The Daedalus Project: Physiological Problems and Solutions

Ethan R. Nadel
Steven R. Bussolari

In April of 1985, a team of engineers and scientists at the Massachusetts Institute of Technology began a research program with the goal of flying an aircraft from the Greek island of Crete powered only by the muscles of the pilot. The project was called Daedalus, in celebration of the mythical Greek inventor who constructed wings of wax and feathers with which he flew from imprisonment on Crete some 3,500 years ago. In some versions of the myth, Daedalus was accompanied by his son Icarus, who flew too close to the sun, against his father's admonition, and fell to the sea when his wings melted.

The route proposed in the Daedalus project, from the port city of Heraklion on Crete to the island of Santorini (or Thíra), was 119 km, more than three times the existing world record for human-powered flight, Bryan Allen's 35-km crossing in 1979 of the English Channel in the *Gossamer Albatross* (Fig. 2). In the years since the record was set, advances in aircraft technology had made our more ambitious attempt possible, although much needed to be learned about the physiology of the human pilot. In fact, the fundamental challenge of human-powered flight is the limited ability of humans to act as a power plant. Preliminary estimates of the aircraft's performance, based on previous designs, indicated that the Daedalus flight would last four to six hours. Before an aircraft could be designed in detail, we needed to learn more about the physiological limits of long-duration exercise and about possible countermeasures that would postpone the onset of fatigue. We sought an engineering model for human power production that we could address with the same analytical tools an aircraft designer would use in matching power plant to airframe. It was that goal which brought the authors—a physiologist and an aeronautical engineer—into collaboration.

The challenge of a human-powered flight lasting up to six hours posed unique physiological problems and required unique solutions

Because an aircraft engine must carry its own weight, its performance is often expressed in power per unit weight or power-to-weight ratio. Preliminary calculations showed that our pilot would be required to produce approximately 3.0 to 3.5 watts of mechanical power per kilogram of body weight to fly at all. Furthermore, because human-powered aircraft require significantly more power to climb than to fly on the level and so generally fly within a few meters of the surface, there would be no time to glide, and the pilot would be required to produce this power continuously, with no rest, for the entire flight.

Figure 1. The *Daedalus* undergoing initial tests at Edwards Air Force Base in California, with coauthor Steven Bussolari, the director of flight operations, following on a recumbent bicycle. (Photograph by Steve Finberg.)

The metabolic cost to the pilot of maintaining the constant mechanical power production of 3.0 to 3.5 watts per kilogram of body weight is relatively easy to determine. Potential energy is converted into mechanical work by the oxidation of stored fuels to generate the high-energy compounds that are necessary for both the contraction and relaxation processes in skeletal muscle (see Ethan Nadel's article in *American Scientist*, July-August 1985, for an expanded account of energy conversion in skeletal muscle). It is generally accepted that in humans only about 24% of the potential energy of these stored fuels can be converted to mechanical work during the metabolic transfers (Åstrand and Rodahl 1986); this value is known as the mechanical efficiency. The remaining 76% is converted directly to heat during these transfers and is of no use to the pilot. Thus, in order to generate mechanical power at the rate of 3.5 W/kg, the pilot would have to maintain a fuel-oxidation rate of 14.6 W/kg, which requires an oxygen uptake of more than 44 ml O_2/(min·kg). The pilot has to sustain this rate of oxygen uptake, without pause, to maintain steady flight. This metabolic cost is approximately the same as that required to pedal a bicycle over level ground at a world-class speed of 37 km/hr (Whitt and Wilson 1982).

The problem unique to the Daedalus project was whether this energy production could be sustained for the anticipated four to six hours of the flight. A thorough review of the existing literature yielded no convincing data for human power production of durations beyond about three hours, and no data taking the sizes or body weights of the subjects into account, which made estimates of specific power nearly impossible (see Whitt and Wilson 1982 for a good summary of the available data). It was clear, therefore, that the Daedalus project would

Figure 2. The 119-km route of the *Daedalus*, a symbolic reenactment of the escape from Crete by the mythical Daedalus on wings he constructed, is more than three times longer than the previous record for human-powered flight, the crossing of the English Channel.

need to conduct its own research in long-duration human power production to identify the potential factors that might promote the onset of fatigue and to determine whether we could eliminate these factors or at least postpone their onset.

Screening for high aerobic power

The first problem that the Daedalus team had to address was whether we could expect to find people who could maintain a constant power output adequate to sustain flight for an extended time. There have been a number of population surveys of maximum aerobic power, or maximum oxygen uptake, two of which are notable: one is the assessment of maximum oxygen uptake in 350 Swedish males and females ranging in age between 4 and 65 years (Åstrand 1960), the other in 184 American male and female army inductees (Vogel et al. 1977). In both surveys the average values of maximum aerobic power were about 25% higher in males than in females when normalized for body weight. In males between the ages of 20 and 25 years old, the maximum oxygen uptake averaged just over 50 ml O_2/(min · kg), which is only marginally greater than the 45 ml O_2/(min · kg) we calculated as necessary to keep the Daedalus aircraft aloft in steady flight, and which is therefore grossly inadequate for a long-distance flight.

Nonathletes rely increasingly on anaerobic processes for energy production at exercise intensities above 60% of their maximum aerobic capacities. The byproducts of anaerobic metabolism are excess lactic acid and hydrogen ions, which alter the optimal intracellular environment and impair the efficiency of the enzyme interactions, resulting in a decrease in the rate of energy production. Based on these values, we predicted that the average young male might be expected to maintain an oxygen uptake of around 30 ml O_2/(min · kg), but not much more, for an extended period.

It was clear that the pilot for the Daedalus aircraft would have to be an extremely well conditioned athlete. Endurance athletes are able to maintain energy production without the production of excess lactic acid during exercise that demands up to 80% of aerobic capacity. Accordingly, we could expect an athlete with a maximum oxygen uptake above 65 ml O_2/(min · kg) to be able to maintain an uptake of around 45 ml O_2/(min · kg) for hours. Therefore, the first goal of the pilot-selection team was to screen applicants for high maximum oxygen uptakes and for high power production at 70% of their maximum capacities (arbitrarily chosen to provide a margin of safety from the excess lactic acid threshold).

Announcements of the search for pilots for the Daedalus project produced 300 applications, a number of these from Olympic-caliber athletes. We invited 25 (24 men and 1 woman) to be tested, all of them either cyclists or triathletes. We had determined that athletes who have been training on the bicycle could be expected to generate power on the Daedalus aircraft the most efficiently, because they had been using the specific muscle groups for cycling in their training regimes. The group of 25 included 4 cyclists from the Greek national team; our hope was to have at least one Greek citizen as a member of our Daedalus pilot team.

The test for maximum oxygen uptake was given on a stationary-cycle ergometer on which the athlete pedaled in a semirecumbent position similar to that in the aircraft. After a warm-up, the athlete began pedaling at his preferred frequency (generally around 76 rpm). At 2-minute intervals, the power required to maintain the same pedaling frequency was increased in increments of 60 watts by tightening the belt around the flywheel. The athlete was encouraged to maintain pedaling frequency for as long as possible despite the increasing load. The test was terminated when the athlete could no longer maintain that frequency and power production declined. During the test, the athlete breathed through a low-resistance, two-way valve, with which his mass flow rate and the amount of carbon dioxide and oxygen in his expired air was continuously monitored. Maximum oxy-

Ethan R. Nadel, a graduate of Williams College and the University of California, Santa Barbara (Ph.D. 1969), is a professor of epidemiology and physiology at the Yale University School of Medicine and is a Fellow of the John B. Pierce Foundation Laboratory. His research focuses on the physiological control of energy exchanges in humans. Steven R. Bussolari is an assistant professor in the Department of Aeronautics and Astronautics at MIT, where he did his graduate work (Ph.D. 1983), and where he now conducts research in aerospace human factors. *The Daedalus project has been supported in part by United Technologies Corporation, Shaklee Corporation, MIT, NASA, the Smithsonian Institution, and several agencies of the Greek government.* *Address for Dr. Nadel: John B. Pierce Foundation Laboratory, 290 Congress Avenue, New Haven, CT 06519.*

gen uptake was established by an inability to maintain pedaling frequency within 10% of the predetermined value, by a leveling off in oxygen uptake with increasing power requirement, and by a respiratory exchange ratio of carbon dioxide to oxygen greater than 1.15, which would indicate a significant hyperventilation resulting from the accumulation of anaerobic metabolites in the blood.

Figure 3 shows the results from a typical test for maximum oxygen uptake. The linear relation shown between oxygen uptake and power output (calculated without the highest value, which always includes an anaerobic component) can be represented by this equation: oxygen uptake = $a + b \times$ mechanical power output, with the value of a representing (at a power output of 0 W/kg) the oxygen uptake contributing to metabolic processes independent of mechanical power output, and with the value of b representing the ratio of oxygen uptake to power output (i.e., the slope of the equation), from which the athlete's mechanical efficiency can be derived. We can determine maximum aerobic mechanical power production by substituting the measured maximum oxygen uptake in this equation. Calculation of mechanical power output at 70% of maximum is accomplished by substituting oxygen uptake at 70% of maximum in the equation and solving for mechanical power.

The average values we obtained for the 25 athletes confirmed that we had indeed selected an elite group for testing. The range of maximum oxygen uptakes was between 59 and 86 ml O_2/(min·kg), certainly representative of highly trained endurance athletes (Åstrand and Rodahl 1986). Not only did the maximum uptakes of our 25 applicants have a much higher average than the values obtained by Vogel and his colleagues in their survey of 184 army recruits—69.2 compared to just over 50 ml O_2/(min·kg)—but it should be stressed that the high values of our group were produced in the semirecumbent position on the cycle ergometer, which characteristically yields values around 8 to 10% lower than the treadmill used in the army survey, because the latter involves a higher mass of active muscles. The aerobic mechanical power output of our athletes averaged 5.25 W/kg at maximum; at 70% of maximum the average was 3.54 W/kg (ranging between 2.87 and 4.23 W/kg), allowing the interpretation that our average applicant would be able to produce sufficient power to maintain steady flight in the Daedalus aircraft. The mechanical efficiency, the power production per unit energy production, averaged 24.1%, close to the expected value for skilled cyclists.

Remarkably, the mechanical efficiency among the 25 athletes ranged between 18.0 and 33.7%, indicating that maximum oxygen uptake alone is not a sufficient predictor of performance. As Figure 4 illustrates, two athletes with nearly identical maximum oxygen uptakes can have widely different efficiencies, 20.1 and 26.6% in the example shown. At 70% of maximum aerobic power output, the values for mechanical power production are 3.31 and 4.21 W/kg, which means that the more efficient of the two is able to generate 27% more mechanical power at 70% of his maximum oxygen uptake. Another way of looking at the difference between the two is that the oxygen uptake necessary to generate a power output of 3.5 W/kg is 74% of maximum in the less efficient athlete and only 59% of maximum in the more efficient athlete, whom we would therefore expect to have a greater endurance.

The reasons for the large range in efficiency are not entirely clear. Certainly, a small part of the variability can be attributed to differences in the recruitment of auxiliary muscle groups not directly involved in mechanical power production. In other words, some of the athletes make greater use of the upper body, which participates only indirectly in power generation on the cycle ergometer. The major part of the variability is probably a consequence of differences among individuals in metabolic machinery; the velocity of muscle shortening, and therefore the economy of tension development, is a function of the genetically determined content of a particular enzyme, myofibrillar myosin ATPase, in the muscle itself.

A question about mechanical efficiency that concerned us from the inception of the project and that was not resolved by the literature was whether the semirecumbent position, which gave the pilot the most freedom to use the aircraft controls, entailed a lower mechanical efficiency than the standard, upright cycling position. Bicyclists have known for years that a recumbent can beat an upright in a race, all other things being equal, but this is largely because of the lower wind resistance offered by the recumbent cyclist's reduced frontal profile (Whitt and Wilson 1982). We therefore tested several of our applicants a second time in the

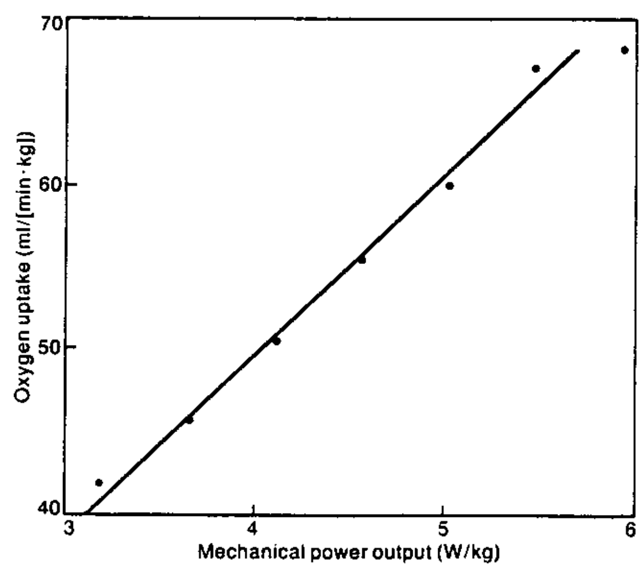

Figure 3. In these typical results of a test for aerobic capacity, each data point represents the athlete's average oxygen uptake during a two-minute interval while pedaling on a cycle ergometer. The power required to maintain a consistent pedaling frequency on the ergometer is increased in successive intervals in increments of 60 watts, and the maximum oxygen uptake is established at the highest power output that could be sustained for an interval. This maximum always includes an anaerobic element (as indicated by the smaller difference in oxygen uptake between the last two readings) and so is discarded when deriving the average linear relation shown, from which the aerobic mechanical power production can be calculated.

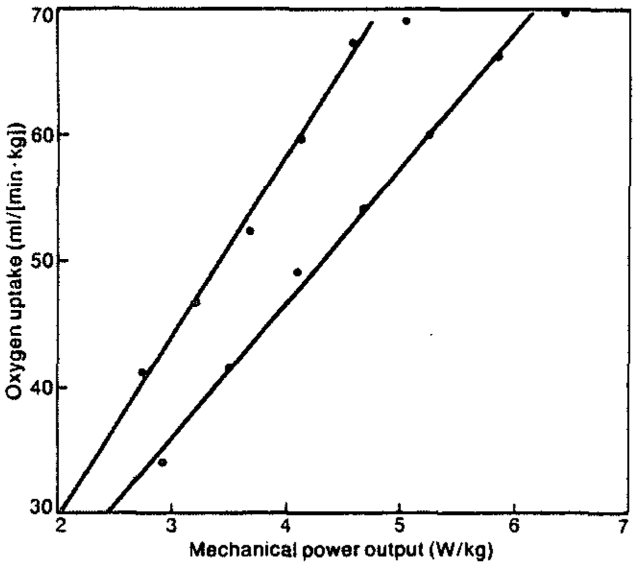

Figure 4. Although the two athletes represented here have nearly identical maximum oxygen uptakes, close to 70 ml O_2/(min · kg), mechanical efficiency—the percentage of energy production (as indicated by oxygen uptake) that results in mechanical power production—is much greater in one athlete (*blue*) than in the other (*gray*).

upright position. As Figure 5 shows, we found no differences in either maximum oxygen uptake or mechanical efficiency between the two positions in experienced cyclists.

Maintaining oxygen delivery

Although we were confident that our athletes were capable of maintaining the necessary oxygen delivery to the active skeletal muscles for a flight of up to 2 hours, we had to examine the issue of maintaining oxygen delivery over 5 or 6 hours, when fatigue in one or more of the links in the oxygen transport chain may begin to occur. Since there is practically no literature on the physiology of exercise that is prolonged for more than 3 hours, we were unable to predict whether this might be the case.

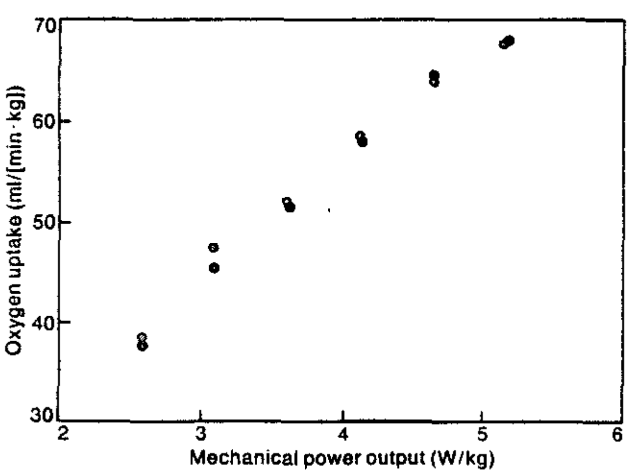

Figure 5. Nearly identical results were produced when the same athlete was tested for maximum oxygen uptake and mechanical efficiency in both the semirecumbent (*blue*) and upright (*gray*) cycling positions.

The issue can be conceptualized by examining the determinants of maximum oxygen uptake:

$$VO_{2\ max} = [HR_{max}][SV_{max}][(aO_2 - vO_2)_{max}]$$

That is, maximum oxygen uptake (ml O_2/(min·kg)) equals the product of the maximum heart rate (beats/min) times the maximum cardiac stroke volume (ml blood/beat) times the maximum of the oxygen content in the arterial blood less the oxygen content in the mixed venous blood (ml O_2/ml blood). The difference between the arterial and mixed venous oxygen contents represents the volume of oxygen extracted by the body.

Any reduction in maximum oxygen uptake during prolonged exercise increases the *relative* cost of maintaining level flight in the aircraft. In other words, since the oxygen requirement to fly the plane is constant, any reduction in the maximum will have the consequence of moving the absolute cost of flying closer to the pilot's maximum ability to generate energy. As such, the production of energy will become increasingly anaerobic, and the production and storage of excess lactic acid and hydrogen ions in the active muscles will hasten the onset of fatigue.

Maximum heart rate is primarily a function of heart size, because the ability of any muscle to conduct the depolarization signal is a function of its mass. Thus, unless the potassium content of the heart decreases dramatically, an unlikely event for heart muscle, there should be no decrease in maximum heart rate during prolonged exercise.

Maximum cardiac stroke volume, however, could well be forced to decline during prolonged exercise as a result of plasma water losses. Marked shifts in body water out of the vascular compartment occur during exercise, both because of the increased capillary blood pressure within the muscles, which promotes a filtration of fluid into the muscle interstitial space, and because of the gradual redistribution of body water that accompanies the evaporative losses from the respiratory and skin surfaces. The rate of skin evaporation will be proportionately greater as the ambient temperature increases. Plasma water losses result in a fall in the cardiac filling pressure and an associated fall in the cardiac stroke volume, since the force of contraction of the heart muscle is a function of its stretch during the preload interval (Starling's law of the heart). The loss of plasma volume is partly offset by such compensations as the shift in water from the other body-fluid compartments and the redistribution of blood flow and volume away from vascular beds that are not directly participating in the integrated response to exercise (Rowell 1983).

Nonetheless, during prolonged exercise it is difficult, if not impossible, to replace completely the water and ions lost in sweat and to avoid the resulting dehydration and loss of plasma volume. Thus, one would expect a progressive decrease in the maximum cardiac stroke volume during prolonged exercise. This was confirmed by Fortney and her colleagues (1983); they artificially expanded and contracted blood volume to show that it has a strong influence on cardiac stroke volume during exercise. Furthermore, when blood volume was low, subjects performing moderately heavy exercise in a warm environment stored body heat at a greater rate than when blood volume was normal. It is

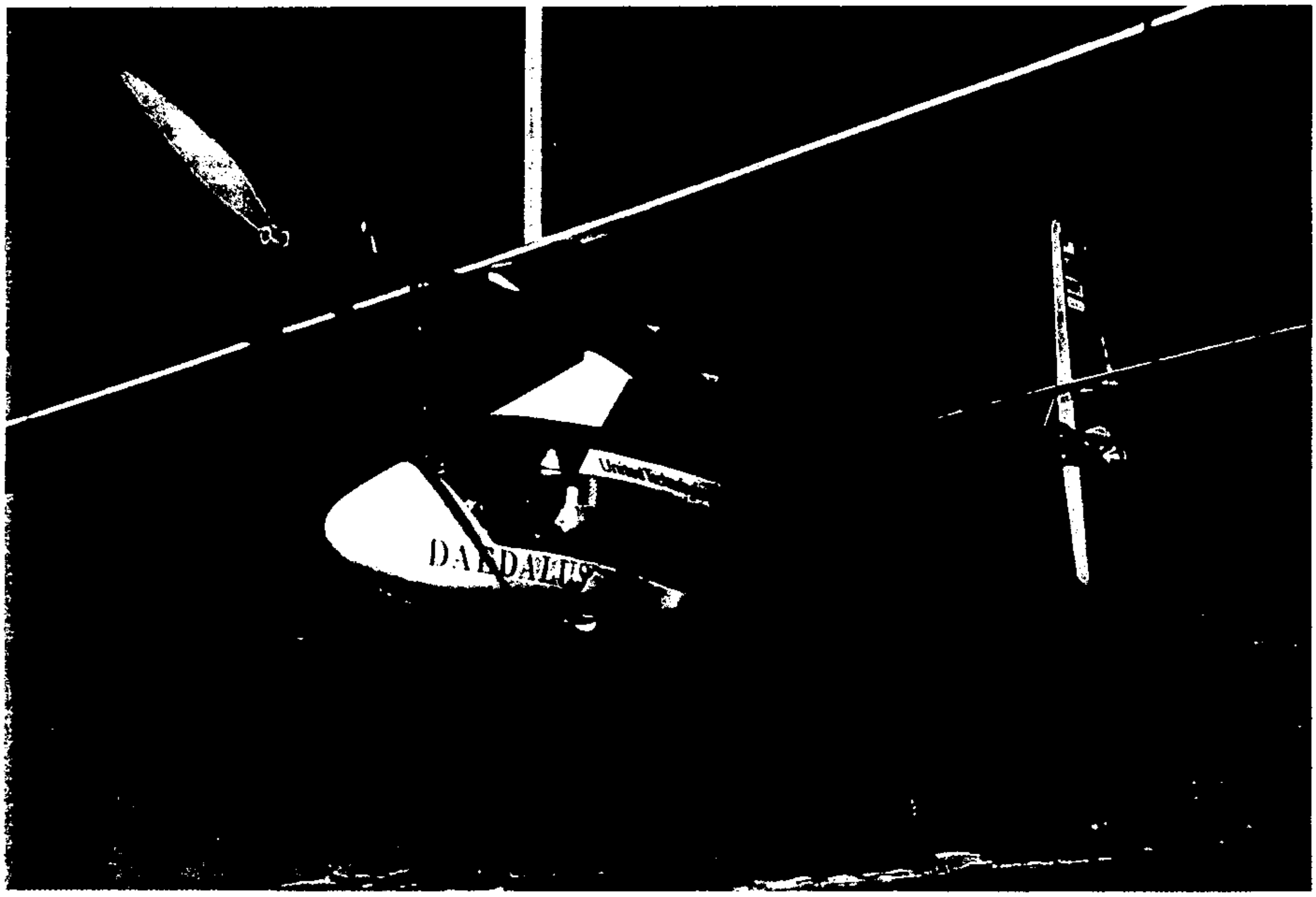

Figure 6. The semirecumbent cycling position completely frees the pilot's hands for maneuvering the *Daedalus*'s controls and, as Figure 5 demonstrates, entails no sacrifice of mechanical efficiency. (Photograph by Mike Smith.)

well known, conversely, that an increase in blood volume—which occurs during training (Convertino et al. 1980)—provides for an increase in maximum cardiac stroke volume and accounts for a good portion of the higher maximum oxygen uptake that is observed (Ekblom 1969).

Maximum oxygen extraction is increased over the course of a training regime by adaptations that increase the maximum blood flow through the muscles (thus increasing the volume of blood in the muscles at any given time), that decrease the diffusion distance for oxygen between the blood capillaries and active muscle fibers, and that increase the aerobic enzymes in muscle tissue (see Nadel 1985). These adaptations partly explain the superior maximum oxygen uptakes of trained athletes. However, during heavy exercise itself, maximum oxygen extraction by the body will be reduced only under extreme conditions in which there is a reduction in muscle blood flow. This could occur during heavy exercise in the heat, which increases the demand for blood flow to the skin, where relatively little oxygen is extracted, and possibly reduces the blood flow to the exercising muscles (Bell et al. 1983; Nadel 1983). There is no doubt that all vascular beds, including those in muscle, participate in reflexes that act to maintain arterial blood pressure.

It is clear that in conditions of high demand, either maximum cardiac stroke volume or maximum oxygen extraction can be reduced, thereby lowering maximum aerobic power. It is also clear that the prevention of a decline in either of these factors during the Daedalus flight would depend in large part on protecting the pilot from dehydration and overheating.

Heat dissipation and hydration

Heat dissipation actually involves two problems. The first is to provide enough air movement through the cabin of the aircraft for convective and evaporative cooling from the skin surface of the pilot. This is an aircraft design problem rather than a physiological problem, although improper design could considerably increase the physiological cost of flying the aircraft. The physiologists could estimate the pilot's heat production reasonably well, and the engineers could then design a ventilation system able to meet the heat-loss requirement. The greater the air flow, the greater the confidence that it would be adequate to provide for optimal cooling. However, with a higher air flow there is a greater induced drag on the aircraft, and the cost of flying increases accordingly. Thus, the challenge for the engineers was to determine the optimal ventilation rate that would ensure evaporation and yet add minimally to the drag.

The second heat-dissipation problem is a physiological one. A person's ability to dissipate the large amount of heat produced during heavy exercise is compromised by increasing dehydration. The body then tends to store heat at a greater rate than when normally hydrated and thus reaches its thermal tolerance limits sooner. There

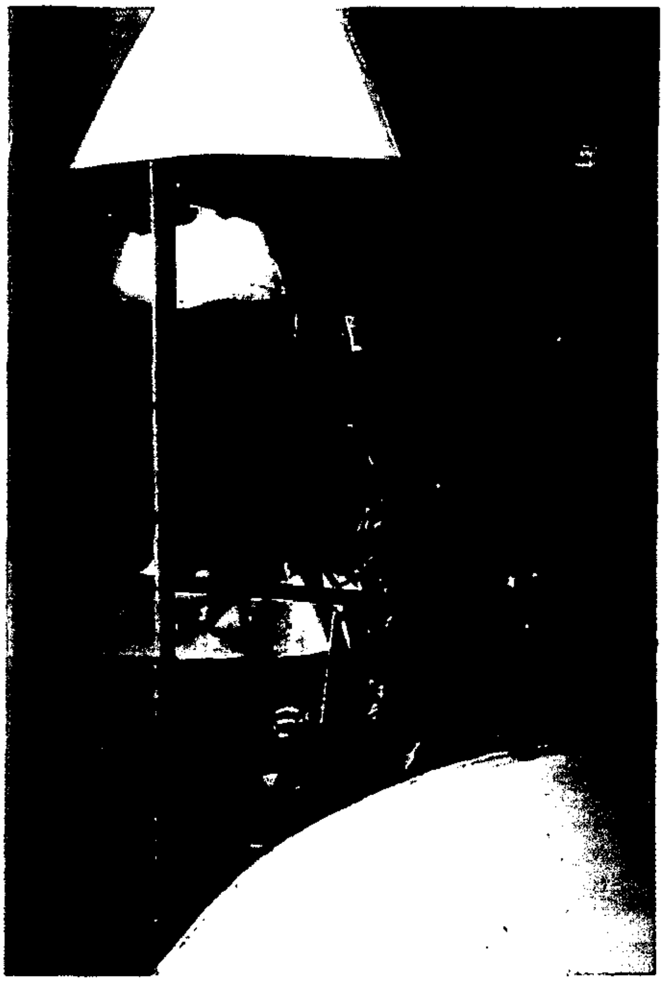

Figure 7. The confined space of the *Daedalus*'s cabin posed a problem for the aircraft's designers—to provide enough airflow to dissipate the considerable heat produced by the human engine without adding too much drag for him to overcome. (Photograph by Mike Smith.)

are two reasons for this. The first is that the ability of the blood circulation to transport heat from the body core to the skin is reduced, because dehydration reduces plasma volume, which in turn stimulates reflexes that increase skin vascular resistance in order to shift blood to the body core (Nadel et al. 1980). The second is that the ability to dissipate heat from the skin surface is also reduced because of a decrease in the sensitivity of the sweat-gland response to an increasing body core temperature (Fortney et al. 1983). Thus, keeping the pilots well hydrated for the entire flight is the key to the prevention of overheating and its associated symptoms, such as light-headedness, disorientation, and fainting.

One problem in maintaining body hydration is that humans have a notoriously poor sense of thirst and do not recognize the characteristics of dehydration until it is too late; hence, it is essential to anticipate the amount of fluid needed by the pilot to complete the flight. The rate of evaporative water loss will be a function of the total thermal load, which is the combined metabolic and environmental loads, and can exceed 30 grams per minute in extreme conditions of heavy exercise in the heat. Since the ill effects of body dehydration begin to occur when the loss of body water exceeds 3% of body weight (at one to two hours in a 70-kg pilot), the ability to exercise will eventually be compromised unless the body water content can be restored at a rate that approximates its rate of loss. Thus, during exercise, the problems of heat dissipation and hydration are combined: the body must produce sweat on the skin surface at a sufficiently high rate to evaporate the metabolic heat produced; concurrently, the body cannot allow its water content to decrease too much, or fatigue will occur as a consequence of the hyperthermia induced by the dehydration.

There is, however, a complicating factor that makes it difficult for humans to remain adequately hydrated, even when they try, in conditions of heavy sweating (Greenleaf 1982). Humans lose sodium in sweat, and the greater the sweating rate, the greater the sodium loss. As a result of the sodium deficit, any attempt to rehydrate with free water will fall short, because the rapid dilution of the blood removes the drive for drinking too soon. Furthermore, dilution of the blood inhibits the release of antidiuretic hormone, thereby stimulating the production of urine by the kidneys and the subsequent loss of water from the body. Thus, when drinking pure water, there is a limitation in the rate of fluid retention as well as in intake.

In a series of recent experiments, Nose and his coworkers (in press) confirmed that humans are able to recover from thermal dehydration much more effectively by drinking a sodium solution than by drinking water alone. Furthermore, recovery of lost plasma volume is more rapid when rehydrating with sodium in the drink. This recovery would presumably improve the body's ability to distribute blood flow to contracting muscles and skin during exercise in conditions of heavy demand.

In anticipating the needs of our Daedalus pilots, we assumed that the same principles concerning the replacement of lost fluid apply during exercise as well as during the recovery from exercise, although this has yet to be demonstrated satisfactorily.

Maintaining fuel delivery

One other major phenomenon that has been implicated in the generation of fatigue during prolonged exercise is a critical depletion of glycogen, the storage form of glucose, from the liver and muscle fibers themselves. Whereas the body contains only a small supply of stored oxygen, enough to support a minute or two of heavy exercise at most, the body's fuel stores contain a sufficient supply of potential energy to sustain activity for days, should nothing else be limiting. Most of the stored energy is in the form of triglycerides in adipocytes, or fat cells, and the remainder is in the form of glycogen. During exercise, the immediate source of fuel for oxidation is the glycogen stored in the muscle itself. As exercise continues, free fatty acids, mobilized from the adipocytes, and glucose, mobilized from the liver, are transported in the bloodstream to the active muscles and are then made available for combustion with oxygen, also transported in the bloodstream. The muscles are able to draw on their stored fuels for energy production and, if necessary, on the fuels delivered as well. The release of glucose from the liver serves to maintain blood glucose at its regulated level and thereby ensures that glucose-dependent tissues—for example, the brain—are not deprived of their fuel source during the heavy demands of exercise.

For years it has been believed that fatigue during prolonged exercise coincides with the depletion of muscle glycogen and that one can postpone the onset of fatigue by eating a carbohydrate-rich diet prior to exercise (Karlsson and Saltin 1971). A recent study has shed further light on this issue; Coyle and his colleagues (1986) demonstrated that fatigue could be postponed by ingesting a glucose drink during prolonged exercise. During trials using a placebo, fatigue (defined as an inability to maintain oxygen uptake at 70% of maximum) occurred at approximately 3 hours, was preceded by a decline in blood glucose, and was accompanied by a depletion of glycogen in the active leg muscles to approximately 23% of the initial value. During trials using the glucose drink, the level of blood glucose did not decline and fatigue did not occur until the fourth hour of exercise; surprisingly, however, muscle glycogen was depleted at the same rate as in the placebo trials. Coyle and his co-workers attributed the postponement of fatigue to the ability of trained athletes to oxidize glucose provided from sources other than muscle (i.e., the drink) during prolonged, strenuous exercise. However, they were unable to explain the source of fatigue, since at the time of fatigue blood glucose was in the normal range, carbohydrate oxidation rate was constant, and muscle glycogen had been at the reduced level for 1 hour.

These data and conclusions provided some optimism that fatigue during heavy exercise might well be postponed significantly, but not that fatigue could be postponed indefinitely. Thus, our challenge became to identify the source of the fatigue that occurred when drinking a glucose solution and to provide our pilots with the means to resist this as well as the fatigue that results from the depletion of the body's glucose stores. Furthermore, we also needed a drink for rehydration, one that could meet not only the fuel requirements of the Daedalus pilots but their fluid and sodium requirements as well, in order to provide optimal resistance against overheating and dehydration. While rehydration drinks exist on the commercial market, our calculations, based on measurements and estimates, showed that none of these drinks quite met the extreme needs dictated by the proposed flight conditions. We intended to use objective data from a 4-hour endurance test—the final phase of the pilot selection process—to develop our own rehydration drink.

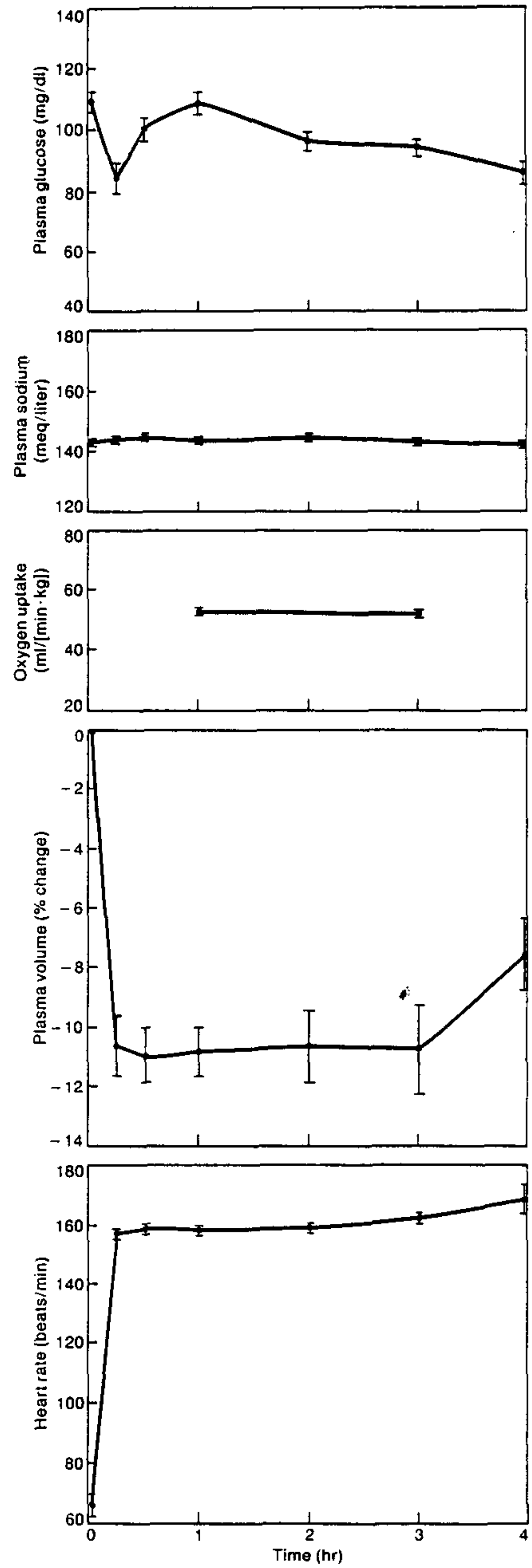

Figure 8. The results of a 4-hour endurance test indicated that the Daedalus flight was within the realm of physiological possibility. All 11 athletes tested (at 70% of their maximum oxygen uptakes) were able to sustain for at least 3 hours the mechanical power output necessary for flight, and 8 were able to sustain it for 4 hours, a period approaching the anticipated 4 to 6 hours of the flight. (There was significantly little variation in the physiological capabilities of this group, as indicated by the small standard deviations.) However, although the athletes were given a commercially available drink containing sodium and glucose that maintained water and sodium homeostasis (as indicated by levels of plasma volume and plasma sodium), the decreasing levels of plasma glucose and the increasing heart rates were potentially debilitating trends if the flight were to continue much beyond 4 hours.

Endurance tests

Of the 25 athletes we tested for maximum oxygen uptake, we selected 11, those with the best results, to undertake a 4-hour endurance test at 70% of their maximum power output in order to assess their abilities to maintain this pace over an extended period. The maximum oxygen uptake of the 11 athletes averaged 71.6 ml O_2/(min·kg), their mechanical efficiency 25.7%, and their aerobic power production at 70% of maximum 3.73 W/kg. The goal of the 4-hour tests was not only to select the final team of 4 or 5 pilots, but also to examine the changes in the important physiological variables during prolonged exercise so that we could anticipate which of these would be the limiting ones.

The 4-hour test, conducted on the same cycle ergometer used in the first round of tests, was given under optimized conditions. The athletes reduced their training intensity and consumed extra carbohydrates in the few days prior to the test. During the test the chamber was kept relatively cool, at 16 to 18°C, to minimize the external heat load, and the athletes drank a commercially available sport drink—7% glucose and 10 milliequivalents (meq) per liter sodium—at a rate of 1 liter per hour. Throughout the test, blood samples were taken and analyzed, oxygen uptake measured, and heart rate recorded.

The results of the 4-hour tests, summarized in Figure 8, gave the Daedalus team confidence that the challenge of maintaining a high power output for an extended period could be met successfully, given the right conditions. Of the 11 athletes who began the 4-hour test, 8 were able to complete it. All 3 who could not became fatigued during the final hour, suffering a decline in power output that manifested itself as an inability to maintain the prescribed pedaling frequency; but there were no specific physiological correlates of the fatigue.

Based on these results, 5 of the athletes were selected as the Daedalus pilots. Their maximum oxygen uptakes averaged 69.9 ml O_2/(min·kg), they could produce an average 3.72 W/kg at 70% of maximum, and they had an average mechanical efficiency of 27.5%. The responsibilities of these 5 were to learn to fly the Daedalus prototype aircraft and to maintain a high level of physical condition.

The results of the 4-hour test demonstrated the importance of supplementing our athletes with a glucose-electrolyte drink. The drinking schedule of 1 liter per hour appeared to have been adequate to prevent dehydration, since the concentration of blood sodium did not increase and plasma volume did not decrease progressively between the first and fourth hours. However, despite supplementation, blood glucose had fallen significantly by the fourth hour, and the heart rate had increased significantly, changes that, had they been allowed to progress, would have led to fatigue. Thus, we felt that our pilots' abilities to maintain glucose, sodium, and water homeostasis in the extreme conditions of the

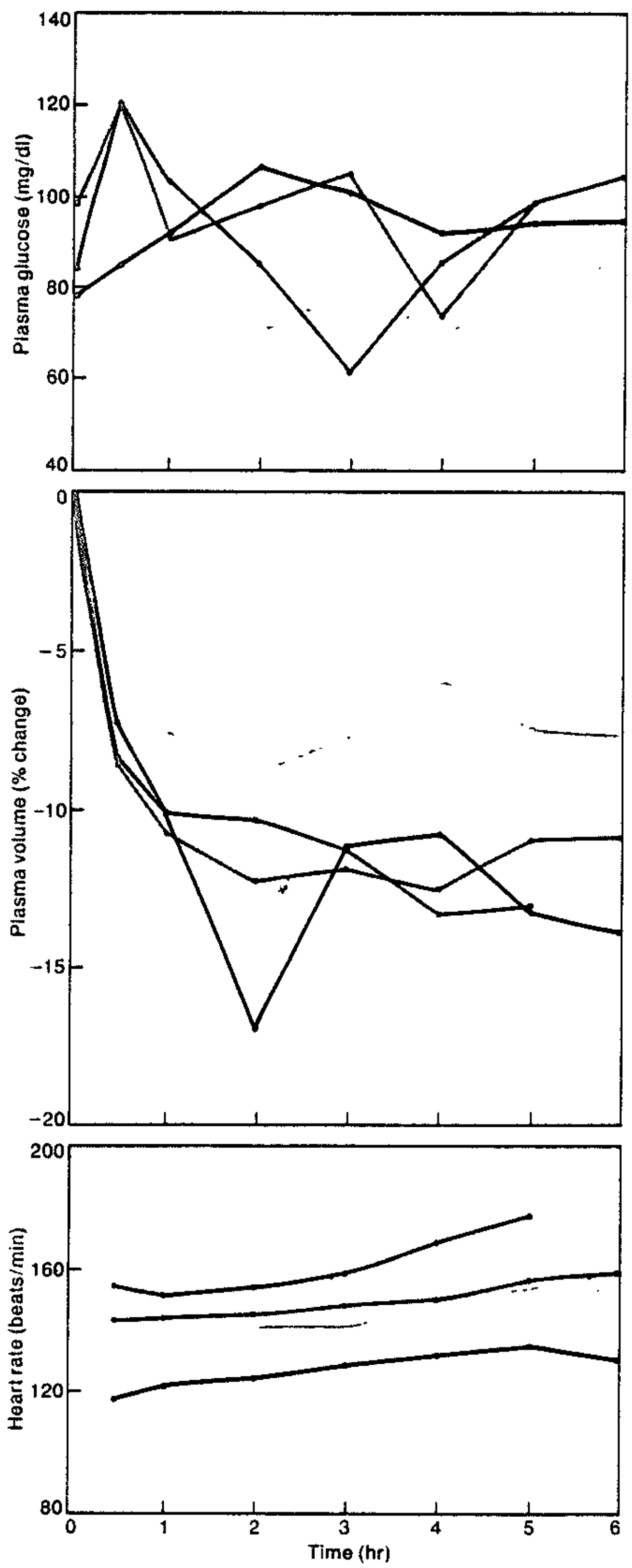

Figure 9. Four Daedalus pilots (each represented by a different colored line) participated in a 6-hour simulation of the Daedalus flight at a power output sufficient to keep the aircraft aloft. (One of the 4 was unable to complete the test because of physical discomfort with the seat of the ergometer.) These results show the effectiveness of a drink developed specifically for the flight: the levels of plasma glucose were maintained and did not decline (in contrast to the results obtained with the commercially available drink, illustrated in Fig. 8); plasma volume did not rise or fall significantly; and only the heart rate of the pilot who stopped showed any significant tendency to approach a limiting level.

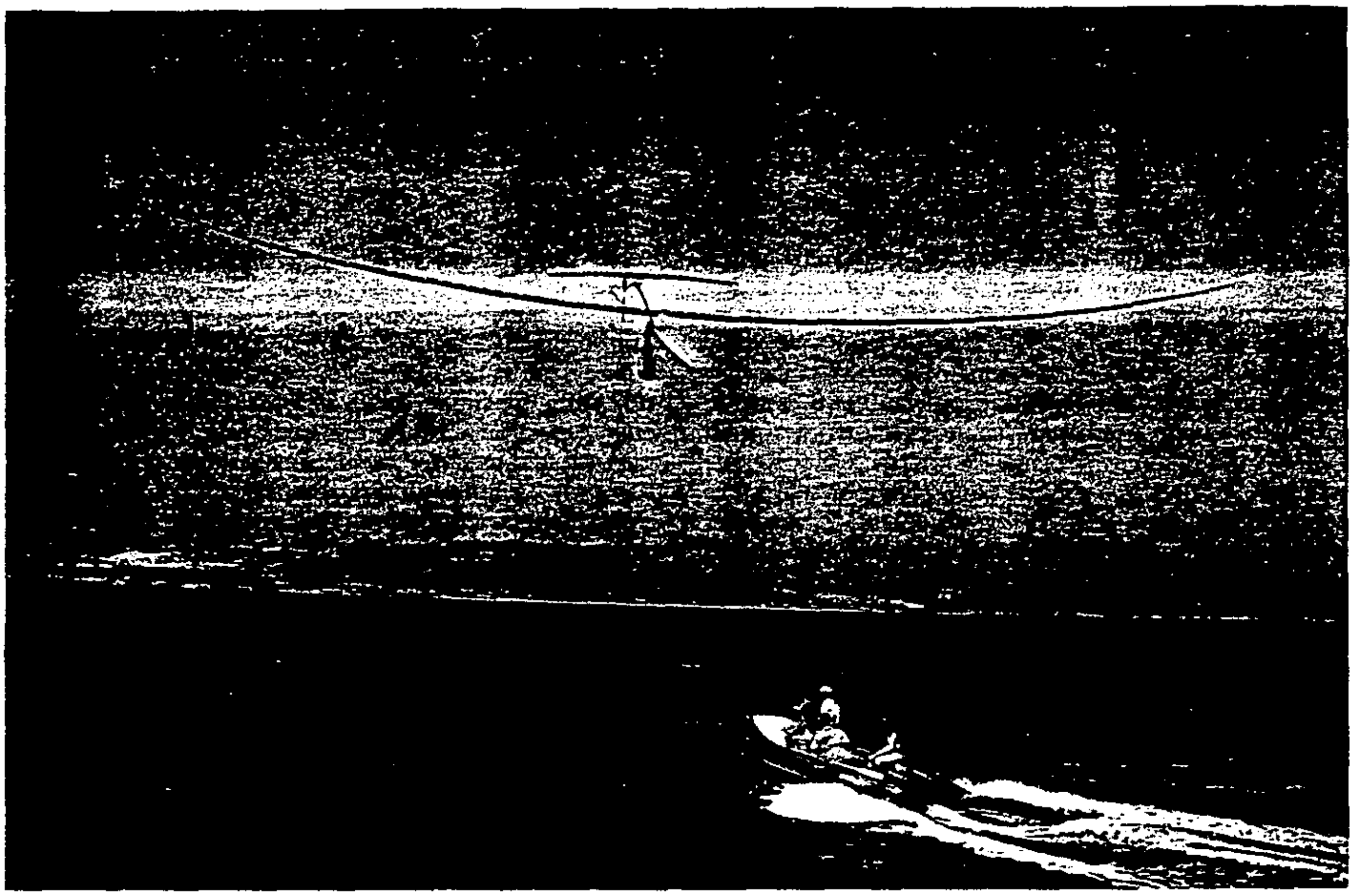

Figure 10. The *Daedalus*, flown by Kanellos Kanellopoulos, near the end of its successful flight from Crete to Santorini on 23 April 1988. (Photograph by Peggie Scott.)

flight could be optimized if we could provide them with a drink that completely compensated for the body's losses during the flight.

Developing the Daedalus drink

Our first approach to developing a drink for the Daedalus flight was to consider the solutions that others had found when confronted with similar problems. Most of the literature we surveyed, including a comprehensive review by Murray (1987) of the characteristics and physiological effects of a number of carbohydrate-electrolyte drinks currently on the market, cited demonstrated improvements in performance in subjects supplemented with either electrolytes or carbohydrates during exercise. However, none of these drinks had sufficient carbohydrates and electrolytes to meet the requirements of the Daedalus challenge, and we therefore had to resort to an empirical approach: we had to estimate the losses of body water, glucose, and sodium during the 6 hours of exercise at a mechanical power production of 3.3 W/kg and to design the drink to replace these losses.

The loss of body water could be estimated from the rate of evaporative heat loss necessary to maintain the internal body temperature at a steady state, which is elevated and constant during exercise. We calculated that a 68-kg pilot with a mechanical efficiency of 24% would produce about 13 W/kg of metabolic heat during steady flight, or around 900 W. Since around 225 W will be transferred directly to the environment in the form of physical work, the remaining 675 W need to be dissipated through evaporative, radiative, and convective heat loss. The rate of heat loss from the body by radiation and convection was estimated as 60 W, assuming an average skin temperature of 33°C, a cabin temperature of 28°C, a heat transfer area of 1.2 m^2, and a heat transfer coefficient of 10 $W/(m^2 \cdot {}^\circ C)$ (Gagge 1972). This left somewhat over 600 W to be dissipated by evaporation. Taking the heat of vaporization into account—0.7 W per gram of water evaporated per hour—we estimated that the pilot would lose on the order of 900 ml of water per hour.

To estimate the rate of glucose uptake by the body during the flight, we assumed that the rate of glucose oxidation would be on the order of 50% of the total fuel oxidation rate (Coyle et al. 1986). Since the total oxidation rate yielded 900 W, we estimated, using the energy conversion of 4.6 W per gram of glucose oxidized per hour, that our pilots would use around 100 grams of glucose per hour while flying the Daedalus aircraft.

The rate of sodium depletion during prolonged, heavy exercise is difficult to estimate, because the concentration of sodium in sweat, which appears to be determined genetically, can range between 10 and 100 meq/liter from person to person. However, as physical fitness increases, sweat becomes more dilute, thereby providing for a relative sodium conservation in conditions of heavy demand. We assumed a sodium concentration of 20 meq/liter, in which case our pilots should lose 18 meq of sodium each hour during the flight, equivalent to a loss of 0.4 grams per hour.

For simplicity's sake we proposed to rehydrate our pilots at a rate of 1 liter of fluid per hour, a rate of fluid ingestion that is clearly slower than the maximum rate of gastric emptying for plain water (Davenport 1982). Although it has been less clear how exercise, the content of the ingested fluids, or both affect the rate of emptying, the consensus is that gastric emptying and the absorption of fluid from the gut are not adversely affected by exercise at intensities below 75 to 80% of maximum in a moderate environment (Murray 1987). Furthermore, the energy content of the fluid appears to be a much more important determinant of the gastric emptying rate, which slows as the energy content increases above a specific threshold, than is the concentration or form in which the energy is carried. It is well known that both glucose and sodium in small amounts will promote increased absorption from the gut (Davenport 1982). We designed our drink with 10% glucose and 18 meq/liter sodium, concentrations estimated to replace glucose and sodium at rates equaling their losses.

Once a prototype drink was concocted and its taste made pleasant, we tested its efficacy at maintaining blood glucose, plasma volume, and body hydration in a simulation of the Daedalus flight on the cycle ergometer at the estimated flight power (3.1 W/kg) and the maximum conceivable duration (6 hours). Four of the pilots participated in the simulation (the fifth was recovering from tendinitis). The drink was given to them at a rate of 1 liter per hour, and they drank at will without excessive prompting. Blood samples were taken at regular intervals, heart rate recorded throughout, and body weight measured at the start and finish. Three of the four pilots completed the simulations (the fourth stopped after 4.3 hours).

The results of the simulation, summarized in Figure 9, showed that the drink performed well. Blood glucose was maintained in all pilots throughout exercise. The relative changes in plasma volume were within the expected range for this intensity of exercise and, most importantly, did not change significantly over the course of the 6 hours. Only the pilot who stopped showed an unduly high heart rate; his initial heart rate was around 10 beats per minute higher than during his previous calibration, and our subjective impression was that he was not pedaling very efficiently because of his discomfort with the Kevlar seat, a discomfort which all four subjects experienced to some degree. All pilots maintained plasma sodium within a reasonable range, and their body-weight losses ranged from 0 to 1.5 kg, indicating that all remained quite well hydrated despite evaporative losses that approximated 1 liter per hour. Three of the four pilots had to urinate during the simulation, another confirmation that their fluid intake was reasonably high relative to their fluid losses.

These simulations supported current concepts about the importance during prolonged exercise of the availability of glucose in maintaining fuel metabolism (Coyle et al. 1986) and of sodium in maintaining body-fluid balance (Nose et al., in press). The simulations confirmed the validity of the empirical approach to designing the drink and were remarkable in demonstrating that our projections were supported by reality, a confirmation that one rarely observes because of the unknown or unanticipated variables that creep into most simulations. Although these were not controlled studies, we concluded that supplementation with appropriate fuel, water, and sodium would indeed postpone the onset of fatigue and enable the pilot to prolong exercise beyond normal limits.

Postscript

At daybreak, 23 April 1988, the *Daedalus* lifted off in front of a 3-knot tail wind with Kanellos Kanellopoulos at the controls. Nearly 4 hours and 119 kilometers later, the *Daedalus* made a water landing into a 12-knot head wind, 9 meters off Parissa Beach on the south coast of Santorini. During the flight, Kanellos drank almost 4 liters of the energy-electrolyte drink. His heart rate, which was telemetered and recorded continuously, never exceeded 142 beats per minute during the flight, confirming our assessments in the laboratory simulation. At no time during the flight were there any indications of impending fatigue.

References

Åstrand, I. 1960. Aerobic work capacity in men and women with special reference to age. *Acta Physiol. Scand.*, supp. 169.

Åstrand, P.-O., and K. Rodahl. 1986. *Textbook of Work Physiology.* McGraw-Hill.

Bell, A. W., J. R. S. Hales, R. B. King, and A. A. Fawcett. 1983. Influence of heat stress on exercise-induced changes in regional blood flow in sheep. *J. Appl. Physiol.* 55:1916–23.

Convertino, V. A., J. E. Greenleaf, and E. M. Bernauer. 1980. Role of thermal and exercise factors in the mechanism of hypervolemia. *J. Appl. Physiol.* 48:657–64.

Coyle, E. F., A. G. Coggan, M. K. Hemmert, and J. L. Ivy. 1986. Muscle glycogen utilization during prolonged strenuous exercise when fed carbohydrate. *J. Appl. Physiol.* 61:165–72.

Davenport, H. W. 1982. *Physiology of Digestive Tract.* Chicago:Yearbook Medical.

Ekblom, B. 1969. Effect of physical training on oxygen transport system in man. *Acta Physiol. Scand.*, supp. 328.

Fortney, S. M., C. B. Wenger, J. R. Bove, and E. R. Nadel. 1983. Effect of blood volume on forearm venous and cardiac stroke volumes during exercise. *J. Appl. Physiol.* 55:884–90.

Gagge, A. P. 1972. Partitional calorimetry in the desert. In *Physiological Adaptations*, ed. M. Yousef et al. Academic.

Greenleaf, J. E. 1982. Dehydration-induced drinking in humans. *Fed. Proc.* 41:2509–14.

Karlsson, J., and B. Saltin. 1971. Diet, muscle glycogen, and endurance performance. *J. Appl. Physiol.* 31:203–06.

Murray, R. 1987. The effects of consuming carbohydrate-electrolyte beverages on gastric emptying and fluid absorption during and following exercise. *Sports Med.* 4:322–51.

Nadel, E. R. 1983. Effects of temperature on muscle metabolism. In *Biochemistry of Exercise*, ed. H. Knuttgen et al. Champaign, IL: Human Kinetic Publ.

———. 1985. Physiological adaptations to aerobic training. *Am. Sci.* 73:334–43.

Nadel, E. R., S. M. Fortney, and C. B. Wenger. 1980. Effect of hydration state on circulatory and thermal regulation *J. Appl. Physiol.* 49:715–21.

Nose, H., G. W. Mack, X. Shi, and E. R. Nadel. In press. Role of osmolality and plasma volume during dehydration in humans. *J. Appl. Physiol.*

Rowell, L. B. 1983. Cardiovascular adjustments to thermal stress. In *Handbook of Physiology. IV. The Cardiovascular System*, chap. 10. Bethesda, MD: Am. Physiol. Soc.

Vogel, J. A., M. U. Ramos, and J. F. Patton. 1977. Comparison of aerobic power and muscle strength between men and women entering the US Army. *Med. Sci. Sports Ex.* 9:58.

Whitt, F. R., and D. G. Wilson. 1982. *Bicycling Science.* MIT Press.