technique, then fold their wings during aquatic operations and perform an oscillating motion of the wings in order to propel themselves. This capability is demonstrated in figure 5.

Figure 5. Multi-modal capability of common guillemot, *Uria aalge*. Reproduced with permission from [31].

The key point to note here is that the alcids use a lift based propulsion mechanism in air and water, but during the aquatic phase the bird utilizes an active upstroke; that is lift is produced on the up stroke as well as the down stroke. This lift based technique is proven to achieve higher propulsive efficiency than drag based propulsion mechanisms [4]. However, the flapping frequencies during aerial and aquatic operations reduce from approximately 9 to 2.5 Hz in the common guillemot [32]. There is debate in the literature as to the level of compromise exhibited by alcids in order to achieve multimodal locomotion. It has been suggested that the stocky wing arrangement found in alcids is due to the adaptation for aquatic locomotion [30], but other suggest this is due to the fact that alcids, when flying, do not need to avoid obstacles and as such do not require wings that allow high manoeuvrability. From a musculo–skeletal point of view, the muscles of the guillemot cannot be optimized to work at both flapping frequencies and as such a level of compromise, harder to quantify than other traits, must be present.

Although not strictly dealing with performance, investigations into the relationship between animal mass and stroke frequency of the flapping motion in air and water demonstrated that these avian species with aerial and aquatic capabilities appear to be outlier species compared with those that only operate with one of the modes [33]. This is shown in figure 6, with the avian species capable of flight and swimming marked by open squares and diamonds respectively (rhinoceros auklet, gold open; Razorbill, brown open; common guillemot, turquoise; and Brunnich's guillemot, green open). This alludes to these species settling on flapping frequencies away from the norm, potentially due to an opted compromise in locomotive performance or an adaptation in physiology.

Research into the physiological adaptations of avian species, comparing birds capable of both aerial and aquatic locomotion to penguin species that no longer have aerial capabilities has shown that the multi-modal birds maintain a closer resemblance to their counterparts with solely aerial capabilities, indicating that the aerial/aquatic species are still well suited to aerial flight, with the additional capability of aquatic locomotion in terms of locomotion functionality [34].

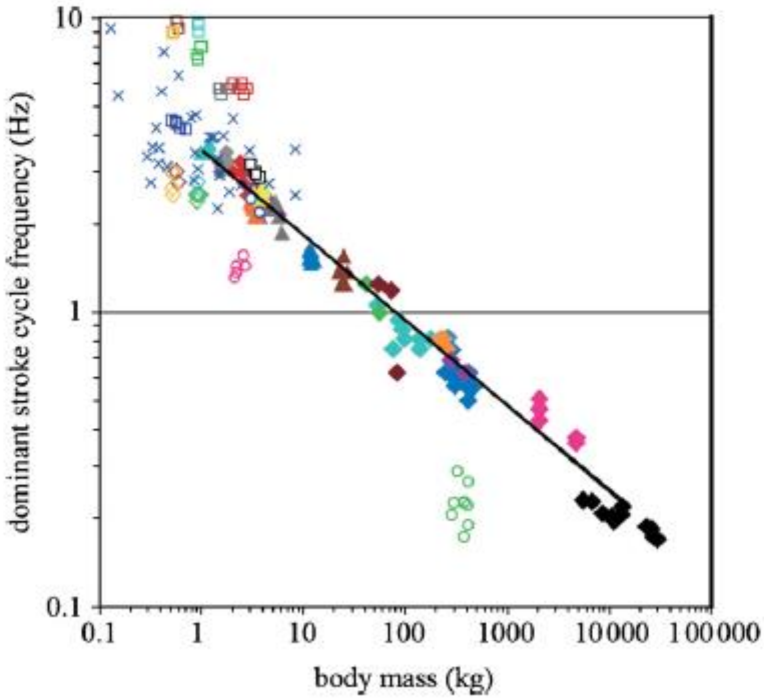

Figure 6. Dominant stroke cycle frequency versus body mass for numerous aerial and aquatic species. Reproduced with permission from [33].

However, research by [35] has compared flight locomotion costs of birds with an aquatic capability with those that have a solely aerial ability. This found that the energy expenditure of the birds with aerial/aquatic capabilities was more than double that predicted by the maximum output line used to represent maximum aerobic capacity in flying birds, as specified in [10]. This is shown in figure 7, within which the murre (i.e. common guillemot) is labelled, representing the aerial/aquatic avian species. Within the animal kingdom, birds remain the best adapted for aerial/aquatic operations utilizing the same propulsive mechanism.

One example amongst mammals that is capable of both aerial and aquatic locomotion is the common brown bat. This species of bat has been observed to swim but does so in a rather poor manner [36]. Although the authors of the original paper do not classify the mode of locomotion, it is apparent from the photographs within the article that a drag based propulsion mechanism is used. This implies an aquatic technique with poor propulsive efficiency. It is clear that the bats aerial performance exceeds that of the aquatic ability, which in actual fact is limited to surface swimming. This is of no surprise if we consider the task-space of the bat which would use the aerial mode of locomotion far more than the aquatic mode, hence a bias in performance towards flight mechanisms. The ability to swim does not appear to have compromised the aerial ability, and much like the aerial/terrestrial bats discussed in the previous section it appears that the ability to swim is a technique that has evolved following the ability to fly.

Insects may appear to be a likely candidate for animals with both aerial and aquatic abilities, utilizing the same propulsive mechanism in each but this is not the case. This is due to the very delicate nature of insect wings. Due to the increased density of water compared with air, it is unlikely that wings originally evolved to work in air would be suitable for use when the loading is that much greater in water. As such no insect species with this ability have been located, however the author would like to stress that cases may exist in the natural world that have not been identified in this study.

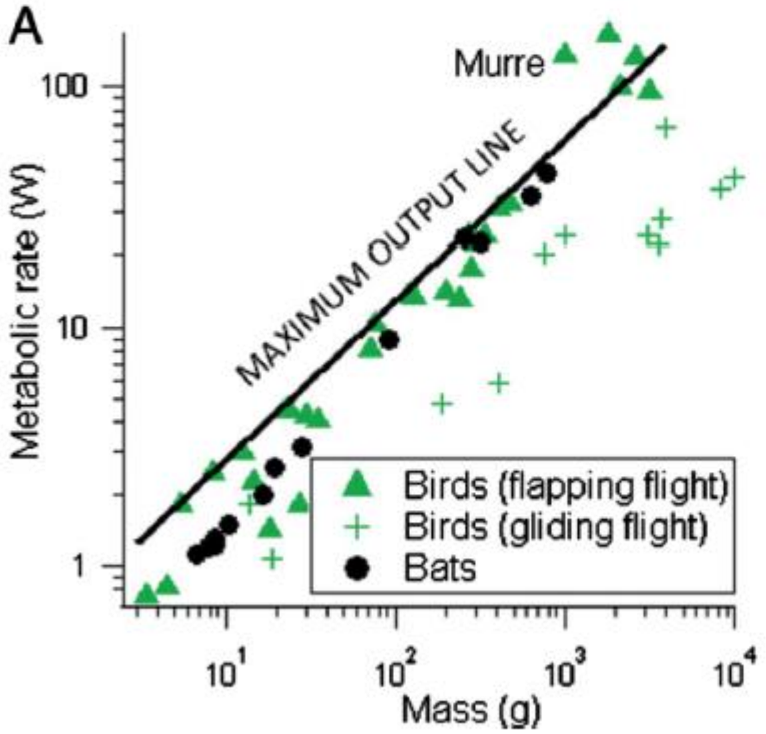

Figure 7. Comparison of power output during flight across different bird species. Reproduced with permission from [35]

2.2.2. Multiple locomotion mechanisms. As highlighted above, insects typically do not use the same mechanism for locomotion in the different mediums, although many examples exist that utilize both modes of transport. To achieve this insects typically use their hexapod gaits in a rowing motion, utilizing a drag based strategy, and then subsequently use wings during aerial operations [4]. As the mechanisms are independent it is again difficult to quantify the compromises exhibited by the various insect species in order to achieve multi-modal operations. From an engineering design perspective, the insects are adept at folding the wings away during aquatic operations, helping to reduce drag. This would need to be considered if trying to replicate the strategies in engineering designs.

Birds once again show considerable adaptability in terms of locomotive performance. Although alcids use the same propulsive mechanism in different mediums, species such as the great crested grebe, *Podiceps cristatus*, use wings in the air and feet during aquatic operations [37]. Furthermore the grebe uses the more efficient lift based propulsion mechanism rather than drag based propulsion mechanisms. Admittedly this technique is highly specialized and other bird species exist that utilize a drag based aquatic propulsion mechanism, such as the European shag, *Phalacrocorax aristotelis* [38].

Quantifying the compromises exhibited by these avian species is once again difficult, with both the same mechanism and independent mechanism solutions offering potential to multi-modal engineering projects. Consideration should therefore be given to the task-space of the animals in question; *alcids*, who hunt fish out in the open sea must actively capture their prey requiring high manoeuvrability, whereas grebes are bottom feeders and hence seek static food sources that do not require the added manoeuvrability. This variance in task-space should therefore be considered when analysing the different measures of performance.

Referring once again to work detailing stroke frequencies of various animals whilst swimming and flying by Sato *et al* [33], analysis of foot propelled avian swimmers was included. Two species of shag, the European shag *Phalacrocorax aristotelis*, and South Georgian shag *Phalacrocorax georgianus* are shown in figure 6 as filled grey diamonds and filled red diamonds respectively for swimming and open grey squares and open red squares for flight. Interestingly these species have evolved a foot size that results in a stroke frequency similar to other swimming specialists. However, aerial stroke frequencies are shown to be higher in the shags than in other species, indicating that they may need the faster flapping mechanism in air to compensate for additional muscle that allows the foot propelling functionality. This demonstrates again the fine balance in compromise that exists when trying to achieve multi-modal functionality.

Fish of the family *Exocoetidae*, commonly referred to as flying fish, are capable of gliding large distances just above the surface of the water. These fish launch from the water to a distance of approximately 1 m above sea level to escape predators and deploy large wings to maintain gliding operations enabling the fish to cover distances well in excess of 50m[39]. The wings that are used during the aerial mode of locomotion are solely used for this purpose, and are deployed upon leaving the water. Whilst submerged the fish use a traditional subcarangiform mode of locomotion using body undulations. They are also known to use their body undulations for short burst whilst airborne to 'run' on the surface of the water to maintain forward velocity. No clear evidence has been located that quantifies the compromise exhibited by the flying fish, it would appear however that the gliding mechanism has evolved alongside the swimming mechanism and as such has not resulted in a detrimental effect on the swimming performance. There will be obvious implications on the fish physiology such as increased muscle required to operate the deployable mechanism that will subsequently incur a greater power requirement during swimming but these would take much more experimental tests to determine the exact contribution and as such can be considered to have a negligible effect on swimming performance during this investigation.

2.3. Terrestrial–aquatic locomotion

The combinations of terrestrial and aquatic modes of locomotion are some of the most common within the animal kingdom. Many animals that predominantly live on land are also able to swim with varying levels of ability. Motivation for terrestrial animals to enter the water ranges from hunting and feeding to migratory requirements. It is also interesting to note that aquatic to land based locomotion founds the basis of evolutionary theories of mobility. Terrestrial and aquatic locomotion modes of animals have been studied extensively in isolation [4, 7].

Of all multi-modal combinations, amphibious animals are by far the most well studied, particularly mammals. Mammals offer an interesting case, in that their lineage can be traced from purely land based to fully aquatic. As such, the transitional nature of locomotion performance has been studied extensively, with work of particular note by Fish and Williams [16, 40–43]. A comparison of the cost of transport associated with fish, marine mammals and semiaquatic mammals is shown in figure 8. This quantifiably demonstrates the greater COT for the semi-aquatic mammals, compared with single mode specialists.

2.3.1. Dual use mechanisms. Utilizing the same mechanism in both terrestrial and aquatic environments is common within the animal kingdom. This combination of abilities also provides some of the clearest compromises exhibited within nature in terms of locomotive ability. Reptiles are some of the most well adapted animals to achieve this combination of modes. The comparison of marine and freshwater turtles encapsulates the very compromises that are being considered here. It has been found that marine turtles that utilize a lift based propulsive strategy can generate twice the propulsive force as freshwater turtles that utilize a drag based approach, and giving further consideration to additional benefits such as the increased streamlining of the body of the marine turtles, results in a maximum swimming velocity six times higher than the freshwater counterpart [44].

However, this increase in aquatic ability has come as a direct result of a decrease in terrestrial ability. Whereas freshwater turtles still retain a terrestrial ability on land utilizing traditional quadrupedal gaits, marine turtles are known to operate in a clumsy and laboured manner, dragging themselves whilst on land [45]. The bias towards the most efficient strategy being used in one medium cannot be considered independently and as such will always result in a detrimental effect on the other mode of locomotion. The adaptation of the fore-limbs clearly demonstrates the varying level of emphasis for performance in one mode of locomotion over another. The transitioning form of turtles limbs can be seen in [46].

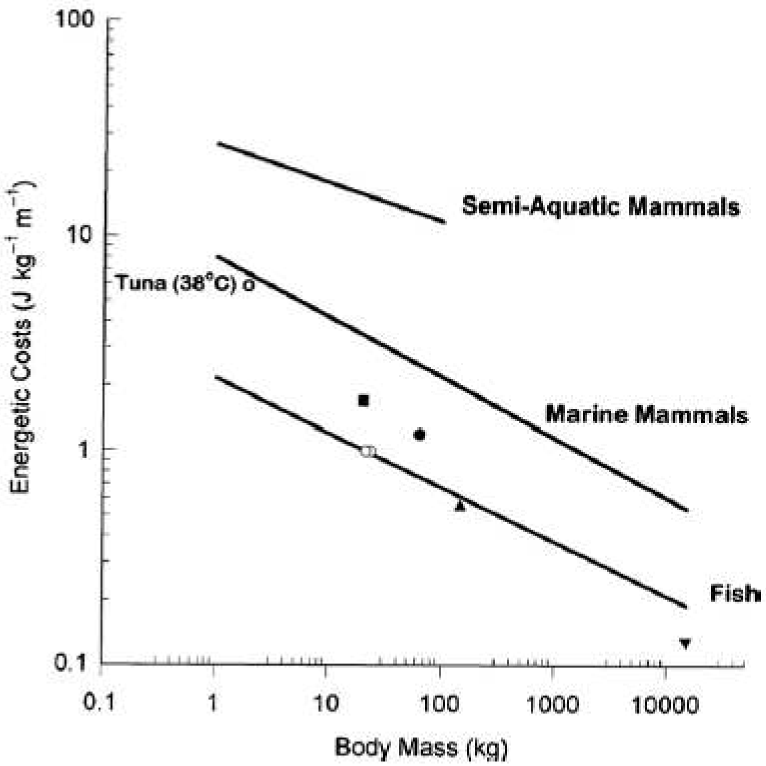

Figure 8. COT comparisons for semi-aquatic mammals, marine mammals and fish. Reproduced with permission from [16].

Remaining with reptiles, various species of snakes have been compared in an attempt to elucidate compromises and trade-offs exhibited in locomotive ability based on conflicting evolutionary optima [47, 48]. The conclusions throughout the literature are that there are compromises within species, with bias towards specific modes, but these evolutionary characteristics remain intricately entwined in physiological adaptations such as reduction of ventral plates and flattening of the tail to aid with aquatic locomotion. Quantifying these adaptations requires further in-depth analysis of specific species. However, it is clear that the undulating mechanism utilized by snakes is a very adaptive mode of locomotion, whereby the body undulation mechanism achieves high levels of competency in both aquatic and terrestrial environments.

Mammals provide another range of animals exhibiting a progression from a predominantly terrestrial life to semiaquatic, with some mammal species maintaining a constant life cycle within water. Much like in turtles, a transition from drag based propulsion to lift based propulsion has been observed in mammals [42]. This shift in propulsion mechanism results in a large increase in achievable propulsive efficiencies, as shown in figure 9. The cost of transport (COT) for a range of semi-aquatic and aquatic mammals confirms that as the animal becomes more specialized for aquatic locomotion, the COT decreases accordingly, as shown in figure 10 [40]. However, although not quantified in Fish's work, it is clear that the terrestrial ability of the animal subsequently decreases. Eventually resulting in the animal being completely water bound. In amphibious mammals, due to physiological constraints the propulsion mechanisms are always related to the protruding limbs. As these evolve into devices capable of increased propulsive efficiencies, the ability on land subsequently decreases.

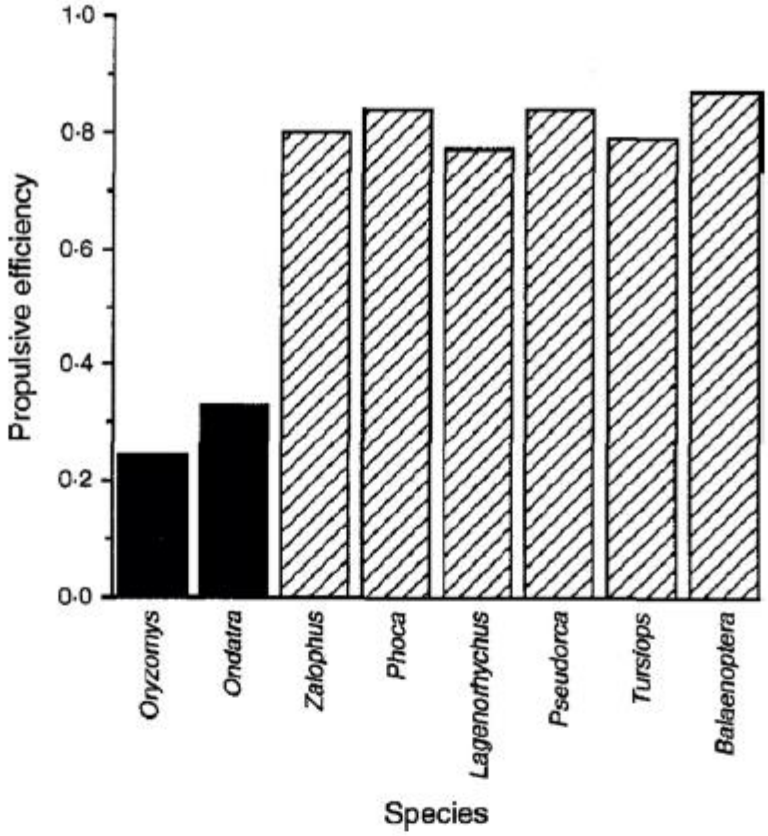

Figure 9. Comparison of propulsive efficiencies between drag-based (solid bars) and lift-based (hatched bars) swimming modes for various mammalian species. Reproduced with permission from the Australian Journal of Zoology 42 (1): 79–101 (Fish, FE). © CSIRO 2004. Published by CSIRO PUBLISHING, Collingwood, Victoria, Australia.

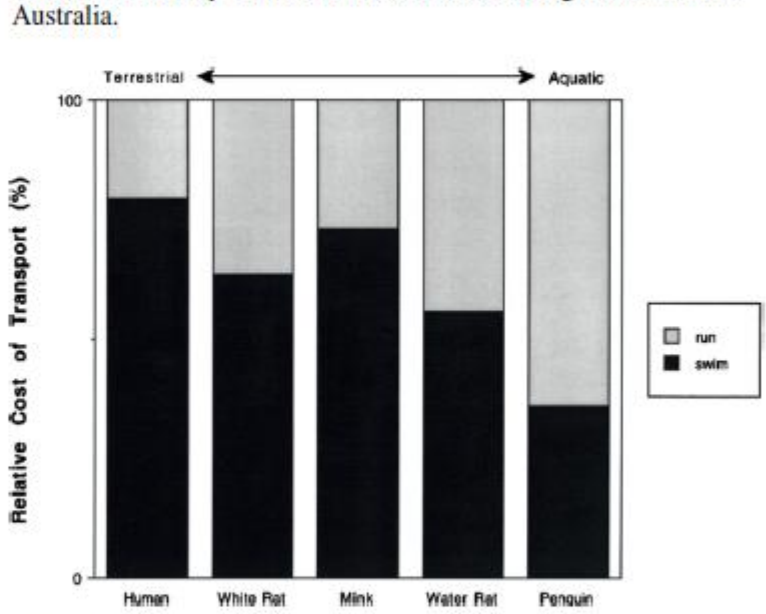

Figure 10. Relative cost of transport for running and swimming of terrestrial, semi-aquatic and aquatic animals. Reproduced with permission from [40].

2.3.2. Multiple locomotion mechanisms. Due to the relative ease in which drag based propulsion can be achieved by limbs that are not particularly specialized for aquatic modes of locomotion, more amphibious examples exist in nature that utilize the same mechanism in both mediums. There are however examples that utilize different mechanisms in each.

Examples of mammals that utilize legs on land and body undulations (including tail motion) in water are those belonging to the subfamily *Latrinae*. The COT of one particular species has been determined for the terrestrial running phase. The North American river otter, *Lontra canadensis*, has been found to have a net COT = 6.63 J kg^{-1} min^{-1} [43]. The energy expenditure of the river otter for running was compared with a terrestrial specialist of similar build (Welsh corgi). It was found that the COT was greater in the otter, indicating that a physiological adaptation to allow swimming with body undulations resulted in a reduction in locomotive efficiency on land. The requirement of an increase in spinal flexion was identified as a key physiological difference leading to the variation in performance.

Reptiles of the order *Crocodilia*, which encompasses crocodiles, alligators, gharial and caiman, utilize tail undulation in water, whilst on land they use their limbs with a quadrupedal gait formation [49]. Although the swimming speeds are slow compared with aquatic mammals and fish, kinematic efficiency has been shown to be comparable to that of fully aquatic mammals and is greater than that of semiaquatic mammals.

Crocodilia maintain a terrestrial ability, but it would be difficult to say that this mode was equal in performance to that during aquatic operations. As the crocodiles task-space sees the animals requiring terrestrial ability for tasks such as nesting and sunbathing, with more dynamic tasks such as hunting conducted from within an aquatic environment, there is little need for truly high performance on land. However they are capable of fast burst of motion on land, but this mode would not be sustainable for long periods, which indicates that it comes at a high energy cost to the animal. Furthermore it does not appear that maintaining the limbs hinders the aquatic performance of the animal; rather it maintains a requirement to nest and rest on shore, with negligible effect on aquatic performance.

Similar amphibious reptiles in terms of locomotive mechanisms are the much smaller newt and salamander, which utilize a quadrupedal gait on land, and body undulations whilst in water, as shown in figure 11 [50]. Locomotive ability aside, this highlights the scalability of this combination of mechanisms. Much like with the *crocodilia*, the terrestrial ability appears to have a negligible effect on the aquatic locomotion, such as increased drag associated with the projected limbs. It would therefore appear that once again that by keeping the mechanisms separate, competent levels of performance on both land and in water are achieved without high levels of compromises being made.

3. Robotic multi-modal vehicles

As research continues new projects are beginning to unravel the prospects of biologically inspired multi-modal robotics. This area is truly exciting as the majority of the past engineering design projects with regards to locomotion have strived to optimize a single modality. Biological systems have not had this freedom and as such have had to develop robust solutions that can function in multiple substrates. Autonomous vehicles that can operate in more than one substrate have not reached mainstream design or use [51], and the projects that do exist tend to lack scalability in the context of broader design. Biological inspiration can help lead towards adaptable, autonomous and scalable future robot designs. The following sections provide successful cases of multi-modal applications.

3.1. Aerial/terrestrial

Platforms with the stated goal of aerial and terrestrial locomotion are few and far between but one such example is the micro air-land vehicle (MALV), an autonomous vehicle capable of both flying and crawling developed at the Naval Postgraduate School, Case Western Reserve University, and the

University of Florida [52], drawing many of its major aspects from biological inspiration. Additionally the Entomopter, another multi-modal MAV, designed to operate with both aerial and terrestrial locomotion [53] developed at Georgia Tech Research Institute can too operate in both substrates. Although the main project aim in both cases was aerial and terrestrial locomotion, both had very different requirements leading to two completely different design solutions, one for operations in open spaces, the other for close quarter's operation such as inside buildings. The MALV can be seen operating in both mediums in figure 12. The biologically inspired aspects of this design are also highlighted within this figure.

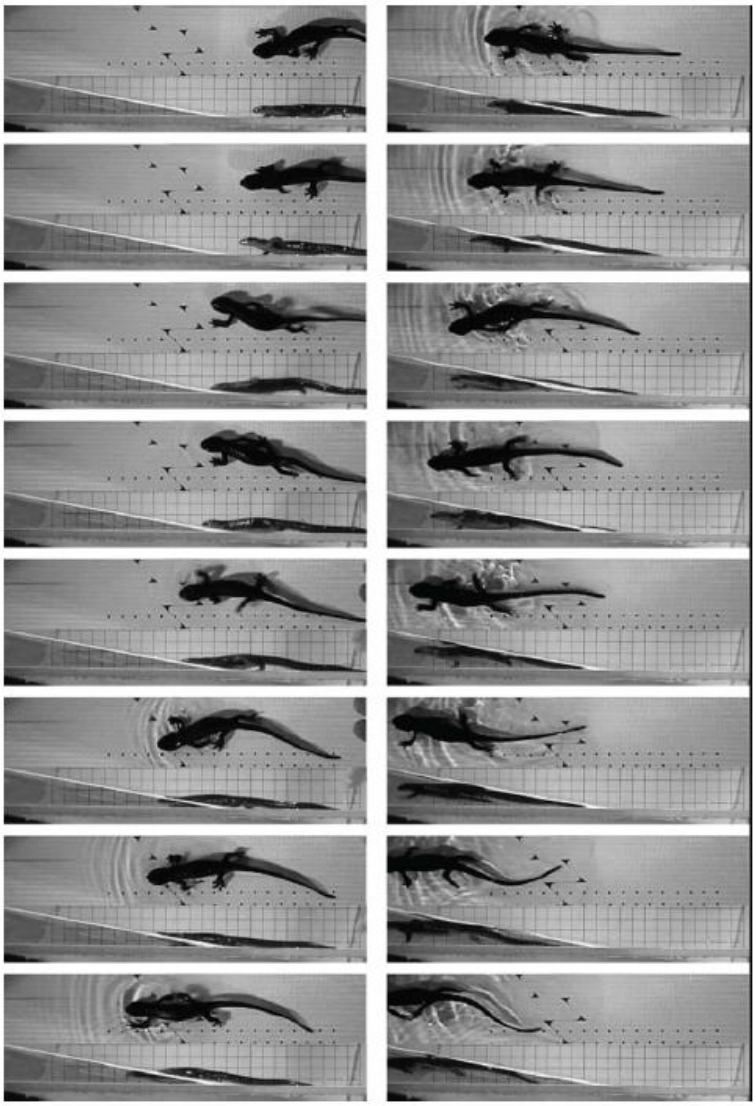

Figure 11. California newt, *Taricha torosa*, transitioning from terrestrial quadrupedal gait to aquatic body undulation. Reproduced with permission from [50].

Another success story lies with the bipedal ornithopter BOLT, from the University of California, Berkeley [54]. This platform achieves its goal of aerial and terrestrial locomotion using flapping wings in air and assisted bipedal locomotion on the ground. Interestingly the wings assist with the bipedal gait whilst completing terrestrial locomotion, identifying a potential advantage to having primarily disparate systems for each mode of locomotion, but not eliminating the potential of using one to aid the other. This trait, as highlighted in the previous sections, is not uncommon in natural systems. Another similar case is with DASH+Wings, a platform that demonstrates that the inclusion of wings on a hexapod robot can actual increase the terrestrial performance [55]. This system also provides a potential insight into the evolutionary process that lead to full flight capabilities in natural cases. Although not fully multi-modal, it clearly draws analogues with the biological systems detailed in the previous sections.

Another team at Stanford University have had success with a robot capable of gliding and perching [56]. Although not strictly multi-modal in that the vehicle does not complete terrestrial locomotion, but simply completes a perching operation, the design itself has taken abstract inspiration from nature in the form of the pads used to enable vertical surface perching. With modifications, the inclusion of an additional mechanism could potentially enable terrestrial operations expanding the task-space of the vehicle to truly aerial/terrestrial operations.

Taking this functionality one step further, a platform capable of climbing and gliding has been developed by [57] which is able to climb prepared vertical walls and complete gliding operations with performance characteristics similar to natural cases from which it drew inspiration.

Figure 12. The multi-modal (aerial/terrestrial) Micro Air Land Vehicle (MALV).

3.2. Aerial/aquatic

Of the multi-modal platforms currently developed, vehicles with the duality of function enabling aerial and aquatic modes of locomotion are by far the most immature of the cases. Although this is true, cases where vehicles can operate with this duality of locomotion have been proposed such as with a recent call from the Defence Advanced Research Projects Agency [58], highlighting the potential usefulness of a vehicle of this type.

Initial work on a vehicle that mimics the ability of the common guillemot, utilizing the same wing in both air and water can be found within [31, 59–63]. This work has begun to lay the foundations of understanding the natural system, which uses the same wings to propel itself in both air and water via a common musculoskeletal driving mechanism. Although starting to unravel the complexities of a vehicle of this type, many obstacles exist before a fully functional platform of this type can be realized.

3.3. Terrestrial/aquatic

At present, few robots have been developed that are capable of multiple modes of locomotion; however the majority of the work appears to focus on swimming/crawling robots. One example uses a snake-like robot design. The AmphiBot I and subsequent design iteration AmphiBot II are capable of both terrestrial and aquatic locomotion by utilizing the undulatory technique of a snake when on land and the anguilliform swimming technique much like a sea snake when in water [64, 65]. This duality of locomotive ability can be seen in figure 14. An alternative robot that uses a combination of wheeled propulsion on land and body undulations in water is the AmphiRobot [66]. This platform differs considerably from AmphiBot II in that it uses disparate mechanisms for the modes of locomotion, although the original inspiration arises from the same amphibious species. In both cases, the use of central pattern generators have been implemented to assist with control of the platforms. A subsequent design iteration, leading to AmphiRobot II has demonstrated locomotive abilities on land and in water [67]. A water tight version in the crawling RHex series of robots has been equipped with fin-like legs that allow it to swim under water [68]. Another similar solution to this has been the adaptation of legged propulsion such as with a surf-zone robot which is currently under development [69]. A major hurdle with any amphibious snake like robot is the need to make the inherently electrical system waterproof, whilst still allowing sufficient dexterity to complete the locomotive movements. This obstacle will be faced by any future research teams and must be given careful consideration.

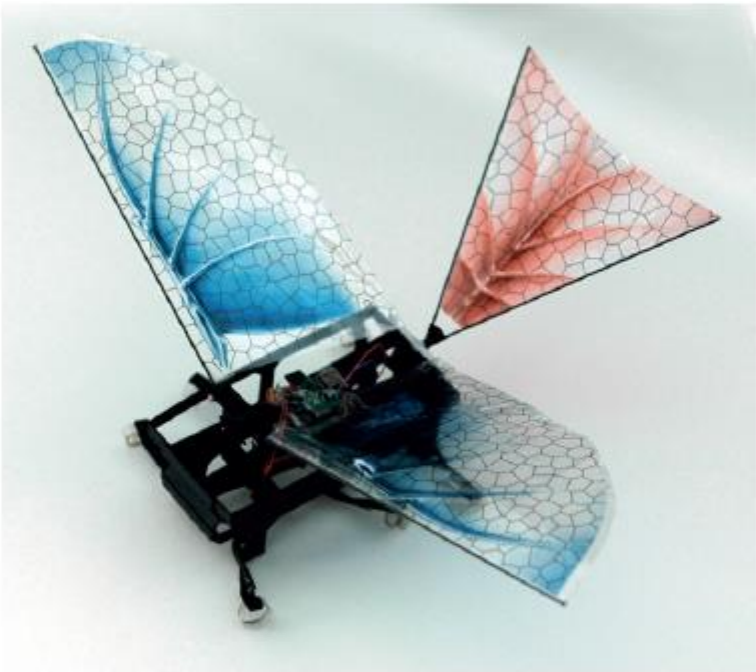

Figure 13. DASH+Wings from University of California, Berkeley. Reproduced with permission from [55].

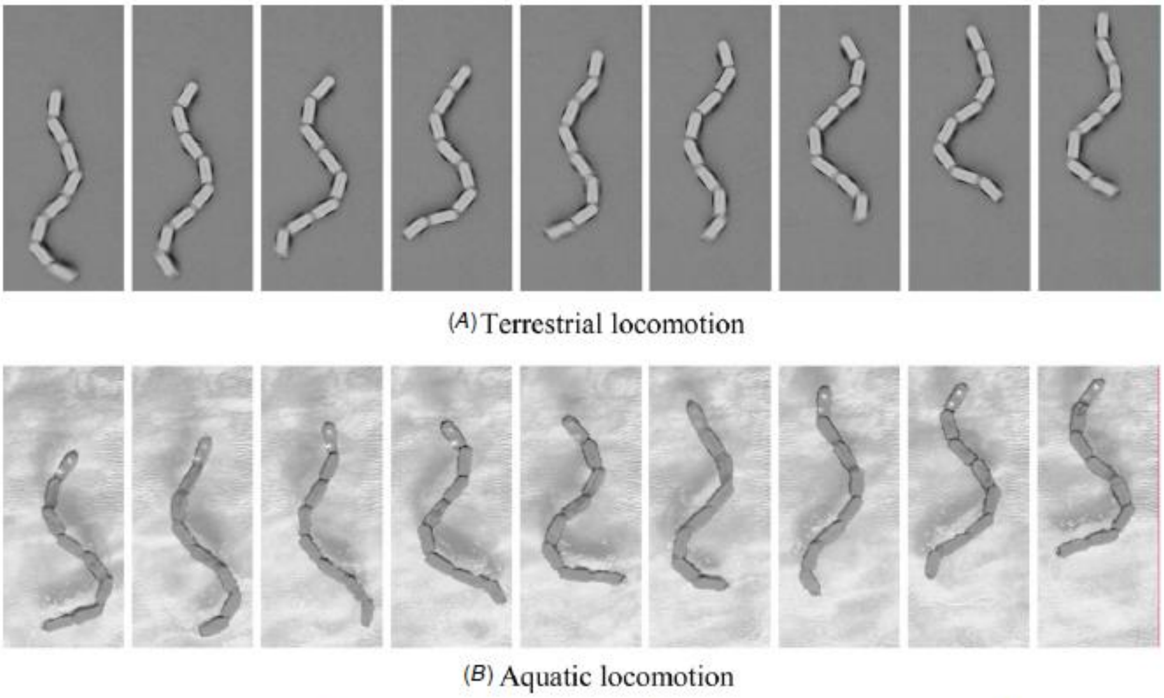

Figure 14. Amphibious snake robot—AmphiBot II. Reproduced with permission from [65].

The above are examples of past and on-going research projects; there is still much more being investigated around the world, drawing inspiration from nature. At the time of this research, no evidence was found of existing robot design projects, biologically inspired or not, that could operate with both aerial and aquatic locomotion, with the exception of the future concepts enabling AUVs with limited gliding capacity to allow aerial deployment [70, 71]. Being able to operate with both aerial and aquatic locomotion is inherently difficult and as such this apparent gap in knowledge is what makes this research into possible design solutions such an exciting direction to take the adaptable process of biological inspiration.

4. Conclusions

Considering all the natural examples shown for aerial/terrestrial operations it would appear that for multi-modal operations of this type, using two distinct locomotive mechanisms are advantageous. This is true for both birds and insects, with birds having the advantage of more feasible scalability of functions. The bats listed are an anomaly to this observation. Further experimental work would be required to determine if the terrestrial ability has led to a decrease in aerial ability within the bat species.

It is also clear that the integration of a mechanism for aerial operations which directly interferes with the mechanism for terrestrial locomotion has a detrimental effect on performance as shown within the mammals. Using a separate mechanism remains preferential when aiming for basic gliding performance.

Within the robotics community, platforms that have aerial/terrestrial capabilities are limited in number but are beginning to show progress. It should be highlighted that all current designs listed utilize independent mechanisms for propulsion in each medium, but in some cases the secondary mechanism (i.e. not the primary driver of the locomotion mode) is used to assist, such as the case with BOLT which uses the wings to help stabilize the platform during terrestrial locomotion. This highlights the potential advantage of having a combination of locomotion mechanisms, even if the benefit is not obvious in the first instance.

For aerial/aquatic operations, birds appear to offer the greatest potential when seeking inspiration. Both strategies involving combined and separate locomotion mechanisms have been successful. The key difference being the techniques that use two distinct mechanisms do not see a trade-off occurring in performance between the two, whereas the same mechanisms do. However, the case that uses the same mechanism for both modes achieves a higher level of performance during aquatic operations. Fully developing an aerial/aquatic robotic vehicle has not yet been accomplished, but as technologies continue in their advancement it is only a matter of time before this capability is realized.

Once again using different mechanisms for each mode of locomotion appear to offer higher levels of performance in both mediums when considering terrestrial/aquatic operations. The transition from drag based propulsion to lift based propulsion can be observed within mammals, resulting in detrimental effects on the terrestrial ability. The combination of body undulations in water and walking on land appear to be the best solution to this problem. However, snaking and anguilliform swimming, although not the most energy efficient modes of locomotion do offer very high levels of mobility in both mediums, utilizing the same locomotion strategy. Depending on the required task-space, this technique does offer much potential. It would appear from this initial qualitative analysis that the two multi-modal operations that would benefit from utilizing the same mechanism in both mediums is the flapping mechanism exhibited by birds in aerial/aquatic operations, and snaking and anguilliform swimming in terrestrial/aquatic operations, a lesser number than the authors had expected. In future mobile robotic platforms, engineers should attempt to identify ways in which discrete locomotion mechanisms can be used to assist additional modes through a secondary function, such as aiding stability, assisting mode transitions and increasing performance.

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