The flying ability of the pterosaur *Quetzalcoatlus northropi* in a reduced gravity

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Abstract

The envisaged flying ability of the gigantic *Quetzalcoatlus northropi* pterosaur has produced ongoing debate since its first discovery, mainly because aeronautical calculations show it is too large to produce continuous powered flight in our gravity. This problem has encouraged a number of authors to suggest that continuous powered flight might be possible in a reduced gravity. This study quantifies the flying ability of a *Quetzalcoatlus northropi* in a reduced gravity of 0.62g (6.08 m/s²). The results show that *Quetzalcoatlus northropi* was capable of producing continuous powered flight in this reduced gravity, allowing its flying ability to be comparable with the largest flying animals of today.

Key words: Palaeogravity, *Quetzalcoatlus northropi,* flying ability.

Introduction to *Quetzalcoatlus northropi*

Pterosaurs have been known for more than two centuries. A pterosaur fossil was found between 1767 and 1784 in the Solnhofen limestone quarry that would later yield the famous fossil bird *Archaeopteryx*. The exquisitely preserved pterosaur skeleton soon began to intrigue the natural historian Baron Georges Cuvier, who was the first to realize that the long fourth finger supported the membrane of a wing. The scientific description of *Pterodactylus antiquus* by Cuvier (1801) was the first pterosaur species to be named and described. Over the centuries of further research it became clear this was only one species of a highly successful group of flying animals with a membrane wing supported on a single digit. Many species also often had a large and bizarre skull and crest. Although they dominated the skies for hundreds of millions of years, ranging from the Late Triassic to the end of the Cretaceous, they are now completely extinct.

The first pterosaurs discovered were relatively small but many new discoveries gradually increased the known size of pterosaurs. By the late 1960s various *Pteranodon* specimens were approaching 7 metres wing span. Since the largest flying animals today have wing spans in the 3 metre range it was recognised that these animals seemed too large to fly, prompting a great deal of debate.

In the early 1970s Douglas Lawson and his colleagues discovered the remains of several large pterosaurs in the Maastrichtian sediments of the Late Cretaceous of North America, placing their age at approximately 68 million years old. One of these fossils was the humerus bone of a gigantic wing that far surpassed the size of any pterosaur wing found previously. Lawson (1975) named the pterosaur *Quetzalcoatlus northropi*. Most recent studies estimate that its wing span was in the 10 to 11 metre range.

The fossil evidence seems to indicate that *Quetzalcoatlus northropi* were spread over a huge area. Fossils have been reported from far afield: Buffetaut *et al* (1997) reported fossils from France, Padian & Smith (1992) and Henderson & Peterson (2006) from Montana, and Godfrey & Currie (2005) from Alberta. All this seems to indicate that *Quetzalcoatlus northropi* was geographically widespread and it has been widely depicted as being able to cover vast distances.

Quetzalcoatlus northropi was as large as a small plane and stood as tall as a giraffe, as shown in Figure 1. Although it has become famous as one of the largest flying animals of all time more recent fossil discoveries indicate that it wasn't the only gigantic pterosaur. It is now considered to be part of a group that demonstrates the spectacular sizes of the largest pterosaurs. Some of the species included in this group are *Hatzaegopteryx*, *Arambourgiania*, as well as *Quetzalcoatlus*. They are larger than every other flying animal known.

It is possible to learn more about the pterosaurs in a variety of publications. The superbly illustrated book *Pterosaurs*, by the palaeontologist Mark Witton (2013) is a good place to start.

FLYING ABILITY IN PRESENT GRAVITY [1g (9.81 m/s^2)]

The flying abilities of the largest pterosaurs have been constantly debated since their first discovery. Many seemed too large to fly. The problem is one of scale. We can predict how a particular quantity will vary if the size of an animal changes. The same aeronautical problems are encountered by birds. If we image a series of "geometrically similar" birds of various sizes, both the mass and volume vary with the cube of the length. However, the power available scales less than the power required to fly as the mass increases. The trend has readily visible consequences so that small birds have power to spare. Large birds often struggle to even take off. It is difficult to establish what the heaviest living bird is but the upper limit seems to be between 12 to 16 kg with a wing span in the 3 metre range. All these observations about flight have profound implications for pterosaurs that were obviously much larger and heavier than current physical limits seem to allow.

When Lawson (1975) first announced the discovery of *Quetzalcoatlus northropi*, with an estimated wing span of between 11 to 21 metres, engineers pointed out that it was impossible for such a large animal to

Figure 1. *Quetzalcoatlus northropi* and a giraffe to the same scale. With an estimated wingspan of 10 metres the gigantic pterosaur would have stood as tall as a modern giraffe. The *Quetzalcoatlus* is a CollectA model that is just about to eat a baby *Alamosaurus*, while the giraffe is a PNSO model.

fly in our gravity, so the palaeontologists must be wrong. The palaeontologists responded that it must be the engineers who were wrong since the animal obviously existed. The debate about its flying ability continued when Langston (1981) published an article about the discovery of *Quetzalcoatlus northropi* in the journal *Science,* estimating the wing span at a conservative 11.2 metres. Most palaeontologists were adamant that *Quetzalcoatlus northropi* could fly even if aeronautical calculations predicted this was impossible. Bakker (1986, p290) perhaps summed up the feelings of most palaeontologists when he reflected that the "…aerial leviathan was stupefyingly large. Mechanical engineers go often astray when analysing the strength of skeletons."

A lot of the research and debate about *Quetzalcoatlus northropi* has focused on how such a large animal could fly. MacCready (1985) collaborated on the construction of a half life-sized robotic model of *Quetzalcoatlus northropi* that could eventually glide. The consensus view between the palaeontologists and engineers who worked on the project was that the mass of the living *Quetzalcoatlus northropi* could not be more than 64kg based on the aerodynamic results from this model.

The suggestion that pterosaurs as a group were remarkably light for their size was continued in a number of studies. Since such an ultra-light body indicated they lacked the muscles to produce powered flight it was proposed that they must have been gliders. Chatterjee & Templin (2004) calculated that an extremely lightweight 70 kg *Quetzalcoatlus northropi* with a 10 metre wing span would need the addition of a downhill run and a headwind to enable it to launch. From then on it would need to stay aloft by gliding from one rising thermal to another.

Sato *et al* (2009) estimated that even smaller pterosaurs such as *Pteranodon* would be unable to produce continuous powered flight based on the flight dynamics of existing animals. They based their conclusions on a study of the flight mechanics of modern day ocean-going albatrosses and petrels. Using their mass dataset they were able to predict that a 5.1 m wing span and 41 kg mass was the absolute limit for pterosaur flight. These limits would imply that many pterosaur species, including *Quetzalcoatlus northropi,* would be incapable of flight in our present environment.

Henderson (2010) estimated the body masses of 14 species of pterosaur using three-dimensional digital models. The largest and most troubling pterosaur was *Quetzalcoatlus northropi*. The estimated mass of 544 kg was considered "astonishingly high". However, it was noted that the previous low mass estimates of 64 kg and 70 kg required "more than 90% of the body filled with air" so were difficult to accept biologically. Henderson (2010, p783) suggested that *Quetzalcoatlus northropi* might have been flightless since,

> "Accepting this possibility releases us from the requirement to generate, and accept, unrealistically low masses and body densities for such large animal. It also frees us from the mental gymnastics required to generate an anatomy with sufficient muscle mass and power to be able to fly when possibly weighing more than thirty times that of the heaviest, living birds such as the 16-kg Kori Bustard (Ardeotis kori) and the Great Bustard (Otis tarda), which may attain 22 kg in some cases. These birds seem to be at the upper mass limit for flying given their apparent difficulty in taking off (Alexander, 1998). A study of the scaling relationships between body mass and the flapping and gliding flight styles in procellariform birds—albatrosses and their closest relatives—predicts an upper body mass limit of 41 kg for this type of flying (Sato *et al.,* 2009)."

Because of these considerations about the high mass Henderson (2010) constructed an alternative model with the body width and depth reduced by 20% and 25% respectively. The total mass of this thinner model was estimated to be 268 kg.

In another study, Witton and Habib (2010) objected to the Sato *et al* (2009) conclusion that many large pterosaurs would be incapable of flight, responding that this limit would imply that "a considerable number of pterosaur taxa had far outgrown the limits of flight." Yet, their own studies indicated that even giant pterosaurs had all the anatomical hallmarks of flight.

Witton and Habib (2010) suggested that pterosaurs were more massive than the superlight versions previously suggested, with *Quetzalcoatlus northropi* predicted to be in the 200-250 kg range. Using the *Flight* computer program of Colin Pennycuick (2008b) they calculated that this more massive pterosaur would need to have about 40% of its body mass as flight muscle to enable it to take off and climb with flapping flight. Unfortunately, the lungs and heart of this pterosaur would be too small to supply the energy and oxygen necessary to keep these flight muscles working aerobically. A 40% flight muscle mass is about twice the muscle mass that the lung and heart could realistically supply. In order to overcome this problem they suggested that the flight muscles only worked anaerobically for short periods of time. Medbo *et al* (1988) measured that the muscles of highly trained athletes can work anaerobically for up to 2 minutes before complete exhaustion, after which there is an accumulated oxygen deficit that must be recovered. Witton and Habib (2010) therefore proposed that a large pterosaur would be capable of powered flight for around a minute before exhaustion forced it to glide, hopefully to a thermal.

Fossil remains seem to indicate that *Quetzalcoatlus northropi* could easily cross oceans. It is very common to hear the assumption that it was able to fly these vast distances. A typical example was contained in the 2011 Sky documentary, *Flying Monsters with David Attenborough,* where we are told that the largest creatures to ever fly "could travel half way around the world in a single flight". This claim is not supported by aeronautical calculations that show *Quetzalcoatlus northropi* would be incapable of fully powered flight in our present environment. Trying to envisage such a large animal as *Quetzalcoatlus northropi* flying in our gravity predicts that the animal had to be a more extreme glider than any animal alive today, whether it was an ultra-light 70 kg animal or a more robust animal. It would be a much poorer flyer than any we know. Observations of modern-day animals that use thermals to provide extra lift indicate that a gliding *Quetzalcoatlus northropi* would have extreme difficulty in crossing any large expanses of water. We can see how difficult it is by observing white storks as they head south to escape the upcoming winter. Half a million journey to Africa across the Mediterranean Sea using thermals to gain heights of a few kilometres. They need the altitude to cross the open water. This is the riskiest part of the journey. Those that haven't gained enough height must begin to flap their wings, starting to burn body fat just to stay airborne. They are now using 20 times more energy than when they were gliding. Since white storks struggle to cross the Mediterranean Sea we know that *Quetzalcoatlus northropi* would struggle even more. The white storks can use prolonged energetic wing flapping if they encounter bad weather. This is not an option available to *Quetzalcoatlus northropi* in a 1g environment since it would be incapable of any prolonged powered flight.

Most writers have considered giant pterosaurs as mere gliders. Their flying ability is predicted to be greatly inferior to birds and bats. Some palaeontologists avoid the problem of imagining such a large flying animal as *Quetzalcoatlus northropi* by assuming it didn't fly. Prentice *et al* (2011) for example discuss the "giant and probably flightless *Quetzalcoatlus*" in their comprehensive review of pterosaur evolution. Most are well aware that we do need "mental gymnastics" to believe that such a large animal was capable of flight. It is clear that reconstructions of *Quetzalcoatlus northropi* all show it would struggle to survive in a 1g environment. It doesn't matter if we imagine an ultra-light or heavier mass pterosaur. All aeronautical calculations illustrate that continuous powered flight is not possible. The reconstructions must resort to imagining that *Quetzalcoatlus northropi* was only capable of gliding from one strong up-current of air to the next. It was an animal only barely capable of level flight so we must wonder how it could manage to catch food, or recover from the weight of prey. This vision of a weak flyer presents additional problems since these up-currents would not be available over water or at night, further limiting its flying abilities. All these problems only arise because we are trying to imagine such a gigantic animal flying in a 1g environment.

FLYING ABILITY IN REDUCED GRAVITY

A number of authors, including Pennycuick (2008, 2015), Sato *et al* (2009), Hurrell (1994, 2011) and others have suggested that a reduced gravity would allow pterosaurs to achieve fully powered flight.

Colin Pennycuick was a leading authority on the mechanics of animals' flight. Amongst his many contributions he advanced our understanding of the relationship between the power of flight muscles, wingbeat frequency and the power density of mitochondria - the "powerhouse" of cells. He produced a computer program, *Flight*, which can calculate flying performance without enquiring if the numbers came from a bird, a bat or a pterosaur. The program was checked against many measurements on birds to confirm that the predictions of the *Flight* program agreed with reality. These studies have highlighted the difficulties that large animals such as pterosaurs would have in finding enough power to fly. In his last 2015 book, *Birds never get lost*, he repeated the judgement he voiced for many years,

> "Among living species, the big birds that can flap well get up to masses of 12 kg, or occasionally to 16 kg, with obvious difficulties in finding enough power to fly. That raises problems, because through the second half of the Cretaceous, there was a wide range of pterosaurs that had wing spans of 5 m and up, against 3 m for modern birds." … "These end-Cretaceous giants were far bigger than giant swans, and there is no way in which they could have flown by flapping flight, under today's strength of gravity. Is it possible that the Earth surface gravity might have been progressively reduced, through the last few mil-

lion years of the Cretaceous?” [Pennycuick, C., & Pennycuick, S. (2015) p 53]

> [Pterosaurs could fly] in late Cretaceous times, because gravity at the Earth’s surface was less than it is now, so they flew more slowly than they would today…” [Pennycuick, C. & Pennycuick, S. (2015), p 152]

Sato *et al* (2009) also suggested that gravitational conditions might be different to those in modern times after concluding that the largest pterosaurs would be unable to fly, based on their studies of modern-day ocean going albatrosses and petrels. The fossil-based estimates of even modest-sized pterosaurs were much larger than the limits indicated by their studies. Sato *et al* (2009) noted that this implied pterosaurs “could not have attained sustainable flight in environments similar to the present”. They suggested that changes in other environmental factors such as the “strength of gravity and density of the air” might explain the appearance of large pterosaurs in the fossil record.

Hurrell (1994, 2011) has also noted that a reduced gravity would enable the largest pterosaurs to fly “with as much grace as today’s birds and bats”.

Calculations of the flying ability of *Quetzalcoatlus northropi* in a reduced gravity are complex. Fortunately, the use of the Pennycuick *Flight* program simplifies this task. We only need to input the variables: mass, flight muscle mass, gravity, wing span and wing area. The rest of the variables can be set to standard values and the program calculates how well this animal could fly.

Mass

Mass estimates for *Quetzalcoatlus northropi* have varied widely. Chatterjee & Templin (2004) estimated *Quetzalcoatlus northropi* had a mass of 70 kg, but this low estimate seems mainly to have been suggested to allow it to glide. Paul (2002, p146) estimated a mass of between 200-250kg and this seems to have been uninfluenced by any worries about its aerodynamic capability. Henderson (2010) estimated a mass of 544 kg or 268 kg for a thinner reconstruction. Witton and Habib (2010) reported that the model of *Quetzalcoatlus northropi* Henderson used was apparently based on proportionally incorrect reconstructions in semi-technical literature. By utilising a more appropriate body length estimate, they calculated the mass estimate for the Henderson *Quetzalcoatlus northropi* model dropped from 544 kg to about 240 kg. Witton and Habib (2010) estimated that the most reliable upper estimate was in the 200-250 kg range.

If a range of large birds are scaled up to the same wing span as *Quetzalcoatlus northropi* various masses are obtained that can be used to provide a comparison. Taking the mass and wing span of a range of larger birds from the *Flight* program and then calculating the scaled mass for a 10 m wing span [$(10/\text{wing span})^3$ x mass] gives: Cinereous vulture: 9.9 kg, 3.04 m, [352 kg], Kori bustard: 11.9 kg, 2.47, [789 kg], Greylag goose, 3.77 kg, 1.6 m [920 kg], Lappet-faced vulture: 6.6 kg, 2.64 m, [358 kg], Wandering albatross: 9.57 kg, 3.06 m, [334 kg]. Whooper swan: 12.5 kg, 2.56 m, [745 kg]. The predicted flight ability of all these animals in a reduced gravity can be checked within the *Flight* program. It is clear that the mass of *Quetzalcoatlus northropi* could easily fall within many of the predicted values in a 0.62g environment. However, most palaeontologists prefer a lower mass estimate.

The mass used for *Quetzalcoatlus northropi* in this paper is 250 kg.

Flight muscle mass

Witton and Habib (2010) found they had to increase the flight muscle mass to 40% to enable their pterosaur to fly for a short time in 1g (9.81 m/s^2) but this flight muscle mass can be reduced to 17% in the reduced gravity of 0.62g (6.08 m/s^2). Since the proportion of flight muscle mass to body mass is reduced to similar levels observed in large birds (Goose - 17%, Bustard – 17%, Vulture – 15 to 17%) we know these flight muscles could be continuously powered by the heart-lung system of the pterosaur.

Gravity

The palaeogravity at the time of *Quetzalcoatlus northropi* has been previously calculated using the weight–mass method [see Hurrell (2020) for an overview of this method and the results obtained]. A tentative formula for the calculation of the relative palaeogravity predicted by this data is:

$$g_a = 0.52.e^{-0.018.a} + 0.47$$

where a is the time before present in millions of years. This formula gives the relative palaeogravity taking the present gravity as 1. If palaeogravity is required in m/s^2 then g_a should be multiplied by 9.81.

This formula indicates that it is likely that a reduced palaeogravity of approximately 0.62g (6.08 m/s^2) existed at the time *Quetzalcoatlus northropi* flew about 68 million years ago. This reduced palaeogravity can be input directly into the *Flight* program.

Wing span

Chatterjee & Templin (2004) estimated *Quetzalcoatlus northropi* had a wing span of 10.4 metres. Paul (2002, p146) estimated a wing span of between 10 to 11 metres. Witton and Habib (2010) used a wing span of 9.64 metre in their flight calculation. The wing span used in this paper is 10 metres.

Wing area

The key parameter that affects the lift-to-drag ratio of a wing is the aspect ratio of the wing. This can be defined in terms of the "plan view" of the wing most simply as the ratio of the overall length of the wings to their average width, or chord. Since wing tips often taper towards their tips the mean chord is often difficult to determine. Because of this the aspect ratio is often defined as the square of the wing span divided by the profile area of the wing. All these parameters are automatically calculated by the *Flight* program from just the wing span and the wing area.

It is sometimes argued that the wing of large pterosaurs must have had a large area to support their mass, but this is incorrect. The aerodynamics of wings is not as obvious as it might first appear. We can't just increase the area of a wing in order to increase lift. In practice, the flow of all fluids seems counter to what we might expect. When a fluid flows from a larger to a smaller diameter pipe for example, the common perception is that the pressure would be greater in the smaller diameter pipe. In fact it is lower. This is explained within the Bernoulli Equation in terms of the energy in the fluid which must be converted into a faster velocity in the smaller pipe thereby reducing the pressure. The same sort of complex relationships mean that a wing that is long and narrow is more efficient than a broad one. It provides more lift because speed is increased due to reduced drag. This type of wing has a high lift-to-drag ratio.

There aren't any fossils indicating the exact wing shape of *Quetzalcoatlus northropi* but we can infer the optimum shape from these various aeronautical considerations. The optimum shape of the wing must account for many differing requirements. Firstly the wing must be as efficient as possible while in flight and this implies a long thin wing so it has a high lift-to-drag ratio. But when landing or taking off the wing needs to present the broadest expanse possible to enable the slowest flight speed possible. A large animal forced to land fast has a much greater risk of injuring itself than one that flies slower with a slightly less efficient wing.

The effect of size is also evident in the optimum shape of the wing due to the lift-to-drag ratio. Vogel (1988, p130-157) for example gives formulas for both the lift and drag based on the shape of the wing outline. Skin friction is the main sort of drag for streamlined aerofoils so the best lift-to-drag ratios are dependent on size. For an aeroplane-sized wing the best ratio may be 25:1, for a locust wing it is about 8:1, for a fruit-fly wing it's less than 2:1. Since *Quetzalcoatlus northropi* is plane sized we would expect it to evolve to achieve a lift-to-drag ratio of about 25:1 for efficient flight. The requirement to land with this high lift-to-drag ratio would imply a high speed landing but this speed is reduced slightly in a reduced gravity.

From these aeronautical considerations it would seem that an optimum wing shape would be 10 metres wide with an area of 7 square metres. This is an aspect ratio of 14.3:1, producing an effective lift-to-drag ratio of 24.8:1 at the minimum power speed of 20.7 m/s. This speed is comparable with the minimum power speed of a Bustard (21.2 m/s), Goose (16.2 m/s), Vulture (16.2 m/s) or Albatross (16 m/s), indicating that the flying ability of *Quetzalcoatlus northropi* would be similar to the large birds we know.

There has been a long debate about the structure and shape of the wing membrane for pterosaurs in general. Most postulate a relatively wide wing profile but some have argued for a narrow wing shape. Padian (1985) noted that this narrow wing would allow the wing to be easily collapsed without loss of aerodynamic competence. The optimum wing shape used in this paper is slightly wider than the narrow version suggested by Padian (1985) so we could imagine *Quetzalcoatlus northropi* being relatively agile in the air as it changed the profile of its wing to suit various flying conditions.

Athletic Flying Ability of *Quetzalcoatlus northropi*

The athletic ability of today's flying animals is related to their size. Small birds can easily take off and land but larger birds clearly struggle. One way of quantifying their athletic ability is to calculate their rate-of-climb. As shown in Figure 2, a comparison of wing span to the maximum rate of climb shows how this variable is a good indication of a bird's athletic ability. The Pennycuick *Flight* program indicates that the maximum rate of climb for *Quetzalcoatlus northropi* in a reduced gravity of 0.62g (6.08 m/s^2) would be 0.425 m/s, indicating that its athletic ability would be comparable with the largest flying animals of today.

Take-off

Trying to reconstruct large pterosaurs capable of flight in 1g has led many palaeontologists to infer that take-off could not occur without assistance from slopes, constant headwinds or cliff edges. A pterosaur adapted to living in a reduced palaeogravity would encounter none of these hindrances.

The 17% flight muscle mass of *Quetzalcoatlus northropi* in a 0.62g (6.08 m/s^2) palaeogravity would enable it to generate enough lift to take off without any further assistance. Slopes, strong winds and cliff edges are no longer required so a pterosaur living in a reduced palaeogravity could live in a much wider range of habitats.

Pterosaurs were quadrupedal while on the ground so Habib (2008) has described how it would seem reasonable to imagine that they launched into the air directly from that position. Their strong arms were particularly well developed around the shoulders so they would be capable of catapulting themselves into the air from a standing start. Far from being weak flyers, pterosaurs could employ their powerful flight muscles to almost explode into the air. This would all happen in a very rapid motion so that even the largest pterosaurs would be clear of the ground in a second or so. Small pterosaurs would be able to spring into the air vertically but the climb angle would decrease with size. The calculated climb rate for *Quetzalcoatlus northropi* in a 0.62g (6.08 m/s^2) palaeogravity is 0.425 m/s so it would require a relatively open environment to take off, free of any trees for example.

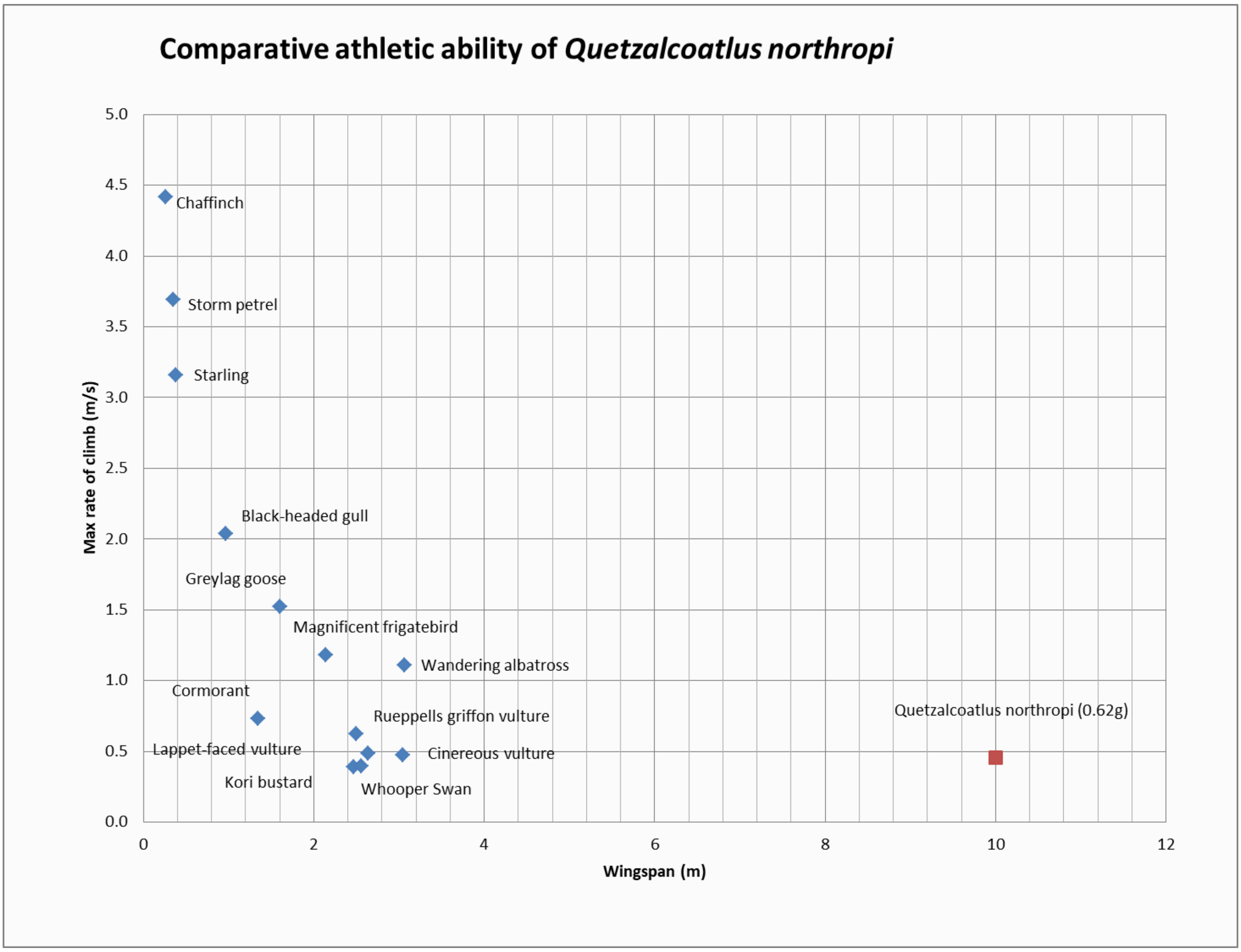

Figure 2. The maximum rate of climb of a flying animal is a good indication of its athletic ability. A range of birds (wingspan, maximum rate of climb) are shown: Chaffinch (0.264 m, 4.42 m/s), Storm petrel (0.36 m, 3.69 m/s), Starling (0.384 m, 3.16 m/s), Black-headed gull (0.967 m, 2.04 m/s), Cormorant (1.35 m, 0.731 m/s), Greylag goose (1.6 m, 1.52 m/s), Magnificent frigatebird (2.14 m, 1.18 m/s), Kori bustard (2.47 m, 0.391 m/s), Rueppells griffon vulture (2.5 m, 0.623 m/s), Whooper Swan (2.56 m, 0.395 m/s), Lappet-faced vulture (2.64 m, 0.487 m/s), Cinereous Vulture (3.04 m, 0.472 m/s) and Wandering albatross (3.06 m, 1.11 m/s). These can be compared with *Quetzalcoatlus northropi* in a reduced gravity of 0.62g (6.08 m/s^2) with a maximum rate of climb of 0.425 m/s, indicating that its athletic ability (in a reduced gravity of 0.62g) would be comparable with the largest flying animals of today.

In the air

In a 0.62g (6.08 m/s^2) palaeogravity environment the flight muscles of *Quetzalcoatlus northropi* can be reduced to only 17% of the total body mass. This low flight muscle mass means the heart and lung system would be able to always supply these muscles so they can operate aerobically. It can continuously flap its wings from the moment it takes off to the time when it lands. This would mean its environment can be substantially different from a glider that must live close to rising air currents.

Landing

A recently discovered trackway of a pterosaur landing indicates this was relatively easy. Mazin *et al* (2009) describe how the footprints of a pterosaur landing indicate that it appears to have lost most of its flight speed before landing to drop onto both feet simultaneously. The entire body must have pitched up so the legs could swing into a landing position. After gently lowering itself onto the floor the animal dropped forward onto its hands in one fluid motion as the wings were folded away.

On the ground

All known pterosaur trackways indicate that they habitually walked on all four limbs. Trackways from giant pterosaurs with an estimated shoulder height of 2.5 metres have been described by Hwang *et al* (2002). The pterosaur footprints are consistently found in front of their handprints, indicating that their hands had to be clear of the ground before the foot was placed on the ground.

Various feeding strategies have been suggested for the large pterosaurs. One proposal was that the largest pterosaurs dined on a range of smaller animals and various eggs. A modern-day comparison might be a heron that regularly feeds on small ducklings – a search on YouTube will show the often brutal way this is accomplished. An interesting comparison is that a human-sized animal of about 70 kg mass would seem to make a convenient-sized snack for *Quetzalcoatlus northropi*. The CollectA *Quetzalcoatlus* model includes a baby sauropod dinosaur that is just about to be eaten. Could it still fly with that added mass? Entering the appropriate figures into the *Flight* program (as a payload mass and assuming the same flight muscle mass) indicates that its rate of climb would be reduced from 0.425 m/s to 0.121 m/s. Our *Quetzalcoatlus northropi* could clearly include a 70 kg mass animal in its diet without critically endangering its flight performance. Time travelling humans would need to watch the skies!

Migrating

All animals need energy to migrate and this energy is in the form of fat. The distance our *Quetzalcoatlus northropi* can fly (its range) depends on the fat fraction and this can be calculated using the **Migrate** function of the *Flight* program.

Choosing **Migrate** in the *Flight* program allows a fat mass to be added. A typical moderate value is a fat fraction of 0.2 (meaning that 20% of the body mass is fat). Setting the **Fat mass** to a moderate 60 kg changes the *Quetzalcoatlus northropi* body mass to 310 kg, since the body mass also includes 60 kg of fat. **Start migrating** now allows the *Flight* program to calculate a power curve, works out the speed and the power, and from that, the rate at which fat is consumed. It calculates that *Quetzalcoatlus northropi* runs out of fat having flown 10,744 km continuously for 98.7 hours. Our *Quetzalcoatlus northropi* could very easily migrate from what is now the USA to Central Europe, crossing the developing Atlantic Ocean in the process.

Changes in Air Density

A popular alternative proposal to a reduced gravity is that the atmosphere was denser during the time of the pterosaurs, allowing them to reach larger sizes. I had many interesting discussions with Robert (Bob) Tuttle in particular about the suggestion that a denser atmosphere would explain the large size of pterosaurs. Tuttle (2015) explains his thoughts in detail in the NCGT Journal. This was a reply to my article, *A new method to calculate palaeogravity,* Hurrell (2014), proposing that fossil feathers could be used to calculate palaeogravity. Tuttle wasn't alone in his views, both the other two responses to my original article also suggested a denser atmosphere might account for the results reported - see Beatty (2014) and Gregori (2015). Various increases in atmospheric density above the present were proposed, Tuttle (2015) suggested between 1.7 to 4.5 times the present atmospheric density while Gregori (2015) suggested between 1.46 and 2.33. Tuttle (2015) also noted that a much more extreme atmospheric density of between 278 to 352 times the present would provide buoyancy for dinosaurs like *Argentinosaurus* and *Tyrannosaurus rex,* so this thick air would also provide buoyant support to the ancient birds and pterosaurs.

Clearly the effects of air density need to be quantified and the *Flight* program allows the calculation of flight performance with an increased air density. With a standard atmospheric pressure (1.23 kg/cu m) the maximum rate of climb in a reduced gravity would be 0.425 m/s. With an increased air density of twice standard (2.46 kg/cu m) the maximum rate of climb drops to 0.383 m/s, at four times standard (4.92 kg/cu m) the maximum rate of climb drops to 0.333 m/s, at fifty times standard (61.5 kg/cu m) the maximum rate of climb drops to 0.171 m/s. The *Flight* program shows that an increased air density increases drag, thereby slowing the airspeed and reducing lift. Clearly an increased air density atmosphere is more difficult to fly in and wouldn't account for the large size of pterosaurs.

Another option is to decrease the air density. Setting this to one third (0.4 kg/cu m) the standard density increases the maximum rate of climb to 0.439 m/s in a reduced gravity of 0.62g (6.08 m/s^2). This small increase in performance is replicated by birds which regularly fly at high altitude, particularly when migrating. However, the increase in performance is relatively minor compared to other factors.

It is clear from these calculations that a change in air density would be unable to account for the large size of *Quetzalcoatlus northropi*.

Conclusions

Aeronautical calculations show that in a palaeogravity of 0.62g (6.08 m/s^2) a gigantic *Quetzalcoatlus northropi* pterosaur, with a wing span of 10 metres and a mass of 250 kg, would have similar athletic ability to the largest birds of today. The main attributes of a gigantic *Quetzalcoatlus northropi* in a 0.62g (6.08 m/s^2) environment would be:

- The flight muscle mass would enable it to generate enough lift to take off without any further assistance, negating any requirements for wind or slope assistance.
- The maximum rate of climb would be 0.425 m/s, indicating that its athletic ability would be comparable with the largest flying animals of today.
- Flight muscles could be continuously powered by the heart-lung system of the pterosaur, negating any requirement to be a glider.
- It could fly 10,744 km continuously on fat reserves, so could very easily migrate from what is now the USA to Central Europe, crossing the developing Atlantic Ocean in the process.
- It could easily include a 70 kg mass animal in its diet without critically limiting its flying ability.

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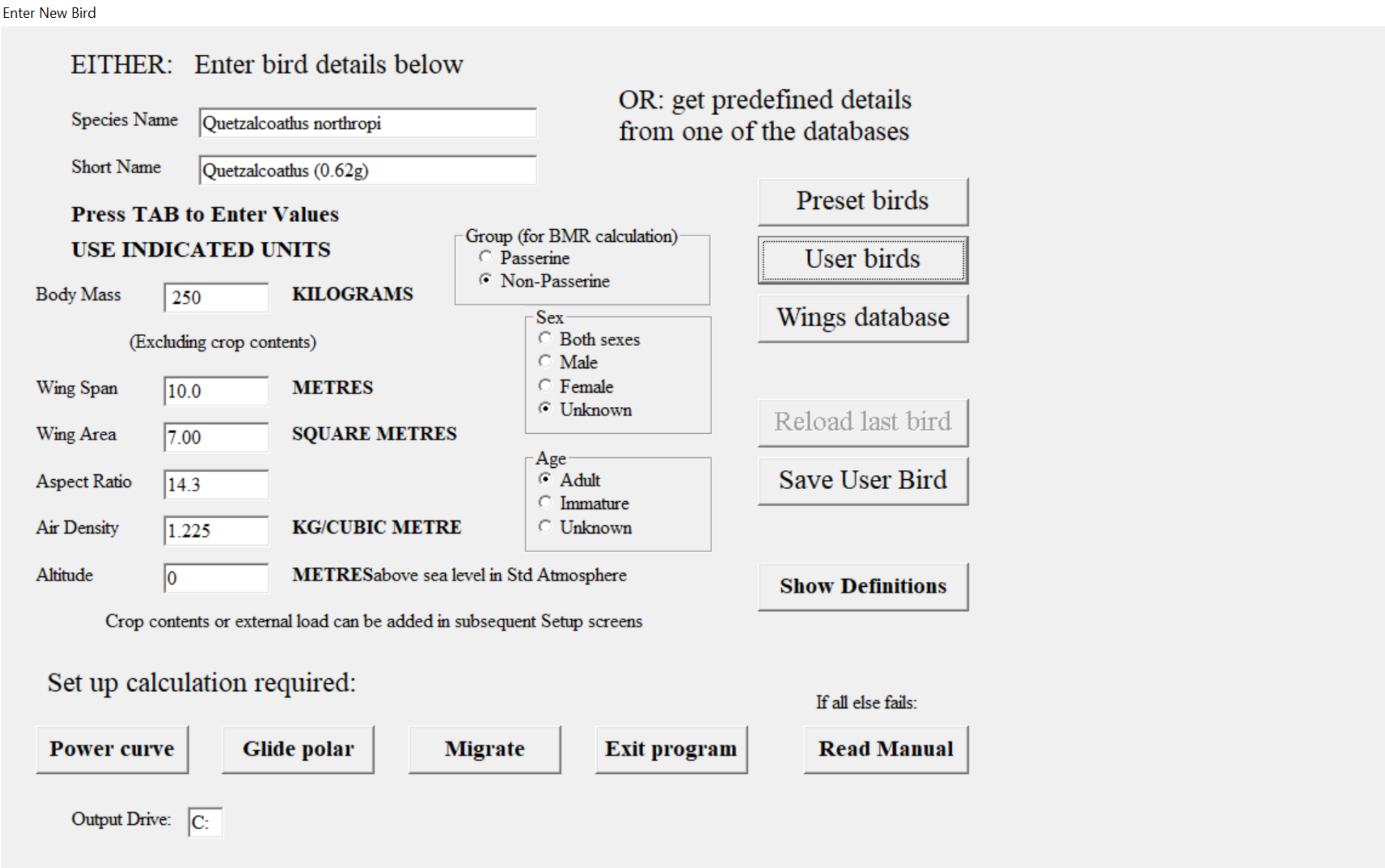
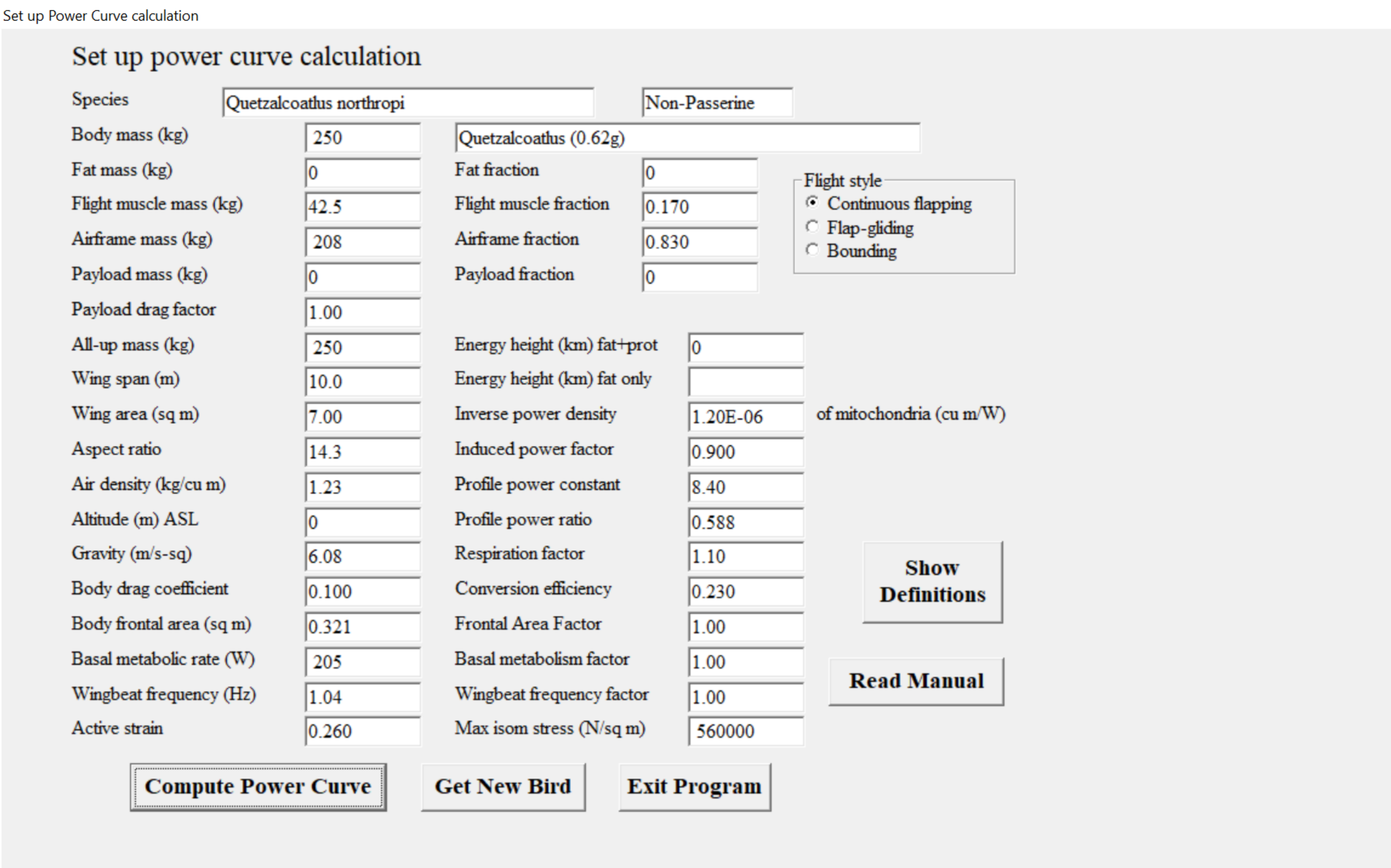
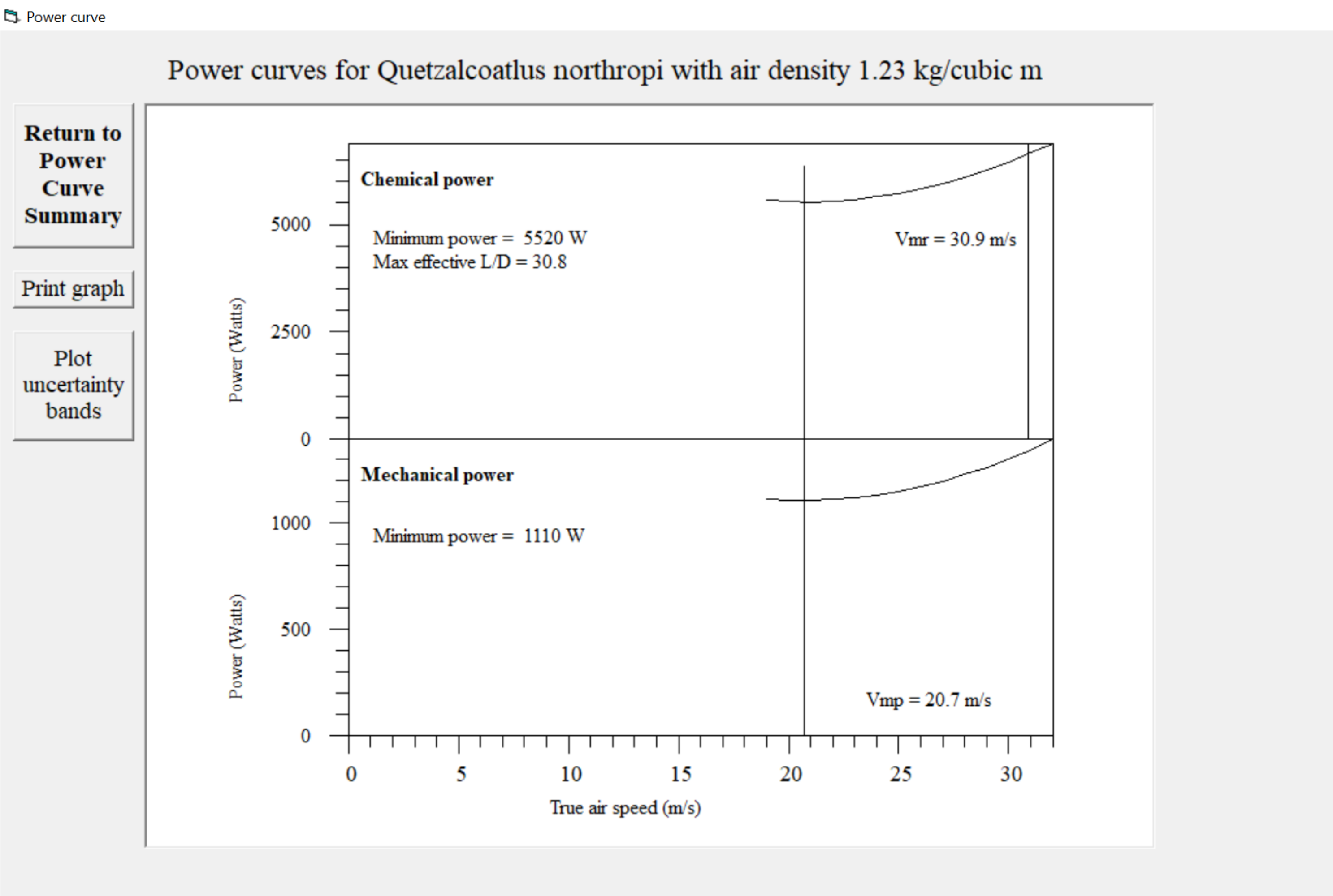
Screen dumps from the Flight program for powered flight






Results summary from Power Curve calculation
Power curve summary
Quetzalcoatlus northropi
Quetzalcoatlus (0.62g)
Show Definitions
Show Graph
Minimum Power (Vmp)
Maximum Range (Vmr)
True air speed (m/s) 20.7 30.9
Equivalent air speed (m/s) 20.7 30.9
Mechanical power (W) 1110 1340
Chemical power (W) 5520 6640
Effective lift:drag ratio 24.8 30.8
Specific work in myofibrils (J/kg) 25.8 31.5
Downwash angle (degrees) 2.11 0.948
Wing Reynolds Number (Mean Chord) 999000 1.49E+06
Body Reynolds Number 917000 1.37E+06
Reduced frequency 0.111 0.0742
Mitochondria fraction (level) 0.0331 0.0401
Mitochondria fraction (climb) 0.0518
Wingbeat frequency (Hz) 1.04
Max rate of climb (m/s) 0.425
Ratios
Vmr:Vmp 1.49
Min chem power:BMR 26.9
Wind Triangle Calculator
Return to Setup
Save power curve as Sheet 1 of a new Excel workbook
4-digit output


Power curve
Power curves for Quetzalcoatlus northropi with air density 1.23 kg/cubic m
Return to Power Curve Summary
Print graph
Plot uncertainty bands
Chemical power
Minimum power = 5520 W
Max effective L/D = 30.8
Vmr = 30.9 m/s
Mechanical power
Minimum power = 1110 W
Vmp = 20.7 m/s
Power (Watts)
5000
2500
0
1000
500
0
0
5
10
15
20
25
30
True air speed (m/s)

Screen dumps for powered flight after eating 70 kg animal

Set up Power Curve calculation

Set up power curve calculation

Species	Quetzalcoatlus northropi		Non-Passerine
Body mass (kg)	250	Quetzalcoatlus (0.62g)	
Fat mass (kg)	0	Fat fraction	0
Flight muscle mass (kg)	42.6	Flight muscle fraction	0.133
Airframe mass (kg)	207	Airframe fraction	0.648
Payload mass (kg)	70.0	Payload fraction	0.219
Payload drag factor	1.00		
All-up mass (kg)	320	Energy height (km) fat+prot	0
Wing span (m)	10.0	Energy height (km) fat only	
Wing area (sq m)	7.00	Inverse power density	1.20E-06 of mitochondria (cu m/W)
Aspect ratio	14.3	Induced power factor	0.900
Air density (kg/cu m)	1.23	Profile power constant	8.40
Altitude (m) ASL	0	Profile power ratio	0.588
Gravity (m/s-sq)	6.08	Respiration factor	1.10
Body drag coefficient	0.100	Conversion efficiency	0.230
Body frontal area (sq m)	0.379	Frontal Area Factor	1.00
Basal metabolic rate (W)	205	Basal metabolism factor	1.00
Wingbeat frequency (Hz)	1.14	Wingbeat frequency factor	1.00
Active strain	0.260	Max isom stress (N/sq m)	560000

Flight style
- (•) Continuous flapping
- ( ) Flap-gliding
- ( ) Bounding

Show Definitions

Read Manual

Compute Power Curve | Get New Bird | Exit Program

Results summary from Power Curve calculation

Power curve summary

Quetzalcoatlus northropi | Quetzalcoatlus (0.62g)

Show Definitions

Show Graph

	Minimum Power (Vmp)	Maximum Range (Vmr)
True air speed (m/s)	22.5	33.4
Equivalent air speed (m/s)	22.5	33.4
Mechanical power (W)	1670	2010
Chemical power (W)	8210	9850
Effective lift:drag ratio	23.2	28.7
Specific work in myofibrils (J/kg)	36.1	44.0
Downwash angle (degrees)	2.29	1.04
Wing Reynolds Number (Mean Chord)	1.09E+06	1.61E+06
Body Reynolds Number	1.08E+06	1.61E+06
Reduced frequency	0.112	0.0753
Mitochondria fraction (level)	0.0499	0.0602
Mitochondria fraction (climb)	0.0566	
Wingbeat frequency (Hz)	1.14	
Max rate of climb (m/s)	0.121	

Ratios

Vmr:Vmp	1.48
Min chem power:BMR	40.0

Wind Triangle Calculator

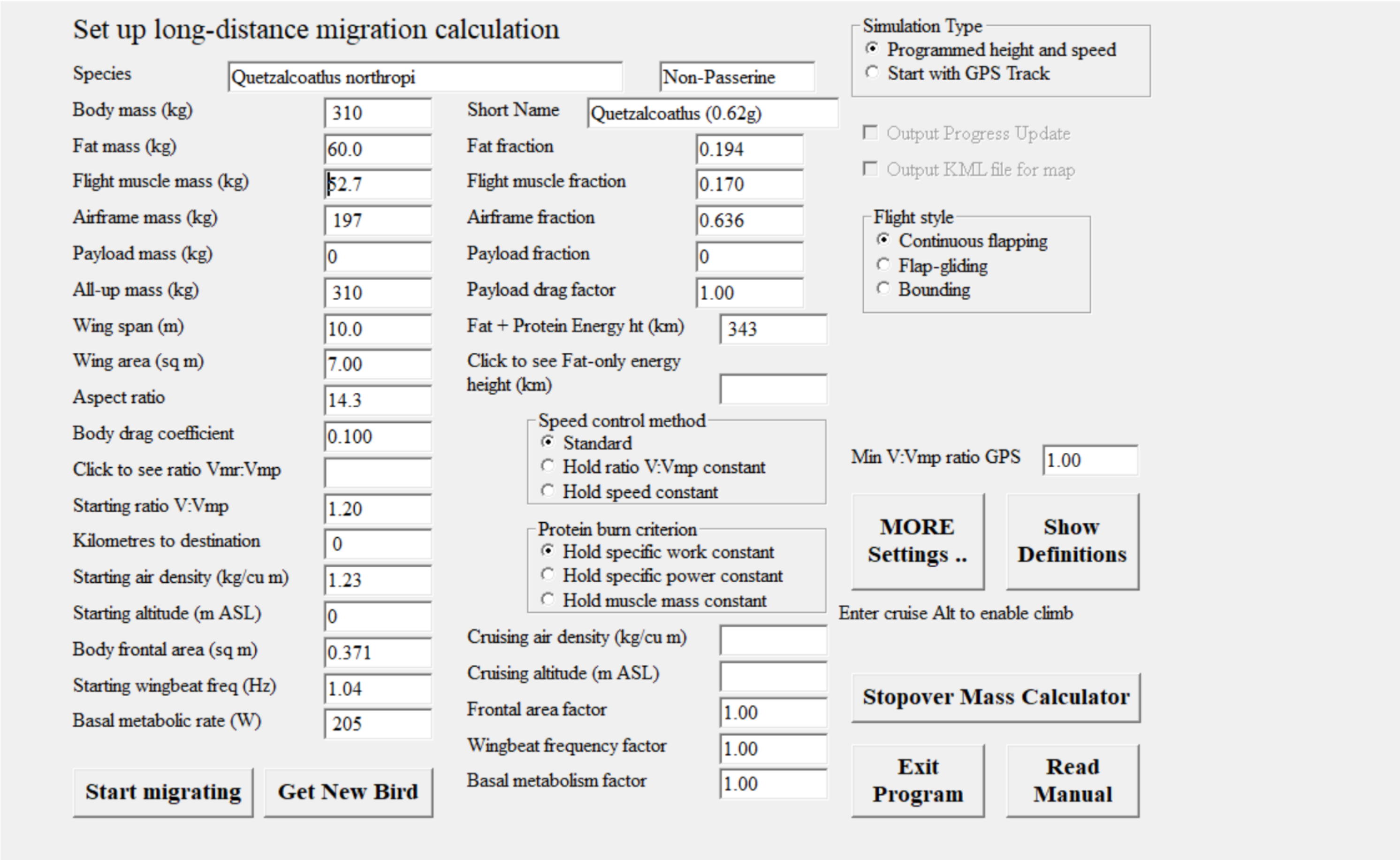
Return to Setup

Save power curve as Sheet 1 of a new Excel workbook ☐

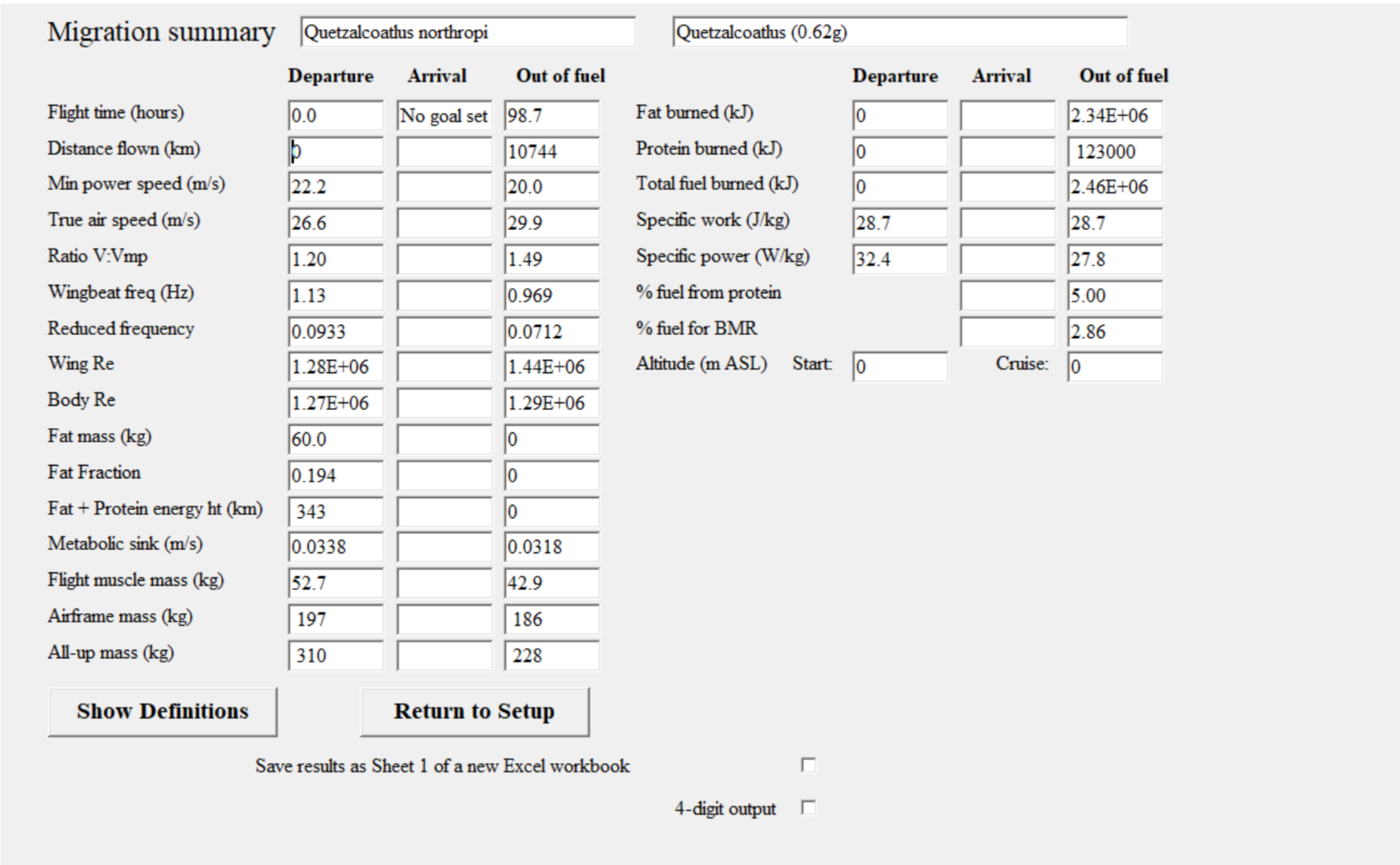
4-digit output ☐

Screen dumps for powered flight long distance migration

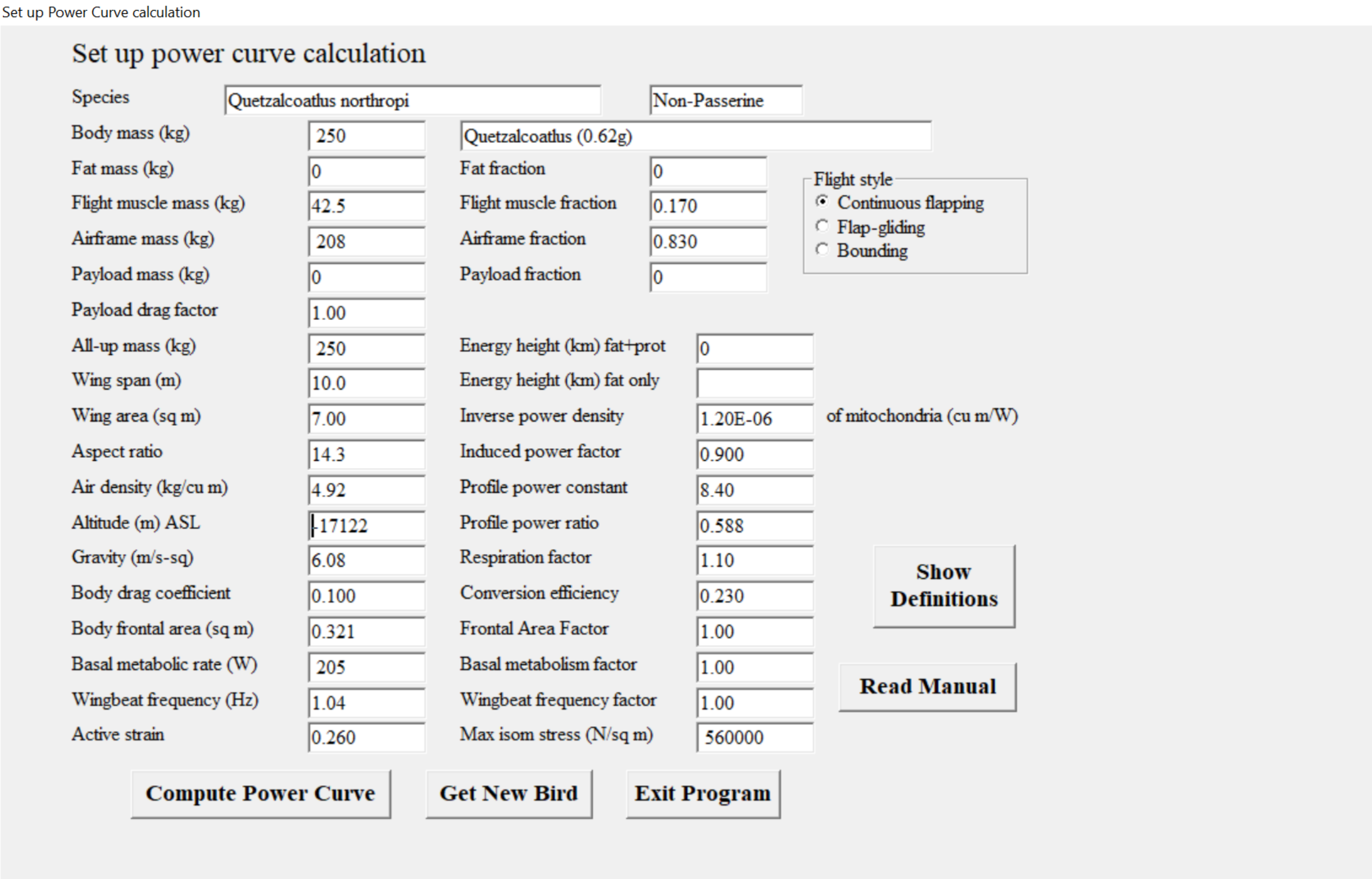
Set up Migration calculation



Results summary from Migration calculation



Powered flight with air density 4 times standard



Set up Power Curve calculation

Set up power curve calculation

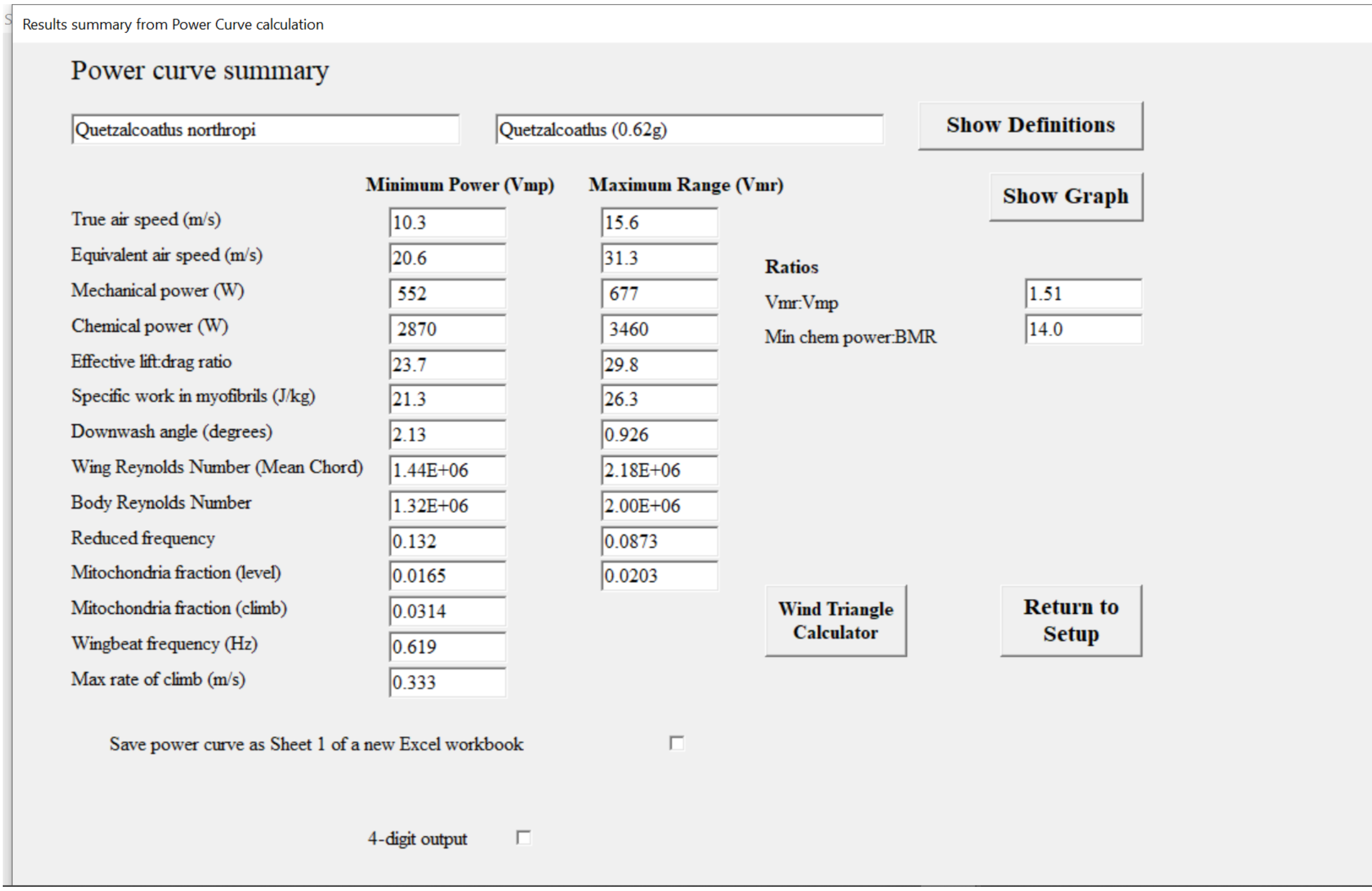
Species	Quetzalcoatlus northropi		Non-Passerine
Body mass (kg)	250		Quetzalcoatlus (0.62g)
Fat mass (kg)	0	Fat fraction	0
Flight muscle mass (kg)	42.5	Flight muscle fraction	0.170
Airframe mass (kg)	208	Airframe fraction	0.830
Payload mass (kg)	0	Payload fraction	0
Payload drag factor	1.00		
All-up mass (kg)	250	Energy height (km) fat+prot	0
Wing span (m)	10.0	Energy height (km) fat only	
Wing area (sq m)	7.00	Inverse power density	1.20E-06 of mitochondria (cu m/W)
Aspect ratio	14.3	Induced power factor	0.900
Air density (kg/cu m)	4.92	Profile power constant	8.40
Altitude (m) ASL	-17122	Profile power ratio	0.588
Gravity (m/s-sq)	6.08	Respiration factor	1.10
Body drag coefficient	0.100	Conversion efficiency	0.230
Body frontal area (sq m)	0.321	Frontal Area Factor	1.00
Basal metabolic rate (W)	205	Basal metabolism factor	1.00
Wingbeat frequency (Hz)	1.04	Wingbeat frequency factor	1.00
Active strain	0.260	Max isom stress (N/sq m)	560000

Flight style
- Continuous flapping (selected)
- Flap-gliding
- Bounding

Show Definitions

Read Manual

Compute Power Curve | Get New Bird | Exit Program



Results summary from Power Curve calculation

Power curve summary

Quetzalcoatlus northropi | Quetzalcoatlus (0.62g) | Show Definitions

Show Graph

	Minimum Power (Vmp)	Maximum Range (Vmr)
True air speed (m/s)	10.3	15.6
Equivalent air speed (m/s)	20.6	31.3
Mechanical power (W)	552	677
Chemical power (W)	2870	3460
Effective lift:drag ratio	23.7	29.8
Specific work in myofibrils (J/kg)	21.3	26.3
Downwash angle (degrees)	2.13	0.926
Wing Reynolds Number (Mean Chord)	1.44E+06	2.18E+06
Body Reynolds Number	1.32E+06	2.00E+06
Reduced frequency	0.132	0.0873
Mitochondria fraction (level)	0.0165	0.0203
Mitochondria fraction (climb)	0.0314	
Wingbeat frequency (Hz)	0.619	
Max rate of climb (m/s)	0.333	

Ratios

Vmr:Vmp	1.51
Min chem power:BMR	14.0

Wind Triangle Calculator | Return to Setup

Save power curve as Sheet 1 of a new Excel workbook

4-digit output