Design 1: Metabolism and Heat Balance of The *Puijila darwini*

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Introduction:

The *Puijila darwini* (figure 1) is a now extinct species of basal pinniped, or seal, with origins in the high arctic that lived during the early Miocene Epoch around 21 to 24 million years ago. A fossil of the species was discovered on Devon Island of Nunavut, Canada in 2008, and is the subject of this analysis. The studied remains were a 65% completed collection of fossilized remains of a male individual of the species (Rybczynski et al., 2009). It was a semi-aquatic, carnivorous, arctoid mammal with a strong resemblance to the present-day river otter (Rybczynski et al., 2009) in size and morphology. With a body resembling an otter and the head and jaw of a seal, the *Puijila darwini* had four legs rather than the four flippers of modern pinnipeds.

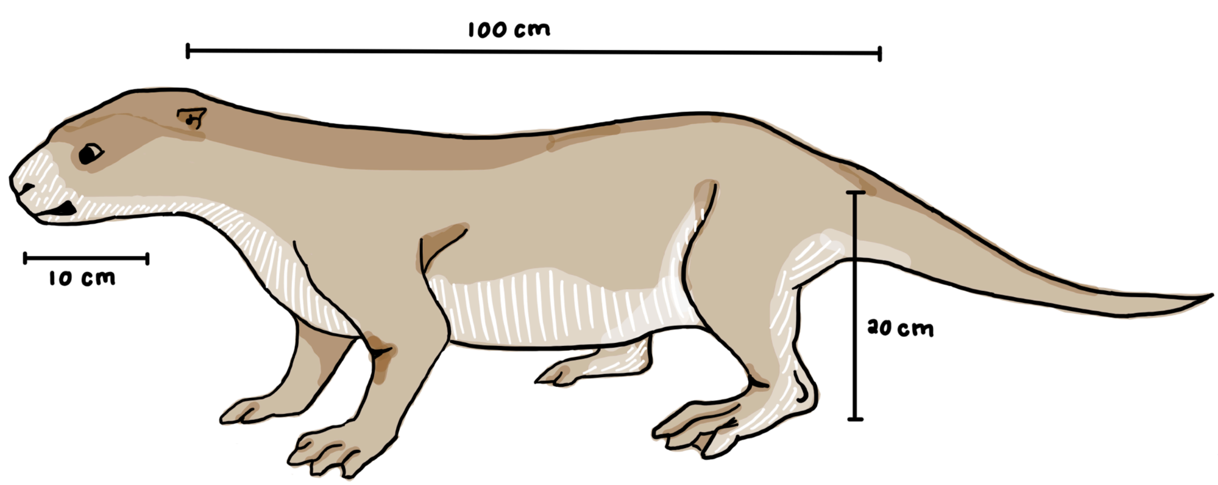

Figure 1. Drawing of *Puijila darwini* with estimated dimensions (Rybczynski et al., 2009).

Its morphology indicates a development towards specialization for marine life with webbed feet, shortened femurs, flattened phalanges, and a pelvis with a short illium (Rybczynski et al., 2009). The most significant of these characteristics is the shortened illium. Such a morphology would have made it very inefficient for the subject to run and jump. Therefore it would have had to expend more energy on terrestrial activities (Rybczynski et al., 2009) and would have experienced more ease of movement in the water. True to its resemblance, the *Puijila darwini* is a direct ancestor of modern day pinnipeds and has a sister relationship with mustelids (otters) (Northover, 2011).

Fossils of the *Puijila darwini* are primarily found in the high arctic where ambient temperatures ranged from $0^{\circ}C$to $11^{\circ}C$ at a yearly average during the Miocene Epoch (Whitlock, 1990). Their habitats consisted of boreal and conifer forests with large sources of freshwater such as lakes and rivers often near coastlines. Their diets most likely consisted mainly of small to medium sized fishes as well as shellfishes (Marshal et al., 2019). While the *Puijila darwini* itself most likely hunted in and resided near freshwater sources (Northover, 2011), their descendents primarily make use of saltwater sources like the ocean. This and the morphology of the fossil indicates that *Puijila darwini* were a significant transitional species between primarily terrestrial, freshwater, animals and primarily aquatic, marine animals such as modern seals and otters.

From our knowledge of morphology, the *Puijila darwini* most likely was an active animal in aquatic settings with a higher efficiency of movement in water than on land and probably spent most of its active time in water. Information about the *Puijila darwini's* habitat shows that it was adapted to colder environments and therefore is predicted to be more efficient in regulating its body temperature in cold environments than in hot environments.

Methods:

Mass Analysis

From the dimensions of the reconstructed *Puijila darwini* fossil, the estimated volume of the subject, in centimeters cubed, was calculated using cylindrical volume equations to account for the body and legs, and a spherical volume equation for the head. Both the radius and length of each body component were measured in centimeters for the calculation.

Body and Legs Volume (cm^3): $V = \pi r^2 l$ Head Volume (cm^3): $V = \frac{4}{3}\pi r^3$

Total Volume (cm^3): $V_t = V_{Body} + (4 \times V_{Leg}) + V_{Head}$

Parameters: Length (l) → centimeters (cm), Radius (r) → centimeters (cm)

The resulting volume was converted into mass in grams by multiplying the sum of the body's volume by the density of water (1g/cm^3) because animals are made of about 70% water.

Mass (g): $M = V_t \times \frac{1g}{cm^3}$

Metabolism

The BMR of the *Puijila darwini,* in joules per hour, was modeled on the allometric equation of small mustelids (Withers, 1992) and calculated using the subject's mass in grams. This equation was used because the *Puijila darwini,* like its descendents, is an endothermic mammal and it is closely related to modern mustelids in morphology and ancestry (Rybczynski et al., 2009).

Basal Metabolic Rate of Small Mustelids (Jhr^{-1}) (Withers, 1992): $BMR = 74.3M^{0.72}$

Parameters: Mass (M) → grams (g)

The behavior of the *Puijila darwini* was predicted with reference to the behavior of modern pinnipeds and mustelids (Marshall, 2019) as well as the subject fossil's morphological traits. Focal behaviors and the time the *Puijila darwini* likely spent on them in a 24 hour period were predicted to create a daily time budget for the animal. These behaviors were grouped into four categories of intensity and assigned multipliers (Withers, 1992) to relate them to the calculated BMR using the following equation.

Metabolic Rates Relative to BMR (Jhr^{-1}) (Withers, 1992): $MR = BMR \times Multiplier$

The metabolic rates calculated include those during rest (RMR), minimal activity (AMR1), regular levels of activity (AMR2), and maximal intense activity (MMR). Resting behaviors included resting, grooming and basking, minimal activity behaviors included walking, feeding, and floating or gliding, regular activity behaviors included swimming and aquatic hunting, and maximal activity behaviors included intense swimming, and running on land (Northover, 2011). These metabolic rates were then used to calculate an estimation of the daily metabolic rate (DMR), in joules per day. This was done by multiplying each metabolic rate by the number of hours per day spent on the metabolic rate's corresponding activities and taking the sum of these components.

Daily Metabolic Rate ($JDay^{-1}$) (Withers, 1992):

$DMR = (RMR \times hr) + (AMR1 \times hr) + (AMR2 \times hr) + (MMR \times hr)$

Heat Balance

Ambient temperatures for the *Puijila darwini's* environment fell in an average yearly range of $0^{\circ}C$ to $11^{\circ}C$ (Whitlock, 1990). The body temperature of the *Puijila darwini* was estimated to be about $38^{\circ}C$, as is common for endothermic mammals (Esslinger, 2011).

Ambient Temperature: $T_{aMin} = 0^{\circ}C,\ T_{aMax} = 11^{\circ}C$ Body Temperature: $T_b = 38^{\circ}C$

To find the metabolic production of heat (Hm) in the subject, the DMR and RMR, in joules per hour, were used as baselines for energy production during rest and during average activity. The resting Hm was used in situations where the subject did not actively move such as during activities like sleeping and basking on land. The active Hm was used in situations where the subject most likely was actively in motion such as when it was in water.

Resting Hm (Jhr^{-1}): $H_m = RMR$ Active Hm (Jhr^{-1}): $H_m = DMR$

The heat transfer due to convection and conduction (Hc), in joules per hour, was calculated using the subject fossil's estimated mass in grams, the difference in ambient to body temperature in celsius, and a conductance variable. The conductance variable itself was calculated based on the estimated mass using the conductance equation for all mammals (Withers, 1992).

Conductance for all Mammals ($Jg^{-1}hr^{-1}{}^{\circ}C^{-1}$) (Withers, 1992): $C = 13.9M^{-0.534}$

Hc (Jhr^{-1}) (Withers, 1992): $H_c = C\ M\Delta T$

Parameters: Conductance (C) → $Jg^{-1}hr^{-1}{}^{\circ}C^{-1}$, Mass (M) → g, Temperature ($^{\circ}C$)

To account for the variety of environmental conditions the *Puijila darwini* experienced, multiple Hc values were calculated. The first set of Hc values accounts for winter conditions on land, in the water, and while basking while the second set of Hc values accounts for the same three situations, but in summer climates. In the winter Hc set, the ambient temperature was set at $0^{\circ}C$ while in the summer Hc set, it was set at $11^{\circ}C$. Additionally, the Hc value in water in both climates consisted of the land Hc value multiplied by 25 to account for an increase in conductivity in water.

The heat transfer due to radiation (Hr), in kilojoules per hour, from the sun was calculated using a set heat gain variable for the sun and the surface area of the animal in centimeters cubed. The surface area of the subject was calculated similarly to how volume was.

Hr ($kJhr^{-1}$) (Withers, 1992): $H_r = (Sun\ Heat\ Gain)(SA)$

Parameters: Sun Heat Gain Variable → $0.180\ kJhr^{-1}cm^{-2}$, Surface Area (SA) → cm^2

The heat transfer due to evaporation (He), in kilojoules per hour, was calculated by multiplying evaporative water loss (EWL) in grams per day by the latent heat of evaporation, a constant with a value of $2.4\ kJg^{-1}$.

He (kJ/hr) (Withers, 1992): $H_e = (EWL\ gDay^{-1})(2.4\ kJ/g)(Day/24hr)$

EWL was obtained through the addition of the *Puijila darwini's* respiratory evaporative water loss (REWL) and cutaneous evaporative water loss (CEWL), both in grams of water lost per day. In both calculations for REWL and CEWL, the difference in water content in the air at the body ($\chi_{exp/body}$) and in the environment ($\chi_{insp/air}$) is used. The water content values are in accordance to the average ambient temperature of $5.5^{\circ}C$and body temperature of $38^{\circ}C$at their respective humidities of 75% and 100% (Whitlock, 1990). The r value for CEWL calculations was set at $150\ sec/cm^2$, a reasonable resistance value for fur mammals (Withers, 1992).

REWL ($gDay^{-1}$) (Withers, 1992): $REWL = (Liters\ Air/Day)(\chi_{exp} - \chi_{insp})$

CEWL ($gDay^{-1}$) (Withers, 1992): $CEWL = (\chi_{body} - \chi_{air})(SA)/r$

Parameters: Resistance (r) → $150\ sec/cm^2$, Water Content at the Body → $\chi_{exp/body} = 43\ mg/L$, Water Content in Air → $\chi_{insp/air} = 5.1\ mg/L$

The heat balance, in kilojoules per hour, of the *Puijila darwini* in varied situations was then determined by taking the sum of each of the calculated components for different conditions. The change in temperature caused by this heat balance was calculated as well.

Heat Balance ($kJhr^{-1}$) (Withers, 1992): $\Delta H_s = H_m \pm H_c \pm H_r \pm H_e$.

Temperature Change ($\Delta^{\circ}C$) (Withers, 1992): $\Delta T = (\Delta H_s)(1/M)(1^{\circ}Cg/4J)$

Based on these calculations, 4 situations were calculated to explore the possible heat balance for the *Puijila darwini* under different conditions. The first and second were daily heat balances that might occur on a normal day in winter or summer. The daily time budget in both seasons was estimated based on the metabolic energy budget as well as on behaviors of modern pinnipeds and mustelids. The third was a heat stress situation taking place in summer climates wherein the subject *Puijila darwini* is imagined to have fallen asleep under the sun for 11 hours, the entirety of its resting period. The last situation is a cold stress situation. It imagines the subject *Puijila darwini* stuck at sea in a winter setting, swimming for 13 hours, the entirety of its active period. In both stress situations, the amount of energy needed to return to a heat balance through swimming or basking is calculated.

Results:

Mass Analysis and Metabolism

From the dimensional analysis of the *Puijila darwini* fossil, the following body mass in grams and surface area in centimeters squared was calculated.

Total Surface Area: $SA_{Total} \approx 4838\ cm^2$ Mass: $m \approx 16169\ g \approx 16.17\ kg$

The following BMR and mass specific BMR were then calculated from these parameters.

$BMR \approx 79659\ Jhr^{-1}$ $BMR/M \approx 4.93\ Jhr^{-1}g^{-1}$

An estimated energy time budget of the *Puijila darwini* is shown in table 1. The most significant metabolic behaviors were seen to be those in RMR followed by those in AMR2 (figure 2), as according to research, the *Puijila darwini* most likely spent the majority of its day resting or basking and then spent most of its waking hours hunting for food or swimming.

Table 1. Time Budget of *Puijila darwini* based on fossil morphology and the behaviors of modern otters and seals (Rybczynski et al., 2009) (Northover, 2011) (Marshal, 2019) (Davis, 2019).

Activity	Estimated Proportion of Day (24 Hr)	Intensity	Multiplier
Resting (RMR)	11hr $\rightarrow \frac{11}{24} \approx 0.46$	1	$\frac{6.3}{4.2} = 1.5$
Minimal Activity (AMR1)	9hr $\rightarrow \frac{9}{24} \approx 0.38$	1	$\frac{8.4}{4.2} = 2$
Activity (AMR2)	3hr $\rightarrow \frac{3}{24} \approx 0.12$	2	$\frac{26.4}{4.2} = 6.3$
Maximal Activity (MMR)	<1hr $\rightarrow \frac{1}{24} \approx 0.04$	3	$\frac{48.1}{4.2} = 11.5$

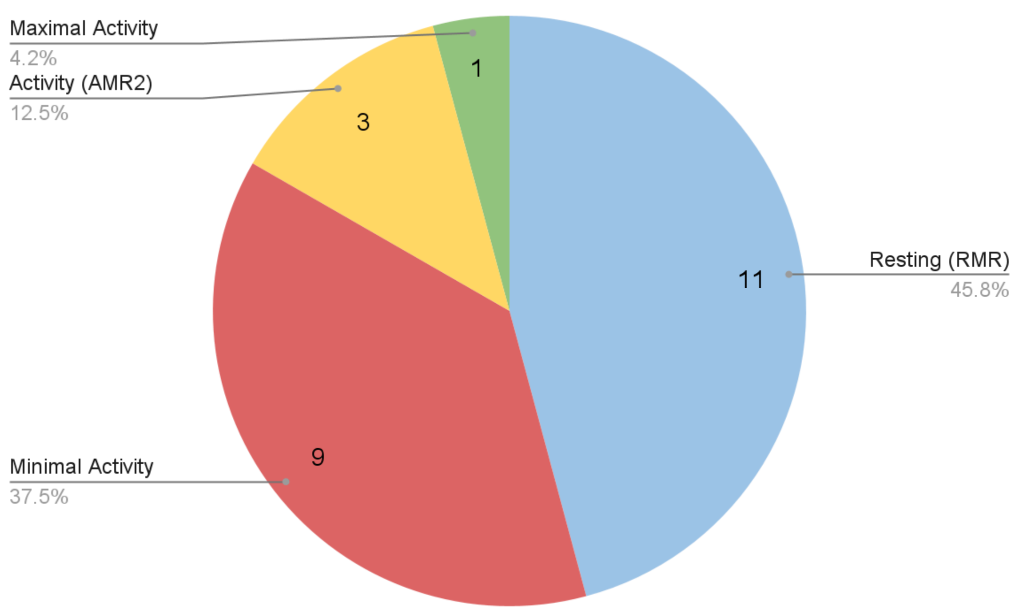

Figure 2. Estimated daily time budget of a male *Puijila darwini* based on observations on fossil morphology and behavioral time budgets of descendents (modern otters, seals).

The RMR, AMRs, MMR, and daily metabolic rate (DMR) were then calculated based on this energy budget and the previously calculated BMR. The resulting metabolic rates are as seen in table 2. Maximal activity (MMR) is seen to be the most expensive form of activity for the *Puijila darwini* while resting is the least.

Table 2. Summary of calculated metabolic rates of the *Puijila darwini.*

Metabolic Type	Rate
Basal: **BMR**	80.0 kJ/hr
Mass Specific Basal: **BMR/M**	4.93 kJ/ghr
Resting: **RMR**	119 kJ/hr
Minimal Activity: **AMR1**	159 kJ/hr
Activity: **AMR2**	501 kJ/hr
Maximal Activity: **MMR**	916 kJ/hr
Daily: **DMR**	5170 kJ/Day
Mass Specific Daily: **DMR/M**	0.320 kJ/gDay

$$DMR/BMR = \frac{5170\ kJ}{Day} \times \frac{1\ Day}{24\ hr} \times \frac{hr}{80\ kJ} \approx 2.7$$

Daily metabolic usage is seen to be about 2.7 times more expensive than the basal metabolic rate of the *Puijila darwini.*

Heat Balance

All heat balance components were first calculated separately according to their corresponding climate and then put together to produce heat balance values for each climate situation. Table 3 shows the resulting values for each component and the full heat balance equation in each situation, as well as the resulting change in temperature in celsius per hour.

Table 3. Summary of heat balance component calculations of *Puijila darwini* and resulting temperature change.

Conditions	Hm [kJ/hr]	Hc [kJ/hr]	Hr [kJ/hr]	He [kJ/hr]	∆Hs [kJ/hr]	∆Temp [C/hr]
Winter Land	215	-48	-	-30.2	137	-0.3
Winter Water	501	-1208	-	-30.2	-737	-58
Winter Basking	215	-48	+871	-30.2	1008	13
Summer Land	215	-37	-	-30.2	149	1.5
Summer Water	501	-913	-	-30.2	-443	-14
Summer Basking	215	-37	+871	-30.2	1020	15

The time budget of an average day in the life of the *Puijila darwini* was estimated for both summer and winter climates. In winter, the *Puijila darwini* was expected to have spent more time basking (Davis, 2019). This is reflected in the following figures 3 and 4 showing the winter and summer time budgets created.

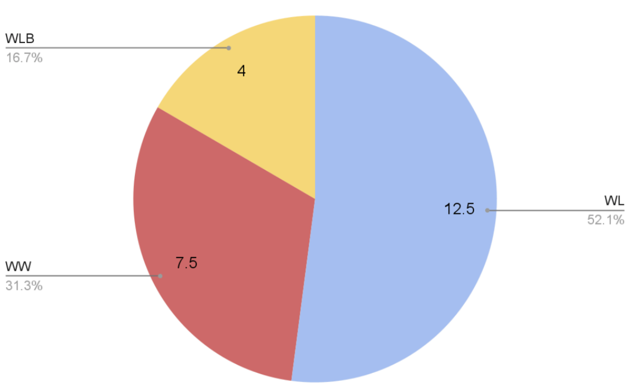

Figure 3. Time Budget of Winter (WLB: Winter basking, WL: Winter land, WW: Winter water)

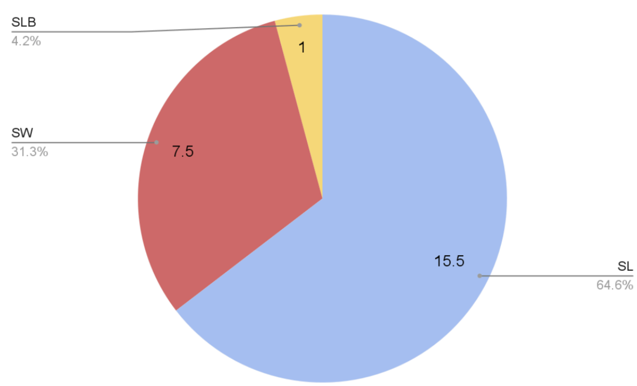

Figure 4. Time Budget of Summer (SLB: Summer basking, SL: Summer land, SW: Summer water)

Based on these time budgets, the following heat balance and change in temperature in winter and summer were calculated (table 4).

Table 4. Heat Balance Situation Summary

Situation	Heat Balance [$\Delta kJ/Day$]	Change in Temperature [$\Delta^{\circ}C/Day$]
Winter	+216	+3.34
Summer	+4.87	+0.08

Cold stress and heat stress situations were also taken into account. In accordance with the parameters stated in the methods, the following heat balance changes were calculated for both stress situations.

Table 5. Stress Situation Summary

Stress Situation	Energy Change [kJ]	Time to Return to Heat Balance [hr]
Heat Stress	11215 kJ (gained from basking)	25 hours of swimming
Cold Stress	9580 kJ (lost from swimming)	9.5 hours of basking

The *Puijila darwini* would gain 11,215 kilojoules of energy and overheat in the heat stress situation. It would take 25 hours of swimming in summer waters to balance out this overheating through loss of heat from conduction in the water. In the cold stress situation, the *Puijila darwini* would lose 9,580 kilojoules of energy that would take at least 9.5 hours of basking to regain.

<u>Discussion</u>:

The *Puijila darwini* expends the most energy when engaging in high activity behaviors such as hunting, and intense swimming as well as low efficiency behaviors such as running. This is reflected in the maximal metabolic rate (MMR) which is seen to be about 11.5 times more expensive than the animal's BMR. Moreover, the daily metabolic rate is about 2.7 times more expensive than the BMR. Both of these observations support the hypothesis that the *Puijila* *darwini* is an active animal because it expends much more energy than its basal energy cost during daily activities. In other words, the *Puijila darwini's* activity levels make it about 2.7 to 11.5 times more expensive to stay alive than it would be if it were a sedentary animal. This is likely affected by its diet and hunting styles. Like modern pinnipeds and mustelids, the *Puijila darwini* fed primarily on small or medium fishes and occasionally on shellfish and they usually hunted alone (Marshal et al., 2019). With smaller prey, hunting needs to be more frequent, and with a lack of teamwork, hunting is less efficient. This behavior would require a high amount of activity and a large amount of energy to fuel.

An endothermic animal, the *Puijila darwini* was most likely a homeothermic, cryophilic animal. The homeothermy of the *Puijila darwini* comes from its high metabolic rates producing heat within its body. It's cryophilia is evident in the ambient temperatures of its arctic habitat going as low or lower than $0^{\circ}C$with a small range of change. We can observe the efficiency of the *Puijila darwini* in cold environments through its bodily temperature changes in the heat balance situations. In a cold environment while practicing winter behaviors such as increased time spent basking, it actually gains more heat energy and therefore more body warmth than in warmer climates (table 4). Moreover, when subjected to heat stress and cold stress situations, the *Puijila darwini* is observed to recover from cold stress over two times faster than what it would take to recover from heat stress (table 5). Both of these experiments show that the *Puijila darwini* is more efficient at thermoregulation in cold conditions than in warmer conditions.

The *Puijila darwini* is a basal pinniped species showing the transition from a terrestrial, freshwater lifestyle to a primarily aquatic environment on coastlines and in oceans. It is thought that this occurred because of the need for a food source in winter when freshwater sources froze over. The *Puijila darwini's* morphology, metabolism, and heat balance all show evidence for this transition. The beginnings of further adaptations to a marine lifestyle are evident in the body of the *Puijila darwini* with its already webbed feet and shortening legs and pelvic bones.

Moreover, the metabolism and heat balance calculations show the *Puijila darwini* was capable of efficient thermoregulation even in cold aquatic environments. It is likely that the next adaptations that occurred were the completion of fins for more efficient swimming or a larger amount of body fat storage like blubber in modern pinnipeds to aid warmth retention.

Abstract:

In this report, the *Puijila darwini* was studied extensively to understand the animal's metabolism and heat balance. The volume and mass were analyzed to determine the BMR and all other metabolic rates such as the RMR, AMR, and MMR. These were then used to estimate the heat balance components Hm, Hc, Hr, and He as well as the heat balance of the *Puijila darwini,* Hs, itself. This information gave a deep insight into the characteristics of an animal already extinct, extrapolated from only its fossil remains. From this information we were able to understand how the *Puijila darwini* regulates its energy in terms of metabolism and heat balance. This allowed us to determine if the *Puijila darwini* was an active or sedentary animal or if it was more suited to cold or warmer environments. These conclusions also gave us the information needed to ask further questions about its evolution leading to modern pinnipeds and how common morphological traits between ancestor and descendant emerged.

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Appendix:

Data:

Dimension Estimations (Rybczynski et al., 2009):

- Length: ~10cm (head), ~100cm
- Radius: ~5cm (head), ~6cm (body), ~1cm (legs)
- Tail Length: ~40cm
- Leg Length: ~20cm from hip/shoulder to ankle

Estimated Surface Area:

- SA of Cylinder (Body): $SA = 2\pi rh + 2\pi r^2 = 2\pi(6)(100) + 2\pi(6)^2 \approx 3996\, cm^2$
- SA of Cylinder (Legs):

  $SA = 4 \times (2\pi rh + 2\pi r^2) = 4 \times [2\pi(1)(20) + 2\pi(1)^2] \approx 528\, cm^2$
- SA of a Sphere (Head): $SA = 4\pi r^2 = 4\pi(5)^2 \approx 314\, cm^2$
- Total Surface Area: $SA_{Total} = 3996 + 528 + 314 \approx 4838\, cm^2$

Mass and BMR Analysis:

- Volume (Cylindrical Body): $V_{Body} = \pi r^2 l = \pi(7)^2(100) \approx 15394\, cm^3$
- Volume (Cylindrical Legs): $V_{Legs} = 4 \times (\pi r^2 l) = 4 \times [\pi(1)^2(20)] \approx 251 cm^3$
- Volume (Spherical Head): $V_{head} = \frac{4}{3}\pi r^3 = \frac{4}{3}\pi(5)^3 \approx 524\, cm^3$
- Mass:

  $m = V_{Total} d = (V_{body} + V_{head} + V_{legs})(\frac{1g}{cm^3}) = (15394 + 251 + 524)\,(\frac{1g}{cm^3}) \approx 16169\, g$

  $16169g \times \frac{1kg}{1000g} \approx 16.17kg$

BMR Equation of Small Mustelids: $BMR = 74.3M^{0.72}$ (Withers, 1992)

$$BMR = 74.3(16169)^{0.72} \approx 79659\, Jhr^{-1} \approx 80\, kJ/hr$$

$$BMR/M = 74.3(16169)^{0.72-1} = 74.3(16169)^{-0.28} \approx 4.93\, Jhr^{-1}g^{-1}$$

O2 Extraction Efficiency 20-25% (Withers 1992) for mammals.

Behavior Data and Time Budget (Based on Modern Otter and Seal):

- Resting (RMR): Resting, Basking, Grooming → 11 hours
- Minimal Activity (AMR1): Walking, Floating/Gliding, Feeding → 9 hours
- Activity (AMR2): Swimming, Hunting (aquatic) → 3 hours
    - Otters and Seals spend the majority of their waking hours foraging/hunting for food in the water (Davis, 2019). But the actual time spent actively hunting was separated between long spans of minimal activity.
- Maximal Activity (MMR): Fast swimming, Running → 1 hour
    - Due to its short ilium in the pelvis, the morphology of the *Puijila darwini* probably did not support efficient running or jumping (intense land activities). Therefore these activities probably took a lot more energy to do than they would in purely terrestrial animals (Marshal, 2019) (Northover, 2011).

Metabolic Rates:

$$RMR = BMR \times 1.5 = 80 \times 1.5 \approx 119\, kJhr^{-1}$$

$$AMR1 = BMR \times 2 = 80 \times 2 \approx 159\, kJhr^{-1}$$

$$AMR2 = BMR \times 6.3 = 80 \times 6.3 \approx 501\, kJhr^{-1}$$

$$MMR = BMR \times 11.5 = 80 \times 11.5 \approx 916\, kJhr^{-1}$$

$$DMR = (RMR \times 11) + (AMR1 \times 4) + (AMR2 \times 8) + (MMR \times 1)$$

$$DMR = (119 \times 11) + (159 \times 9) + (501 \times 3) + (916 \times 1) \approx 5170\, kJ/Day$$

Mass Specific DMR: $DMR/M = 5170/16169 \approx 0.320\ kJg^{-1}day^{-1}$

Heat Balance Variables:

- Ambient Temperature (Year Round Average in Habitat) (Whitlock, 1990): $T_a = 0 - 11^{\circ}C$

  → Taking Average: $T_a = 5.5^{\circ}C$

  - Average Winter Min: 0C
  - Average Summer Max 11C

- Body Temperature (Based on Otter Body Temperature) (Esslinger, 2011) :$T_b \approx 38^{\circ}C$

Heat Balance (All values and equations from Withers, 1992): $\Delta H_s = H_m \pm H_c \pm H_r \pm H_e$

Heat Balance in Winter:

- Winter Land (WL): $\Delta H_s = 215 - 48 - 30.2 \approx 137\ kJ/hr$
- Winter Water (WW): $\Delta H_s = 501 - 1207 + 871 - 30.2 \approx -737\ kJ/hr$
- Winter Land Basking (WLB): $\Delta H_s = 215 - 48 + 871 - 30.2 \approx 1008\ kJ/hr$

Heat Balance in Summer

- Summer Land (SL): $\Delta H_s = 215 - 37 - 30.2 \approx 149\ kJ/hr$
- Summer Water (SW): $\Delta H_s = 501 - 913 + 871 - 30.2 \approx -443\ kJ/hr$
- Summer Land Basking (SLB): $\Delta H_s = 215 - 37 + 871 - 30.2 \approx 1020\ kJ/hr$

Hm: Based on Metabolic Rates

- Hm on Land (Resting) Based on DMR ($RMR = 5170\ kJ/Day$) → $H_{ml} = 215\ kJ/hr$
- Hm on Water (Active) Based on AMR2 ($AMR2 = 501\ kJ/hr$) → $H_{mw} = 501\ kJ/hr$

Hc: Based on C equation for Mammals (Withers, 1992)

- Winter: $C = 13.9M^{-0.534} = 13.9(16169)^{-0.534} = 0.0786$

  $\rightarrow H_{cw} = C_w M\Delta T = (0.0786)(16169)(38 - 0) \approx 48311\, J/hr \approx 48\, kJ/hr$
- Summer: $C = 23.5M^{-0.534} = 23.5(16169)^{-0.534} = 0.1329$

  $\rightarrow H_{cs} = C_s M\Delta T = (0.1329)(16169)(38 - 11) \approx 36540\, J/hr \approx 37\, kJ/hr$
- Water increases both of these by a factor of 25
  - Winter (In Water): $H_{cww} = H_w \times 25 \approx 1207\, kJ/hr$
  - Summer (In Water): $H_{csw} = H_s \times 25 \approx 913\, kJ/hr$

- $C = 20.5M^{-0.426} = 20.5(16169)^{-0.426} = 0.3302$
- Winter: $H_{cw} = CM\Delta T = (0.3302)(16169)(38 - 0) \approx 202919\, J/hr \approx 203\, kJ/hr$
- Summer: $H_{cs} = CM\Delta T = (0.3302)(16169)(38 - 11) \approx 90779\, J/hr \approx 91\, kJ/hr$
- Water increases both of these by a factor of 25
  - Winter (In Water): $H_{cww} = H_w \times 25 \approx 5073\, kJ/hr$
  - Summer (In Water): $H_{csw} = H_s \times 25 \approx 2269\, kJ/hr$

Hr: Negligible in Shade

- Heat Gain from Sunlight (Withers, 1992): 0.180 kJ hr^-1 cm^-2
- $H_r = (Heat\ Gain\ From\ Sun)(Exposed\ Skin) = (0.180)(SA) = (0.180)(4838)$

  $H_r \approx 871\, kJ/hr$

He: $H_e = (Evaporative\ Water\ Loss)(Latent\ Heat\ of\ Evaporation) = (EWL)(2.4\, kJ/g\ water)$

$= (302)(2.4) \approx 724\, kJ/Day \rightarrow 30.2\, kJ/hr$

- Experimental Water Content of air at Tb = 38C and 100% humidity: $\chi_{exp} = 43\, mg/L$

- Inspiratory Water Content of air at Ta = 5.5C and 75% humidity:

$\chi_{insp} = 6.8\, g/m^3 \times \frac{1000mg}{1g} \times \frac{1m^3}{1000L} = 6.8\, mg/L$ (On Land) → $6.8 \times 0.75 \approx 5.1\, mg/L$

- Body Water Content at 38C and 100% humidity: $\chi_{body} = 43\, mg/L$ (On Land)
- Air Water Content at 5.5C and 75% humidity: $\chi_{air} = 6.8\, mg/L$ (On Land) →

  $6.8 \times 0.75 \approx 5.1\, mg/L$

- $EWL = REWL + CEWL = 196 + 106 \approx 302\, g\, water/day$
  - $REWL = (Liters\ air/day)(\chi_{exp} - \chi_{insp}) = (5170)(43 - 5.1) \approx 195941\, mg$

    $\approx 196\ g\ water\ lost\ through\ breathing\ per\ day$
    - Liters of Air per Day:

      $L/d = (Liters\ O_2/Day)/[(0.2\ Liter\ O_2/Liter\ Air)(\%\ Extraction)]$

      $= (\frac{6883\ kJ/Day}{20\ kJ/Liter\ O_2})/[(\frac{0.2}{1})(0.25)] \approx 5170\ L_{air}/Day$
  - $CEWL = (\chi_{body} - \chi_{air})(SA)/r = (0.0379)(4838)/(150) \approx 1.22\, mg/s$
    - $\approx 1.22\, mg/s \times \frac{3600s}{1hr} \times \frac{24\ hr}{I\ Day} \times \frac{1g}{1000\ mg} \approx 106\ g\ water\ lost\ per\ day$
      - r = 150 sec/cm (Withers, 1992) → Mammal with fur (high resistance)
      - $\chi_{body} - \chi_{air} = 43 - 5.1 = 37.9\, mg/L \times \frac{1L}{1000cm^3} = 0.0379\, mg/cm^3$

Temperature Change

$\Delta T = (\Delta H_s)(1/M)(1^{\circ}Cg/4J)$

Winter:

- WL: $\Delta T = (137 \times 1000)(1/16169)(1^{\circ}Cg/4J) \approx 2.12\ ^{\circ}C$
- WW: $\Delta T = (-737 \times 1000)(1/16169)(1^{\circ}Cg/4J) \approx -11.4\ ^{\circ}C$

- WLB: $\Delta T = (1008 \times 1000)(1/16169)(1^{\circ}Cg/4J) = 15.6\ ^{\circ}C$

Summer:

- SL: $\Delta T = (149 \times 1000)(1/16169)(1^{\circ}Cg/4J) \approx 2.30\ ^{\circ}C$
- SW: $\Delta T = (-443 \times 1000)(1/16169)(1^{\circ}Cg/4J) \approx -6.84\ ^{\circ}C$
- SLB: $\Delta T = (1020 \times 1000)(1/16169)(1^{\circ}Cg/4J) \approx 16^{\circ}C$

Example Daily Temperature Situation in Winter with Relation to Daily Time Budget

- RMR 11 hours (Basking and Resting) → 4 hours basking (WLB), 7 hours resting (WL)
- AMR1 9 hours (Swimming, Walking, Feeding) → 5 hours on land (WL), 4 hours in water (WW)
- AMR2 3 hours (Hunting) → 3 hours (WW)
- MMR 1 hour (Running, Intense Swimming) → 0.5 hour (WW), 0.5 hours (WL)

$\Delta H_s = (WLB \times 4) + (WL \times 12.5) + (WW \times 7.5) = 216\ kJ/Day$

$\Delta T = (216)(1/16169)(1^{\circ}Cg/4J) \approx +3.34\ C/Day$

Example Daily Temperature Situation in Summer with Relation to Daily Time Budget

- RMR 11 hours (Basking and Resting) → 1 hour basking (SLB), 10 hours resting (SL)
- AMR1 9 hours (Swimming, Walking, Feeding) → 5 hours on land (SL), 4 hours in water (SW)
- AMR2 3 hours (Hunting) → 3 hours (SW)
- MMR 1 hour (Running, Intense Swimming) → 0.5 hours (SW), 0.5 hours (SL)

$\Delta H_s = (SLB \times 1) + (SL \times 15.5) + (SW \times 7.5) = 4.87\ kJ/Day$

$\Delta T = (4.87)(1/16169)(1^{\circ}Cg/4J) \approx +0.08\ ^{\circ}C/Day$

Heat Stress Situation: The *Puijila darwini* is an arctic mammal. What would happen if it were subject to an environment much warmer than it is accustomed to? Based on the average summer climate of the environment (~20C at 75% humidity). Assume the Puijila fell asleep in the sun, basking, for 11 hours, its full resting time. It does not swim on this day. How long would it have to swim to return to heat balance?

$\Delta H_s = (SLB \times 11) + (x) = 0 \rightarrow x = -(1020 \times 11) \approx -11215\, kJ$

$x = (SW \times hr) \rightarrow hr = x/SW = (-11215/-443) \approx 25\, hr$

Cold Stress Situation: Based on the winter situation and minimum winter temperatures (~ -17C at 75% humidity). What would happen if the Puijila swims for too long in cold waters? (13 hours in winter waters, its full active time). How long would it have to bask in the sun to return to heat balance?

$\Delta H_s = (WW \times 13) + (x) = 0 \rightarrow x = -(-737 \times 13) \approx 9580\, kJ$

$x = (WLB \times hr) \rightarrow hr = x/WLB = (9580/1008) \approx 9.5\, hr$