What selective forces produced eco-geographic patterns in human mid-facial morphology?

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Introduction

For many years anthropologists have known that the shape of the nose varies geographically and climatically, with tall, narrow noses generally found in cold, dry climates, and broader, shorter ones in hot, humid areas (Carey and Steegman 1981; Thomson and Buxton 1923; Williams 1956). Inter-population studies have shown that the mid-facial skeleton reflects climatic adaptations better than other parts of the cranium (Hall 2006; Roseman and Weaver 2004). To provide an evolutionary explanation for these patterns, anthropologists have argued that nasal complex variations affect how air is conditioned to meet the requirements of the lungs, and conditioning air requires energy.

Energetics in Pre-Industrial People

An evolutionary approach requires us to think about energy costs in non-industrial societies where people do more physical work and have less food available. Energetics theory (Ulijaszek 1995), as applied in this project, suggests that selection favors mid-facial and nasal adaptations that are energy-efficient in a population's native habitat. Animal studies have shown that mammals and birds, who as endotherms consume 5 to 10 times the energy that comparably sized reptiles do, have elaborated turbinates at the front of the nasal airway to help them conserve moisture and heat (Hillenius 1994; Geist 2000). Similar concepts have been shown to apply to variation among humans living in different environments (Shea 1977).

This pilot project's goal was to develop an experimental protocol to test whether subjects with different nasal and mid-facial shapes differ in their ability to conserve energy, given specific temperature and humidity conditions. Our pilot study with 12 subjects cannot test this hypothesis; it tested whether our measurement instruments and our protocols are appropriate for a large study.

Hypothesis

Relatively narrow, tall, deep nasal morphologies retain more heat and moisture in a cold/dry experimental condition, and broader, shorter nasal structures perform the task of dissipating heat and moisture better under hot/humid experimental conditions.

Experimental Lab Conditions

We recruited young adult male subjects to test measures of their breathing at different simulated temperature and humidity levels in the University of Oregon's Environmental Chamber in the Human Physiology Department. We tested them at rest and during exercise, using nose-only and mouth-only breathing in these conditions

1) Moderate/indoor conditions (20°C; specific humidity ~11.2 g/kg);
2) Cold/dry typical of Wales, Alaska (-12° C; specific humidity ~1.2 g/kg);
3) Hot/humid typical of Calcutta, India (35°C; specific humidity ~ 22). Subjects' breathing was recorded for four minutes each sitting quietly, pedaling on a cycle ergometer at 20%, 40%, and 60% of workload associated with the subject's maximum VO2 cycling rate.

After each session we asked subjects about their comfort level and specific stresses in each climate condition and breathing type.

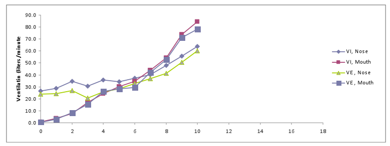
Mattie Bridgmon prepares equipment before a cold-chamber experiment.

Subject Characteristics

Our subjects were male students of ages 18-28, all healthy and non-smoking. We sought subjects with ancestry from different climatic zones to achieve morphological diversity, reasoning that similar mid-facial measurements are found in populations from similar climates and that these morphologies are adaptive. We sought subjects whose ancestors came from countries lying between the tropics of Cancer and Capricorn in Africa, Asia, and the Americas; and subjects with ancestors from northern parts of Eurasia and native North America. We did not achieve the 50:50 ratio we wanted as only three had ancestry in a hot, humid climate and the ancestry of the other nine was in dry, cold ones; in a larger study we would work to achieve a better geographic spread.

Measuring Max VO2

In measuring subjects' maximum VO2 we used two separate expiration tubes, one collecting air from the nose and the other from the mouth. This allowed us to chart the subject's breathing pattern.

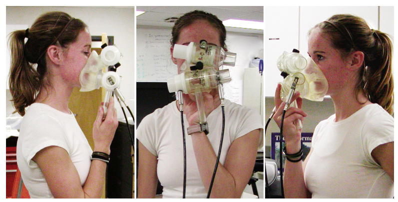


A typical subject's breathing during a max VO_2 test; VI= Ventilation during inspiration and VE=Ventilation during expiration; minutes are recorded on the horizontal axis.

The subject started by breathing primarily through the nose but quickly increased mouth breathing. At maximum VO_2, he is using both channels, with more air going through the mouth than the nose.

Physiological Measurements

Standard physiological measures such as heart rate, VO_2, total ventilation, and respiratory rate, were recorded continuously. In addition, we measured temperature and humidity of expired air with a dedicated humidity/temperature sensor-transmitter in the tube leading from the mask. Adaptations to a basic breathing mask were complex and cumbersome.

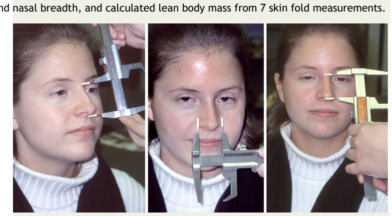


The weight of the mask and the bulk of the air tubes made fitting the mask to the subject a challenge. During nose-breathing we had to adapt the same mask to individuals of different sizes. Straps on the mask helped, and we checked for leaks around the face; when needed, we inserted a gel to obtain a good seal. Fitting was easier during mouth breathing because we could pinch the nose shut and use a relatively simple device to capture air, but this still involved several heavy tubes.

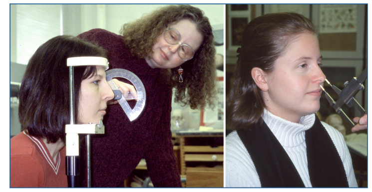
Because VO_2 was consistently lower during nose-breathing than mouth-breathing, we questioned whether part of the difference could be explained by leakage. In this poster, we analyze correlations between measures of nose morphology and 2 ratios: expired temperature recorded at Moderate/indoor conditions to temperatures at Cold/dry and at Hot/humid conditions.

Anthropometric Measurements

We took standard anthropometrics: weight, stature, sitting height, shoulder width, hip breadth, head length, head breadth and upper facial height, nasal height and nasal breadth, and calculated lean body mass from 7 skin fold measurements.

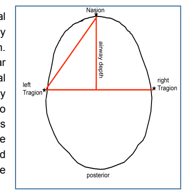


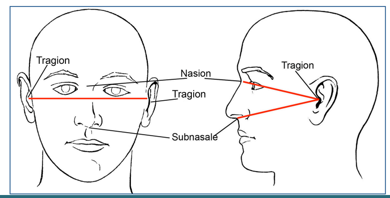
Qualitative observations were made to characterize the projection of the nose; the direction of the nares (down, lateral, or forward); and nose shape as matched to a diagram. We estimated the volume of the external nose using a formula based on height, breadth, nasion to pronasale and pronasale to subnasale developed by mathematician David Bash. We chose a few rarely used measurements and developed new ones: breadth of the nasal bridge, nasion to pronasale, pronasale to subnasale, angle of nose with forehead, nostril length (both sides), and nostril breadth (both sides).



Measuring projection with angle (left) and pronasale to subnasale.

To include the size of important internal nasal structures (Dempsey et al. 2002; Yokley 2006) we devised the measure Airway depth. Tragion (T), at the upper anterior of the ear opening, is a a fleshy proxy for the skeletal point porion. We estimated depth by measuring Tragion to Nasion, Tragion to Subnasale, and Tragion to Tragion. For this analysis we used Tragion to Nasion and the mid-point of Tragion to Tragion and applied these in a right triangle formula to produce the length of the third side, Airway depth.





Subject Variability

We found considerable variation among our 12 subjects; the majority, but not all, completed their VO_2 test with more mouth-breathing than nose-breathing. Work rates associated with maximum VO_2 varied from 225 to 400. Other characteristics were varied too:

- **Lean body mass: 87.4% to 95.5%;**
- **Nose volume: 7.26 sq. cm to 12.37;**
- **Nasal breadth: 2.8 to 4 cm;**
- **Nasal height: 4.8 to 6.6 cm;**
- **Airway depth: 8.45 cm to 11.6.**

Temperature of expired air varied little during the Moderate/indoor phase, quite a lot during the Cold/dry phase, and little during the Hot/humid phase. Expired relative humidity varied little during the Moderate/indoor or Cold/dry phases, but slightly more during the Hot/humid phase. Total Ventilation and VO_2 varied throughout. Measures of a subject's total heat and water loss during all phases, at rest and during exercise, were estimated with formulas that used Total ventilation as well as temperature and relative humidity. All data were entered into an Excel table for analysis.

Statistical Analysis

These ratios were created:

1. **Expired Temp (Moderate/indoor)/ Expired Temp (Cold/dry)**
2. **Expired Temp, (Moderate/indoor)/ Expired Temp (Hot/humid)**

Expectations are that a person well-adapted to cold would have a ratio >1 in #1, with nasal-breathing values higher than mouth-breathing. Correlations between these values and Nasal height, Nasal breadth, Nose volume, and Airway depth in nose-breathing and mouth-breathing trials at rest were made to see whether morphology mattered. A parallel set of ratios using relative humidity in place of temperature produced so little variation among subjects that no further tests were useful. In the cold/dry series, subjects' expired nose temperatures were lower than at moderate temperature and usually – but not always – higher in nose-breathing.

Nose ratios	Mouth ratios
1.466	1.766
1.678	2.131
3.150	1.484
3.031	1.453
2.039	1.448
1.000	1.000
2.217	1.419
1.862	1.265
1.662	1.410
2.207	1.556
1.633	1.248
1.838	1.404

The average nose-breathing ratio was 1.982 compared to 1.465 for mouth-breathing. Correlations with 4 anthropometric measures were interesting but puzzling. The hypothesis predicts that Nasal height and Airway depth would correlate positively with nasal-breathing ratios, and that Nasal breadth would do the opposite. No expectation was made for correlations with Nasal volume.

Anthropometric measures	Correlations with nasal-breathing ratios	Correlations with mouth-breathing ratios
Airway Depth	0.439	0.319
Nasal Height	-0.487	-0.309
Nasal Breadth	-0.453	0.431
Nasal Volume	-0.355	0.004

Cold/Dry Conditions

Most unexpected was that Nasal height produced a negative correlation with the ratio of indoor to cold expired air temperature. It is interesting that Nasal breadth correlations between the two types of breathing were opposite.

Using the ratio of Moderate/indoor to Hot/humid temperature, the average nose-breathing ratio was 0.755 and it was 0.802 for mouth-breathing. The most interesting correlations between anthropometric measures and ratios were negative correlations with Airway depth and Nasal volume, which link greater heat expiration during the Hot/humid trial in subjects with larger noses and deeper airways.

Anthropometric measures	Correlations with nasal-breathing ratios	Correlations with mouth-breathing ratios
Airway Depth	0.669	-0.343
Nasal Height	-0.239	-0.310
Nasal Breadth	-0.098	0.159
Nasal Volume	-0.605	-0.462

Hot/Humid Conditions

General Observations

1. Subjects experienced more stress during the hot/humid trial than during the cold trial. One subject could not get enough breath to go beyond the 40% level using nose-breathing.

2. During mouth-breathing, many experienced thirst, whereas many found nose-breathing more difficult; they felt they did not easily get as much air as they wanted.

3. Output physiological measures – VE, VO_2, measures of expired heat, relative humidity, and heat loss in kilo-calories – differ in nasal and mouth breathing within the same subject and between subjects.

Conclusions

Breathing is the *sine que non* of life and exploring how natural selection maximizes energy use in adapting populations to particular environments deserves further study. This pilot study developed and tested old and new anthropometric and respiration measures with 12 subjects. Most but not all proved useful and appear to have been recorded reliably. Interviews with subjects produced insights about comfort level suggestive of morphological and behavioral adaptations.

Variation evident in charts of nose-breathing and mouth-breathing in maximum VO_2 tests were insightful and in a larger sample can be associated with measures of morphology.

In expanding the study, we need to develop a way to make mask attachments fit securely and confidently on every individual. We may consider omitting measures that appear not to be needed. We should investigate whether the sensor recording humidity should be more sensitive or placed differently.

With a larger sample it is important that we have an equal balance of subjects with ancestry from distinctly different parts of the world. In this analysis we compared subjects to themselves under different lab conditions to avoid problems caused by confounding variables, but in a larger sample we could compare groups of subjects and control for factors such as weight and lean mass.

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