Criteria for Aerial Locomotion in Exoplanetary Atmospheres: Revisiting the Habitable Zone for Flying Lifeforms

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Liquid water is widely regarded as a hallmark of planetary habitability but, whilst its presence may be a prerequisite for life, aerial locomotion imposes additional constraints on the somewhat over-simplistic concept of a circumstellar habitable zone. Could animals of comparable physiology to birds be envisaged sustaining flight without environmental assistance on super-Earth planets of terrestrial density? A quantitative evaluation of flight athleticism in avian species provides the basis for extrapolation here. At constant atmospheric fraction, assuming a plentiful supply of combustible gas, the "aerial locomotion zone" would be restricted to planets $\lesssim 6.86$ $M_\oplus$. However, due to the inevitable thermal impediments at higher altitudes, it is conceivable that the majority of the Earth's avian species could evolve sufficient athleticism for flight on temperate isoatmospheric planets of up to 15 $M_\oplus$, without adjustments in body mass.

1 Introduction

Birds, bats, insects and pterosaurs have independently surmounted the challenges of actively-powered flight [1], perhaps during hyperoxic episodes in the Earth's history [2]. Avian species span some four orders of magnitude in body mass [3] yet birds of all sizes undertake arduous seasonal migrations [4,5]. Flight is a complex and intrinsically dangerous activity especially in arboreal environments, over mountainous terrain, in regions where birds of prey are prevalent or during unfavourable weather [6]. Thus, there is a need for sophisticated neural control [7]. Exoplanet discoveries continue apace [8,9] and NASA's Kepler mission has already established that those of 1–2 Earth radii ("super-Earths") are remarkably abundant [10]. Neutrally buoyant aquatic animals are immune to changes in gravity and land animals can evolve sturdier bones or additional legs to cope with conditions on more massive planets. However, the feasibility of environmentally unassisted flight in stronger gravitational fields is clearly an intricate issue meriting more detailed scrutiny.

The Earth's oxygenated air provides birds not only with a breathable atmosphere but also a medium for generating propulsion and weight support during flight [11]. Consequently, gravity, atmospheric density and the chemical composition of an atmosphere influence the prospects for aerial locomotion. There is no evidence that the laws of physics vary either with time or location, so animals that are as anatomically and physiologically well-adapted to flight as any living here could have evolved elsewhere in the universe. This analysis therefore commences by evaluating the athleticism of Earth's avian species during environmentally unassisted horizontal flight. The limits of flight athleticism on Earth are then used as a basis for extrapolation to different planetary environments, leading to criteria that are likely to be satisfied if circumplanetary atmospheres are compatible with flight.

2 Flight power and athleticism

The following analysis concerns flying animals capable of supporting their own weight in still air conditions, building upon an established result from aerodynamic theory pertaining to hovering flight [12]. If a bird's wings have combined area A_{wing} and the air they sweep is on average accelerated to a downward velocity v_a then the volume of air being swept in unit time is $v_a A_{wing}$. In an atmosphere of density ρ, the mass of this parcel of air is $m_a = \rho v_a A_{wing}$ and so the rate of change of momentum in the air is $m_a v_a = \rho v_a^2 A_{wing}$. For a bird of body mass m_b, Newton's second law requires that this equals the bird's weight $m_b g$ which allows the downward velocity of the air to be obtained as $v_a = \sqrt{m_b g/\rho A_{wing}}$. The power required during hovering is the rate at which kinetic energy is imparted to the air

$$P_{hov} = \frac{m_a v_a^2}{2} = \frac{\rho A_{wing} v_a^3}{2} = \frac{1}{2}\sqrt{\frac{m_b^3 g^3}{\rho A_{wing}}}. \qquad (1)$$

Providing only a small fraction of the power relating to forward horizontal flight, P_f, is required to overcome the drag associated with forward motion, it can be argued that P_f and P_{hov} should scale almost identically. If, furthermore, avian anatomy scales isometrically then $A_{wing} \propto m_b^{2/3}$ and

$$P_f \propto \left(\frac{m_b^7 g^9}{\rho^3}\right)^{1/6}. \qquad (2)$$

For an individual animal this simplifies to $P_f \propto \sqrt{g^3/\rho}$, a term which concisely encapsulates environmental conditions. Thus, flight becomes more challenging on planets with stronger gravitational fields and reduced atmospheric densities [13]. On Earth, flying birds and flightless birds are delineated by the boundary $\sqrt{g^3/\rho}$ =27.7 m³ s⁻³ kg⁻¹ᐟ². Departures from isometry are likely [14] and the allometrically

neutral relationship $A_{wing} \propto m_b^{2/3}$ is only marginally compatible with empirical data – actual wing measurements suggest $A_{wing} \propto m_b^{0.780 \pm 0.112}$ [15] . This implies the following modification involving an exponent $\alpha = 0.110 \pm 0.056$,

$$P_f \propto m_b^{1+\alpha} \sqrt{\frac{g^3}{\rho}}. \qquad (3)$$

Since $\alpha > 0$, mass-specific flight power, P_f/m_b, generally increases with body mass [12]. A quantity χ is now introduced which is directly proportional to the mass-specific flight power needed to fly horizontally in still air. It is adopted as a proxy for flight athleticism and defined as

$$\chi = \left(\frac{m_b}{\tilde{m}}\right)^\alpha \sqrt{\frac{g^3}{\rho}} \qquad (4)$$

where $\tilde{m}$ is a fiducial mass term used for normalisation and can be arbitrarily chosen. In particular, heavier animals capable of flight in hypodense air would score well on this measure. At a similar airspeed, aerodynamic drag is of less concern to large birds, in keeping with the earlier assumption that $P_f \propto P_{hov}$.

3 Aeronautical limits

Avian lungs utilise a cross-current airflow assisted by a complementary vasculature allowing for efficient gas exchange [16], advantageous during high altitude flight where the partial pressure of oxygen is reduced. At least three species appear to be capable of entirely self-powered flight 7000 m or more above sea level. An iconic example is the bar-headed goose, *Anser indicus*, whose seasonal migrations involve navigating the Himalaya [17] and the prominent obstacle of the Tibetan plateau. Having been satellite-tracked at 7290 m [18] they are more tolerant of hypoxia than brent geese, *Branta bernicla*, which have difficulty crossing the Greenland icecaps at altitudes of 2500 m [19]. Despite a body mass placing them in the 98th percentile of bird species [3], they have also been observed flying in formation at almost 8000 m by mountaineers climbing the Annapurna massif [20]. A number of cardiovascular, pulmonary, morphological and biochemical adaptation mechanisms could be responsible for this striking athleticism including high ventilation rates [21], relative immunity to respiratory alkalosis and haemoglobin of superior O_2 affinity, higher cardiac output [17] and tissue enhancements such as cardiac hypertrophy, greater capillary density and mitochondrial abundance [22].

Alpine choughs, *Pyrrhocorax graculus* also inhabit the Himalaya. Nesting as high as 6500 m [17], they have been known to follow climbers on Everest at altitudes approaching 8200 m – within the mountaineering "death zone". Small birds such as choughs readily take to the air but swans are much larger and typically require 15–20 wingbeats to become aloft when taking off from water, even though they can obtain

some acceleration and weight support from webbed feet. On becoming airborne they continue to gain speed and gradually start to ascend, necessitating continued effort [23]. Thus, unlike smaller birds for which a short period of anaerobic exertion is adequate for take-off, swans must demonstrate aerobic athleticism at the commencement of each flight. This applies also to juveniles – cygnets only start to fly at 4–5 months of age. The athleticism demanded by take-off may confer upon swans an ability to sustain high altitude flight, even if they are not ecologically coerced to do so. Lowland species may be incapable of take-off in hypodense air but that does not preclude, *per se*, an ability to fly high – even though swans tend not to during migration [24]. In still air conditions, flying low in dense air facilitates flight – in accordance with (4). However, strong tailwinds capable of drastically curtailing migration times and total energy expenditure are sometimes available, especially at higher altitudes. During lengthier migratory flights, the additional costs of ascent and high altitude cruising can easily be fully recovered. In the cold and featureless seascape of the north Atlantic, which is neither conducive to the generation of strong thermals nor orographic updrafts, a flock of some 30 whooper swans, *Cygnus cygnus*, was detected in 1967 by radar then visually identified by a pilot to be flying at 8200 m with a ground-speed of 38 m s^{-1} towards the end of a ~1000 km migration from Iceland to the UK [25].

The air density at 8200 m is 0.513 kg m^{-3}. Setting $\tilde{m} = m_w = 11$ kg, the mass of a whooper swan, and making allowances for variations in α, the maximum value of χ at which flight is possible at this altitude is 42.8 m^3 s^{-3} kg$^{-1/2}$ for whooper swans, 34.1–39.8 m^3 s^{-3} kg$^{-1/2}$ for bar-headed geese and 22.4–34.6 m^3 s^{-3} kg$^{-1/2}$ for Alpine choughs. Results for various species are presented in Fig. 1. Whooper swans appear to top the list for avian athleticism making them well-suited for astrobiological extrapolations. To compete, bar-headed geese, would need to be capable of flight at altitudes of 9.4–11.7 km, which seems unrealistically high [18].

4 Planetary environments

The radii, R, of terrestrial super-Earths are expected to scale with M, the planet mass, as $R \propto M^{0.274}$ [26]. Hence, surface gravity, g_s, should scale as $g_s \propto M^{0.452}$. The effective increase in sea level on a super-Earth planet with a similar water content to Earth can be estimated from the relationship plotted in Fig. 2. It is also relevant to mention that enhanced gravity tends to attenuate topographical features such as mountains and ridges. Super-Earth planets are variously taken to have a mass of 1–10 $M_\oplus$ or a radius of 1–2 $R_\oplus$ (1–12 $M_\oplus$) where the subscript $\oplus$ denotes the Earth. This analysis considers the slightly expanded range 1–15 $M_\oplus$ in order to encompass the largest planets capable of possessing hexagonally close-packed iron at their core [27, 28]. On Earth, a whooper swan can fly in air of density as low as $\rho_w = 0.513$ kg m^{-3}. Since athleticism is not an environmental variable, the min-
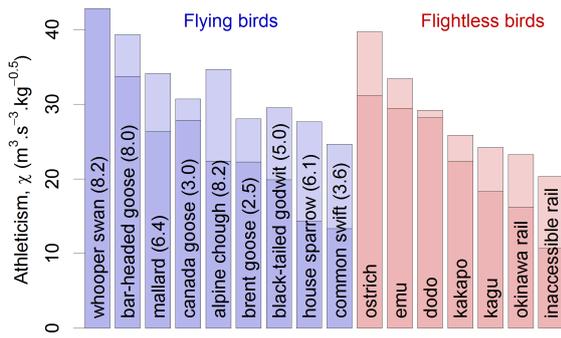
Fig. 1: Flight athleticism, χ, for various species. Estimated maximum altitudes are given in km (in parentheses) for unassisted flight. Selected results are also provided for flightless birds assuming (mostly with undue optimism) that they might be capable of flying in air slightly denser than that of sea level. Lightly shaded areas represent the uncertainty in the allometric scaling exponent, $0.054 < \alpha < 0.166$, using a fiducial mass $\tilde{m} = 11$ kg.
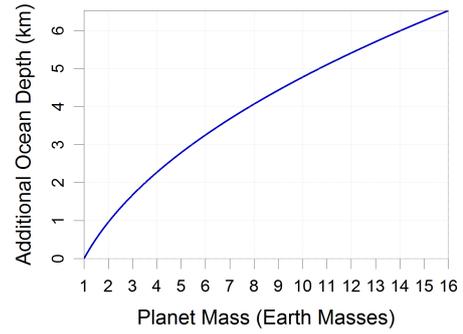

Fig. 2: Planets more massive than Earth but with an identical water fraction ($V_{H_2O} \propto M$) would have somewhat deeper oceans, the additional depth (in km) being at least $2.6\,[(M/M_\oplus)^{0.452} - 1]$ depending on topography. However, if planetary water is exclusively delivered from space via comets and asteroids whose spatial distribution varies little with galactic location, one would anticipate ocean depths to be largely independent of planet mass.

imum air density required by whooper swans on other planets is $\rho_{min} = \rho_w (M/M_\oplus)^{1.356}$. For a 15 Earth-mass planet, $\rho_{min} = 20.18$ kg m^{-3}.

As with discussions of circumstellar habitable zones, some simplifying assumptions are helpful. Due to uncertainties such as cloud cover, humidity levels and fluctuations in atmospheric heating due to planetary rotation, an isothermal model atmosphere is adopted. In hydrostatic equilibrium the ideal gas law predicts that air density, ρ, is proportional to air pressure, $p = \beta\rho$. According to the International Standard Atmosphere, β has a value of about 82714 m^2 s^{-2} for a temperature of 15°C at sea level where $\rho = 1.225$ kg m^{-3}. Gravity is taken to be insensitive to changes in altitude, z. By considering the weight of a thin horizontal layer of air,

$$\frac{dp}{dz} = \frac{dp}{d\rho} \times \frac{d\rho}{dz} = \beta\frac{d\rho}{dz} = -\rho g_s. \tag{5}$$

The air density at height h is obtained by integrating from $z = 0$ to $z = h$,

$$\beta\left(\ln\rho - \ln\rho_s\right) = -g_s h, \tag{6}$$

where ρ_s represents the air density at the surface. Thus, $\rho = \rho_s \exp\left(-g_s h/\beta\right)$ and the total mass contained by the atmosphere below height h is

$$M_h = 4\pi R^2 \int_0^h \rho(z)\,dz = \frac{4\pi\beta\rho_s R^2}{g_s}\left[1 - \exp\left(\frac{-g_s h}{\beta}\right)\right]. \tag{7}$$

M_h converges as $h \to \infty$ to yield the total mass of the entire atmosphere,

$$M_{atm} = \frac{4\pi\beta\rho_s R^2}{g_s}. \tag{8}$$

For an isothermal atmosphere, under the assumption of spherical symmetry, half the air mass lies below a scale height $\hat{h}$ given by

$$\hat{h} = \frac{\beta\ln 2}{g_s} = \frac{\beta\ln 2}{g_\oplus}\left(\frac{M_\oplus}{M}\right)^{0.452}. \tag{9}$$

This expression is entirely independent of ρ_s. Plots of surface gravity, planetary radius and atmospheric scale height against planetary mass are provided in Fig. 3.

5 Criteria for aerial locomotion

From (8) we have $\rho_s = g_s M_{atm}/4\pi\beta R^2$. Recalling that $g_s \propto M^{0.452}$ and $R \propto M^{0.274}$,

$$\rho_s = \frac{g_\oplus M_{atm}(M/M_\oplus)^{0.452}}{4\pi\beta R_\oplus^2 (M/M_\oplus)^{0.548}} \propto M^{0.904}\left(\frac{M_{atm}}{M}\right). \tag{10}$$

Since $g_s = g_\oplus (M/M_\oplus)^{0.452}$, the quantity $\sqrt{g_s^3/\rho_s}$, a factor previously found to be proportional to the power required by flight, can be expressed as follows

$$\frac{g_s^3}{\rho_s} = \frac{4\pi\beta R_\oplus^2 (M/M_\oplus)^{0.096}}{g_\oplus M_{atm}}\left[g_\oplus(M/M_\oplus)^{0.452}\right]^3$$
$$= \frac{4\pi\beta R_\oplus^2 g_\oplus^2}{M_{atm}}\left(\frac{M}{M_\oplus}\right)^{1.452}, \tag{11}$$

$$\sqrt{\frac{g_s^3}{\rho_s}} = \gamma\left(\frac{M}{M_\oplus}\right)^{0.226}\sqrt{\frac{M}{M_{atm}}} \tag{12}$$

where $\gamma = 2g_\oplus R_\oplus\sqrt{\pi\beta/M_\oplus} = 0.026$ m^3 s^{-3} kg$^{-1/2}$. The maximum mass of an isoatmospheric planet (i.e. having a ratio M_{atm}/M identical to Earth's) that is compatible with flight for

Fig. 4: For isoatmospheric planets the Earth-equivalent air density, ρ_{eq}, at the athleticism of zero-altitude flight, is inversely related to the surface gravity of a planet, $\rho_{eq} \propto 1/g_s$.
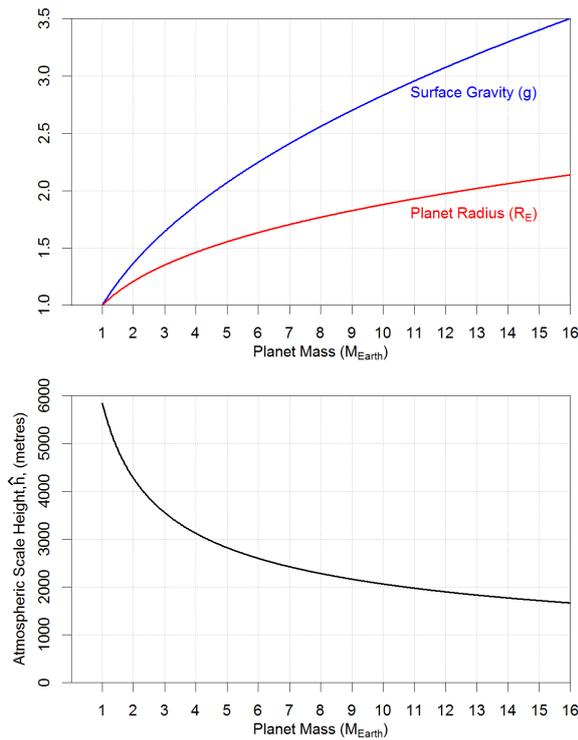
Fig. 3: Upper panel: planetary radius and surface gravity obey simple power law relationships according to planetary mass, $R \propto M^{0.274}$ and $g_s \propto M^{0.452}$ respectively. Lower panel: the scale height of the atmosphere, $\hat{h} = \beta \ln 2/g_s$, is independent of the surface air density and hence total mass of the atmosphere. It decreases for larger planets since a higher surface gravity is better able to confine the atmosphere close to the surface.

a whooper swan can be obtained by requiring that $\rho_s = \rho_{min}$. This implies that $\rho_w(M/M_\oplus)^{1.356} = \rho_\oplus(M/M_\oplus)^{0.904}$, and

$$M = M_\oplus \times \left(\frac{\rho_\oplus}{\rho_w}\right)^{1/0.452} \approx 6.86 M_\oplus. \quad (13)$$

The surface gravity of this planet of 6.86 $M_\oplus$ would be 2.388g. The maximum range and minimum power airspeeds of flying birds are expected to vary as $\rho^{-0.5}$ [12]. The surface air density of an isoatmospheric 6.86 Earth-mass planet would be $\sim 5.68\rho_\oplus$ so a typical airspeed of 21 m s^{-1} for a swan [24] might decline to 8.8 m s^{-1}, roughly the pace of an elite 400 m runner. In this same 2.385g environment, however, most people would struggle to walk at all and horses would be incapable of standing.

Since $P_f \propto m_b^{1+\alpha} \sqrt{g^3/\rho}$ and $\rho_s \propto M^{0.904}$, the flight power at zero altitude on isoatmospheric planets scales as $P_f \propto M^{0.226}$. Because $M/M_\oplus = (g_s/g_\oplus)^{1/0.452}$, it is apparent from (13) that $g_s/g_\oplus = \rho_\oplus/\rho_s$ for the limiting planet mass. Therefore, a particularly simple i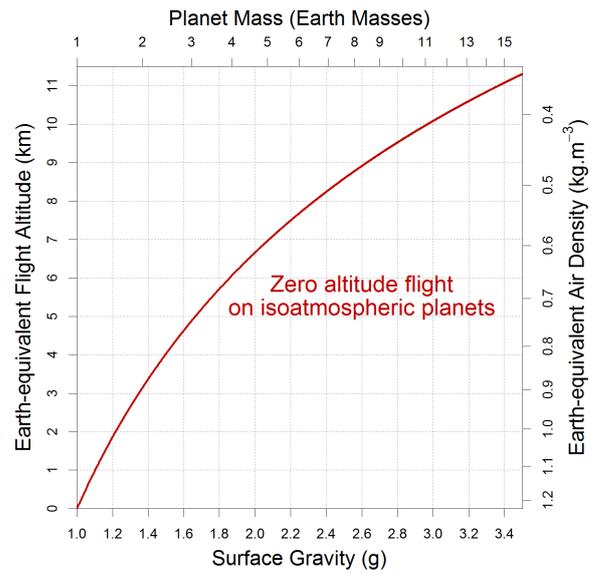nverse relationship exists, $\rho_{eq} \propto$ $1/g_s$, allowing translation of the surface gravity of an isoatmospheric planet to the Earth-equivalent air density (and hence also equivalent maximum flight altitude via the International Standard Atmosphere). Results are presented in Fig. 4.

Might smaller birds be capable of flight on an isoatmospheric planet of 15 Earth masses? The surface air density would be $1.225 (M/M_\oplus)^{0.904} = 14.17$ kg m^{-3}, lower than the minimum air density required by whooper swans for the same planet mass, $\rho_{min} = 20.18$ kg m^{-3}. Since $\chi \propto \rho_s^{-1/2}$, flight athleticism would have to be boosted by a factor of 1.1934. To achieve this, body mass could be reduced so that $m_b < m_w$ and flight would become feasible on a 15 Earth-mass planet if $m_b = m_w \times 1.1934^{-1/\alpha}$. Hence, flying animals of 0.42–3.8 kg or less (according to the value of α) may be capable of aerial locomotion on a 15 Earth-mass planet if they can match the flight athleticism of a whooper swan. Some $\sim$88% of species have a body mass below 0.42 kg and $\sim$99% have a body mass below 3.8 kg [3].

For an isoatmospheric 15-Earth mass planet one finds that $\sqrt{g_s^3/\rho_s} > 51.1$ m^3 s^{-3} kg$^{-1/2}$. On Earth this is equivalent to $\rho < 0.36$ kg m^{-3} or flight at altitudes $\gtrsim 11$ km. Even if smaller birds lack the athleticism of whooper swans, some may be able to fly in such rarefied air. The possibility could be investigated using a hypobaric wind tunnel operated at a comfortable flight temperature. Ruby-throated humming-birds, which have a body mass of only 2–6 grams, can sustain hovering at densities down to 47% that of sea level air (0.576 kg m^{-3}) [29,30]. In forward flight, this species is likely to be capable of flying in yet more rarefied air. However,
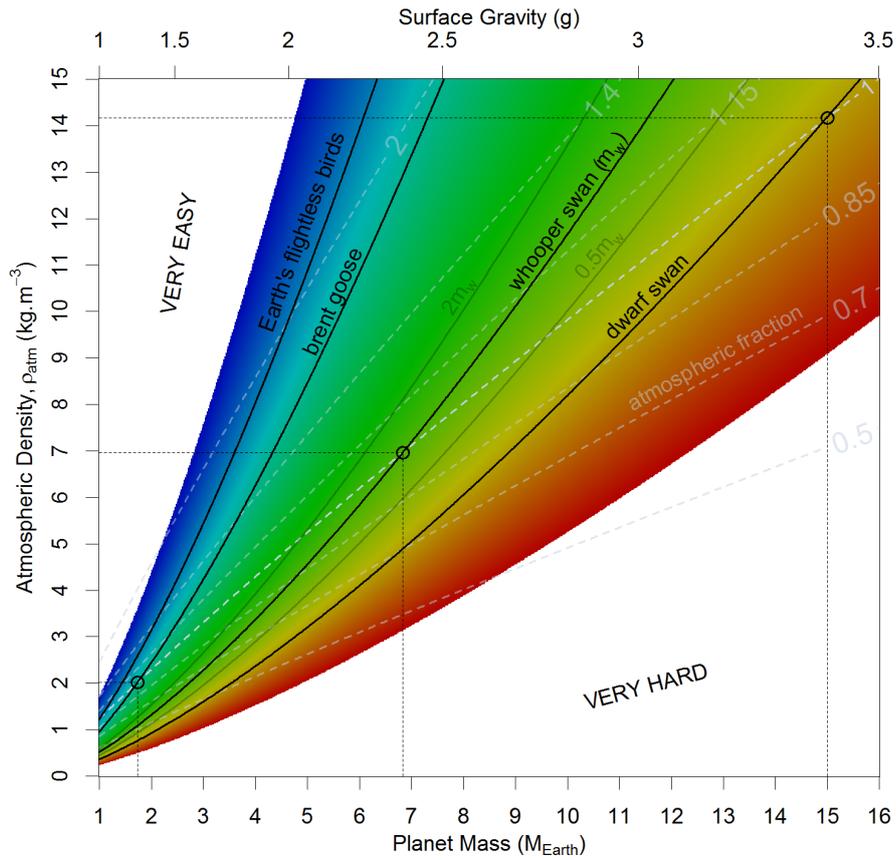
Fig. 5: Flight power (effort increases from blue to red) is a function of planet mass (or surface gravity) and atmospheric density. Conditions compatible with aerial locomotion lie upward of the solid contours. An 11 kg whooper swan appears capable of unassisted horizontal flight on isoatmospheric planets up to 6.86 $M_\oplus$. The influence of doubling or halving body mass relative to the whooper swan is shown for α=0.11. The trace marked *dwarf swan* corresponds to a hypothetical flying animal of the same flight athleticism as a whooper swan but of body mass 0.04–0.34m_w (corresponding to 0.054 < α < 0.166). Dashed contours represent atmospheric mass content relative to the Earth's fraction (862 parts per billion).

even then, due to its relatively small body mass, it is unlikely to challenge whooper swans for flight athleticism. The same argument applies also to flying insects.

Sufficient information has now been collected to describe circumstances compatible with environmentally unassisted circumplanetary flight in which buoyancy effects can be safely ignored. A planet would ideally occupy an orbit within the conventional circumstellar habitable zone [31] and, based upon the flight athleticism of whooper swans, the following criterion should also be satisfied:

$$\left(\frac{m_b}{m_w}\right)^\alpha \sqrt{\frac{g_s^3}{\rho_s}} \lesssim 42.8 \quad \text{m}^3\,\text{s}^{-3}\,\text{kg}^{-1/2}. \tag{14}$$

By virtue of (12), an equivalent formulation involving only normalised mass terms is possible

$$\left(\frac{m_b}{m_w}\right)^\alpha \left(\frac{M}{M_\oplus}\right)^{0.226} \sqrt{\frac{M}{M_{atm}}} \lesssim 1646. \tag{15}$$

Limitations in respiration or gas perfusion could potentially impinge upon the present analysis but oxygen delivery is not constrained in birds by the pulmonary system [23] and, in more inert atmospheres, flow-through breathing arrangements requiring little or no biomechanical effort can be imagined. Changes in atmospheric composition are likely over geological timescales [2]. Thus, it would ideally be useful to know whether an exoplanetary atmosphere has remained breathable and non-toxic for sufficient time to support the evolution of complex organisms.

Another factor which might well impact on these results is a change in atmospheric temperature, T_{atm}. The molar mass of the air, $M_{air} = 0.029$ kg mol^{-1}, the air temperature, T_{air}, and the universal gas constant, $R_{air} = 8,314$ N m mol^{-1} K^{-1}, obey the relationship $\beta = R_{air}T_{air}/M_{air}$. Since both γ and M_{atm} are linearly dependent on β, the value of $\sqrt{g_s^3/\rho_s}$ is proportional to $\sqrt{\beta}$. Since the value of β adopted here corresponds to an air temperature of 15°C, different atmospheric
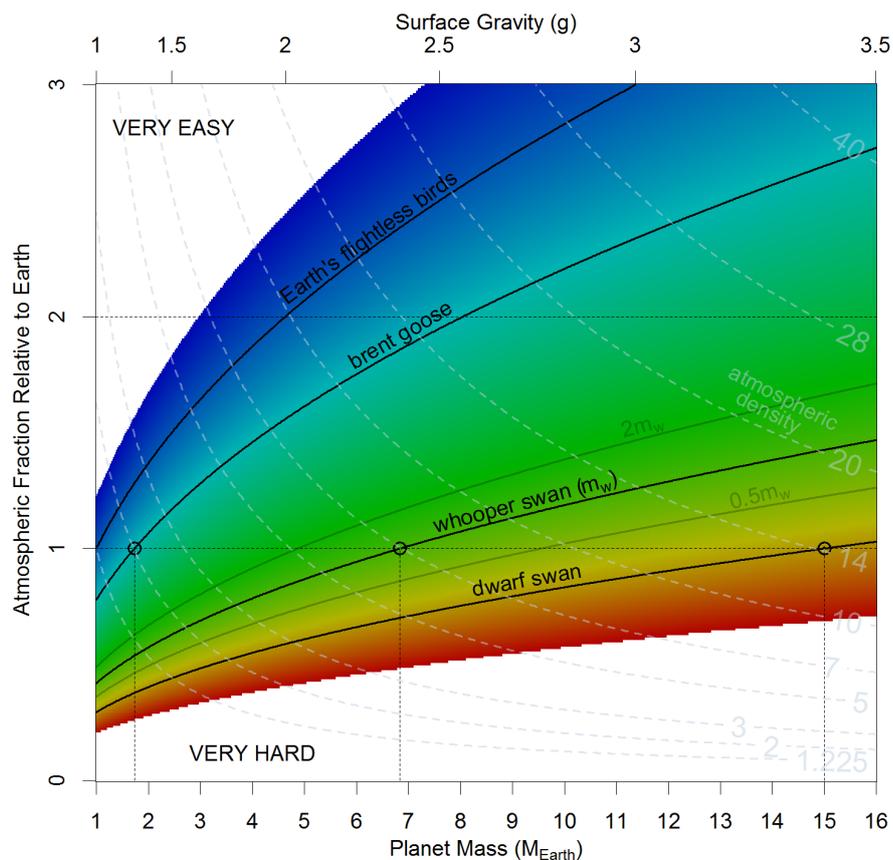
Fig. 6: Flight power according to planet mass and the atmospheric fraction relative to that of the Earth. Aerial locomotion is possible upwards of the solid contours. Dashed contours here represent the surface density of the atmosphere ($kg\,m^{-3}$), and correspond to isobars for the isothermal atmospheric model used here.

temperatures can be accommodated by applying a correction factor of $\sqrt{288.15/T_{atm}}$ to the right-hand sides of the inequalities (14) and (15).

The results of this analysis are presented graphically in Figs. 5 and 6. These limits are likely to be somewhat cautious since it is possible that, with determined effort, whooper swans may be capable of flying higher than the flock sighting at 8200 m. Although it has been conjectured that their initial ascent was aided by lee waves, such assistance would not have been present during the sea crossing from Iceland to Scotland [24]. Furthermore, this species regularly takes off in the dense air present at sea level which prohibits the evolution of larger wings that would tend to facilitate flight at extreme altitudes. Flying animals of extraterrestrial origin may not have been subjected to evolutionary pressures of this kind, particularly if their planets lack elevated land masses obstructing low altitude flight.

6 Discussion

Expressions (14) and (15) present criteria for aerial locomotion to be realistically possible in circumplanetary atmosphe-res. Comparisons of relative flight power under different environmental circumstances can utilise the expression $P_f \propto \sqrt{g_s^3/\rho_s}$. This predicts, for example, that flight in conditions resembling Saturn's moon Titan would be ~ 23 times easier than at sea level on Earth. The wing-scaling exponent α has a small but positive value [15]. If this holds for a wide range of body masses then one can envisage animals flying in such conditions which are larger than any that have ever graced this planet. However, transport costs (or the energy/distance ratio), should approximately scale as $m_b^{0.7}$ during flight but only $m_b^{0.6}$ for running [1]. Above a certain body size, therefore, terrestrial locomotion would be energetically favoured to flight, though transit times might increase.

A primary finding is that, in the presence of a breathable atmosphere, winged animals of a body mass resembling the majority of the Earth's indigenous avian species could potentially evolve the ability to fly on isoatmospheric planets of at least 15 $M_\oplus$ ($g_s = 3.4g$). However, this work also highlights how even mildly reduced atmospheric fractions might potentially prohibit aerial locomotion. Novel techniques capable of remotely determining atmospheric composition, sur-

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face atmospheric density and oceanic coverage could therefore be useful in augmenting future exoplanetary searches. Even worlds entirely covered in water could host flying animals. If in time the Earth were to become an ocean planet through continuing bombardment by comets and meteorites then seabirds could emulate penguins by mating, laying eggs and incubating them on floating icebergs.

That birds possess superb navigation skills has long been apparent but only recently have we appreciated that numerous species are adept problem-solvers [32] with an innate ability to fashion tools [33]. Eurasian Magpies (*Pica pica*) have demonstrated self-recognition when confronted with a mirror, a trait commonly associated with self-awareness [34]. Most birds are proficient hunters, potentially capable of stimulating the evolution of higher intelligence in land-based prey – such as our early mammalian ancestors. That cannot be said of insect-like creatures, which should in general cope more comfortably with higher gravitational fields due to the advantages of relatively small body masses and large area to volume ratios, facilitating respiration.

Flapping flight is a highly effective mode of locomotion for animals possessing sufficient athleticism. However, as aerial manoeuvres demand considerable coordination and spatiotemporal awareness, and body weight is critical, evolutionary pressures arise for efficient neurochemistry and neuroarchitecture. Volant organisms may well have played a pivotal role in shaping the Earth's natural history, enriching its biodiversity and accelerating the evolution of intelligent life. Avian species demonstrated considerable resilience in surviving the ecological catastrophe responsible for the extinction of most dinosaurs. In times of adversity, an ability to swiftly and efficiently relocate over planetary distances and flexibly forage on both land and sea may assist the propagation of flying animals over geological~stellar timescales. Accurate determination of whether circumplanetary flight is possible should not be overlooked if future missions to extrasolar worlds are intent on maximising the chances of encountering complex lifeforms and, perhaps, even extraterrestrial civilisations of comparable sophistication to our own.

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