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Deborah A. Burgoon
The University of Montana

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Brain Cooling and the Rete Mirabile Ophthalmicum in the Calliope Hummingbird (Stellula calliope)

by

Deborah A. Burgoon

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Brain Cooling and the *Rete Mirabile Ophthalmicum* in the Calliope Hummingbird (*Stellula calliope*) (pp.36)

Directors: Drs. Delbert L. Kilgore, Jr., and Phillip Motta

All species of birds in which the relationship between brain and body temperature has been examined are capable of maintaining a lower brain than body temperature and possess a *rete mirabile ophthalmicum* (RMO), the vascular heat exchanger that functions to cool the brain. The Zebra Finch (13 g; *Poephila guttata*) has a reduced brain cooling ability and an RMO that consists of few vessels comparison to that of other birds. The presence of the reduced RMO has been suggested as the reason for the reduced cooling ability in this species. The relationship between the complexity of the RMO and brain cooling, particularly in species smaller than the Zebra Finch, needs to be examined further. The present study was undertaken to determine whether the Calliope Hummingbird (2.5 g; *Stellula calliope*) maintains a lower brain than body temperature and to determine if the anatomical complexity of the RMO reflects this ability.

Twenty-seven measurements of brain and body temperature were obtained from eleven birds. Brain, body, and air temperature were measured simultaneously and continuously. A bird was maintained at a particular air temperature until brain and body temperature were stable. The bird was then exposed to a second temperature. Three birds were sacrificed and latex injected into the aorta to study the vascular anatomy.

Calliope Hummingbirds are capable of maintaining their brain lower than body temperature at body temperatures above 40°C. The magnitude of this difference is within the range of temperature differences in other species studied under similar conditions. This hummingbird possesses an RMO consisting of only 2 - 4 arteries and 2 veins. This suggests that the reduced cooling ability in the Zebra Finch is not necessarily due to the reduced number of vessels in the RMO since Calliope Hummingbird possesses structure with less vessels yet is still capable of cooling the brain.

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Brain Cooling and the _Rete Mirabile Ophthalmicum_

Introduction

Evidence indicates that many species of mammals, perhaps all birds, and some reptiles, can maintain their brain at temperatures cooler than their body (Baker 1979, 1982; Baker & Hayward 1968; Baker et al. 1974; Caputa et al. 1976; Crawford 1972; Taylor 1966; Taylor & Lyman 1972; for birds see below). The maintenance of a cooler brain is important to an organism's tolerance of environmental temperatures that are equal to or exceed body temperature (Carithers & Seagrave 1976). By maintaining a higher body temperature the difference between air and body temperature is reduced and the rate of heat gain from the environment decreased (Calder & King 1974; Kilgore et al. 1976; Weathers 1981). When the reverse is true, that is when body temperature exceeds air temperature, a gradient for heat loss by way of non-evaporative means is preserved (Calder & King 1974; Kilgore et al. 1976; Weathers 1981). These thermal relationships are important for water conservation, especially for small organisms. In addition, the heat that is stored by raising the body temperature can be dissipated by non-evaporative means at times when the environment cools (King & Farner 1961; Kilgore et al. 1976; Weathers 1981).

In order to benefit from the advantages of a controlled hyperthermia, an organism must cope with the effects of an elevated body temperature to which the brain is especially vulnerable (Burger & Fuhrman 1964). Various hypotheses have been proposed to account for the lethal effects of heat on tissues. Heat may inactivate enzymes or shift the equilibrium of an enzyme to favor an inactive form (Johnson et al. 1954 cited from Burger & Fuhrman 1964). Changes in intra- and intermolecular bonding of cell membranes may also be responsible for heat damage (Belehradek 1957). Increases in the concentrations of ammonia, urea, cholesterol, and acid phosphatase have been used as indicators of heat damage to tissues (Burger & Fuhrman 1964; Fuhrman et al. 1944). The concentrations of these compounds have been found to increase in the cerebral cortex tissue of albino rats at 43°C. Maintaining a cooler brain than core temperature may be one method of avoiding heat damage and death. If the brain is kept cool tolerance to elevated deep body temperature is extended (Carithers & Seagrave 1976).

To date the relationship between brain and body temperatures has been examined in many species of birds, passerine and non-passerine, ranging in size from the Zebra Finch (13 g) to the Rhea (35 g; Bech & Midtgård 1981; Bernstein et al. 1979a; Bernstein et al 1979b; Crowe & Withers 1979; Kilgore et al. 1973; Kilgore et al. 1976; Kilgore et al. 1979; Kilgore et al. 1981; Richards 1970, 1971; Schmidt & Simon 1979; Scott & Van Tienhoven 1971). In most birds this body-to-brain temperature difference ranges from 0.50°C (Pekin Duck, Schmidt & Simon 1979) to 2.13°C (Helmeted Guineafowl, Crowe & Withers 1979; Appendix I: A.) with a mean of 0.96°C.

The maintenance of a cooler brain temperature in birds is accomplished by a vascular network of small arteries and veins, the _rete mirabile ophthalmicum_ (RMO), in which arterial blood supplying the brain exchanges heat with venous blood cooled by evaporation and convection in the buccopharyngeal cavity, beak, nares, and eyes. The RMO is located between the posteroventral border of the orbit and the external acoustic meatus. The arterial portion of the rete is formed from branches of the Arteria ophthalmica externa. Arteries distal to the rete anastomose with intracranial branches of the Arteria carotis interna and thereby supply blood to the brain. The venous component of the RMO is composed of veins returning from the beak, eyes, nasal and buccal surfaces, areas of evaporative cooling. The veins forming the RMO include the Vena palpebralis dorsostralis, the V. ophthalmotemporalis, the V. maxillaris, and the V. facialis (Baumel 1975, 1979; Crowe & Crowe 1979; Kilgore et al. 1976; Richards 1970; Appendix I: B).

Several experiments offer evidence for the role of the RMO in lowering brain temperature. Kilgore et al. (1979) found that when arterial flow to the RMO was blocked the normal pattern of body-to-brain temperature difference (i.e. brain temperature lower than body temperature) was reversed with brain temperature always higher than body temperature. This suggests that the RMO plays a central role in maintaining the body-to-brain temperature difference. Bernstein et al. (1979a) blocked the avenues of evaporative water loss from the heads of pigeons by bypassing the buccopharyngeal cavity, and sealing the beak, nares, and eyes. When this was done the body-to-brain temperature difference was reversed or eliminated. Without cool blood returning from the nasal and buccal surfaces, the beak and eyes, there is no heat exchange in the RMO so that blood arrives at the brain at body temperature. Pinshow et al. (1982) further examined the effects of corneal convection on brain cooling. They found that during experiments where air, simulating air flow at flight speeds, was blown across the ocular surface, the body-to-brain temperature difference was increased from the resting value of 2.6°C to 3.5°C. When these experiments were repeated with the eyes sealed the body-to-brain temperature difference was not different from resting values. The results obtained by Pinshow et al. (1982) suggest that blood cooled while flowing through the ocular vasculature contributes to the venous flow through the RMO. This cool blood may contribute to heat exchange in the RMO.

All species of birds studied thus far have been shown to possess a <u>rete mirabile ophthalmicum</u> and are able to cool their brain. The Zebra Finch (<u>Poephila guttata</u>), however, appears to have a reduced brain cooling ability. The mean body-to-brain temperature difference is much lower, (0.18°C compared with 0.96°C), than in other species studied (Bech & Midtgård 1981). In addition, the RMO in the Zebra Finch is reduced in size in comparison to that of other birds. The presence of a reduced RMO, which may simply be the result of the small size of the Zebra Finch, has been suggested as the reason for the reduced cooling ability in this bird (Bech & Midtgård 1981). A comparative study of the vascular anatomy of the RMO in birds also noted that smaller birds have a simple rete compared to larger species (Midtgård 1983). This relationship between the anatomical complexity of the RMO and brain cooling, particularly in species smaller than Zebra Finches, needs to be examined further. Therefore, the present study was undertaken to determine whether the Calliope Hummingbird (_Stellula calliope_), a bird with a mass of only 2.5 grams, maintains a cooler brain than body temperature and to determine if the anatomical complexity of the rete reflects this brain cooling ability.

MATERIALS AND METHODS

Preliminary experiments were conducted during July and August of 1982 using slightly different methods and procedures, as noted below, from those used in subsequent experiments performed in June and July of 1983. The different procedures yielded statistically indistinguishable results so the data have been combined for analysis. Seven female and four male Calliope Hummingbirds were used in these experiments. The mean body mass of females was 2.6 g and 2.5 g for males (Appendix II). All birds were captured using a mist net and were maintained in captivity on a diet consisting of a sugar solution, a protein solution supplemented with vitamins, and live *Drosophila* (Appendix III).

THERMOCOUPLES

Welded copper-constantan thermocouples were used to measure brain, colonic, and air temperatures. Thermocouples were constructed from either 0.12 mm (36 Ga.) or 0.05 mm (44 Ga.) wire (Omega Engineering, Inc.) and were coated with polyvinyl. Colonic probes had a final diameter of 0.2 mm while brain probes had a final diameter of either 0.1 mm or 0.2 mm. Epoxy cement was used to stiffen those thermocouples constructed from the 0.05 mm wire.

SURGICAL PROCEDURE AND THERMOCOUPLE PLACEMENT

Surgery was performed under general anesthesia. Equithesin (2.5 µl/g; prepared as suggested by Fedde 1978) given intramuscularly was used to anesthetize birds in the preliminary experiments. Subsequently, ketamine hydrochloride (0.1 mg/g) also administered intramuscularly was used (Burgoon & Opalka in prep; Appendix IV). A medium plane of anesthesia was induced (Altmann 1980; Kirkby 1980). A warming tray, set at 40°C, was used to maintain the bird's body temperature during anesthetization with ketamine since the anesthetic results in a drop in body temperature (Fedde 1978).

The birds were restrained during surgery in a flannel jacket similar to that described by Lasiewski (1962). A sagittal incision was made in the skin off the midline of the skull. Great care was taken not to sever or damage the hyoid apparatus. The hyoid apparatus was moved aside and in some cases was retracted by gently inserting suture material under the apparatus. A hole was made in the skull using a 22 gauge hypodermic needle. The thermocouple was inserted 2.75 mm into the brain. The placement left the tip positioned no more than 0.5 mm dorsal to the chiasma opticum in the regio preoptica hypothalami (Baumel 1979). The thermocouple emerging from the skull was bent at a 90 angle, placed flat along the top of the skull, and secured using dental cement (3M Silar Restorative Material). A cement (Duro Super Glue) was also used to close the skin. Polyethylene tubing (PE-10) was placed over the wires protruding from the incision to give extra support. All birds were allowed at least 24 hours to recover from surgery before being used in experiments. Thermocouple placement was verified by post mortem examination.

TEMPERATURE MEASUREMENTS

All thermocouples were calibrated using an NBS traceable thermometer. The standard errors (imprecision) of temperatures obtained during calibration do not exceed 0.01°C. The systematic error of temperature measurements also does not exceed 0.01°C. Imprecision and systematic error are used here as recommended by Eisenhart (1968).

Air, brain, and colonic temperatures were measured simultaneously and continuously during an experiment. Air and colonic temperatures were air using a multichannel potentiometric recorder (Honeywell Electronik 16). The emf of the brain thermocouple, which is directly proportional to the difference between the hot junction (the brain) and the cold junction (a reference water bath), was read on a digital multimeter (Keithley, model 160; Appendix I: C).

EXPERIMENTAL PROCEDURE

Birds were maintained in captivity for at least two weeks prior to surgery. All experiments were conducted between 0900 and 1700 hours in a constant temperature chamber (Precision Scientific Incubator Model 805) in which the desired temperature (±0.1°C) could be maintained. The colonic probe was inserted 0.5 cm into the colon and the brain thermocouple soldered to lead wires. Birds were exposed to air temperatures ranging from 30°C to 44°C. During an experiment birds were held at a particular air temperature until brain and colonic temperatures were stable (±0.1°C) for 15 minutes. The air temperature was then raised approximately 4°C. Individual birds were exposed to between one and seven different air temperatures during a 0900-1700 time period, with most being exposed to only three. In some instances individual birds were exposed to only one temperature on a particular day and then were studied again on the following day.

VASCULAR ANATOMY

The vascular anatomy of three birds was studied. The birds were sacrificed, the aorta cannulated, and Microfil (Canton Bio-Medical Supply) injected to facilitate identification of the vessels. The birds were then dissected and the vascular anatomy examined.

STATISTICS

An F test, from the Analysis of Variance on the regression, was used to test whether the relationships between brain and body temperatures, and between body and air temperatures, were linear.

Hollander's test (Daniels 1978) was used to test whether the slopes of the least-squares regression lines relating brain and body temperatures were different from unity.

RESULTS

Twenty-seven measurements of brain and body temperature were obtained from these experiments with eleven birds.

COLONIC TEMPERATURE

Colonic temperature in the Calliope Hummingbird increases linearly with air temperature. This relationship can be seen in Figure 1 and is described by the least-squares regression equation:

$$T_{Cl} = 0.53T_{Amb} + 19.87 \quad (S_{Y \cdot X} = 1.21;\ r = 0.86)$$

where T_{Cl} is colonic temperature and T_{Amb} is ambient temperature. The relationship between colonic and air temperature is linear ($F=84$, $df=1,25$, $p \ll 0.001$).

BRAIN TEMPERATURE

Brain temperature exceeded colonic temperature at low body temperatures but was lower than body at high body temperatures. This relationship is shown in Figure 2 and is represented by the equation:

$$T_{Br} = 0.52\ T_{Cl} + 19.38 \quad (S_{Y \cdot X} = 0.58;\ r = 0.92)$$

where T_{Br} is brain temperature and T_{Cl} is body temperature. The relationship between body and brain temperature is linear ($F=125$, $df=1,25$, $p \ll 0.001$). The slope of the regression line (0.52) is statistically less than one at $\alpha = 0.005$, indicating that the body-to-brain temperature difference is not the same over the range of body temperatures recorded in this study.

The regression line relating brain and colonic temperature intersects the isothermal line at a body temperature of 40.4°C, which is near the typical normal body temperature for non-passerines (Dawson &

Figure 1. Relationship between body and air temperatures in the Calliope Hummingbird. The solid line represents the least-squares regression fitted to the data. The dashed line is the isothermal line shown for comparison. The least-squares equation is inset.

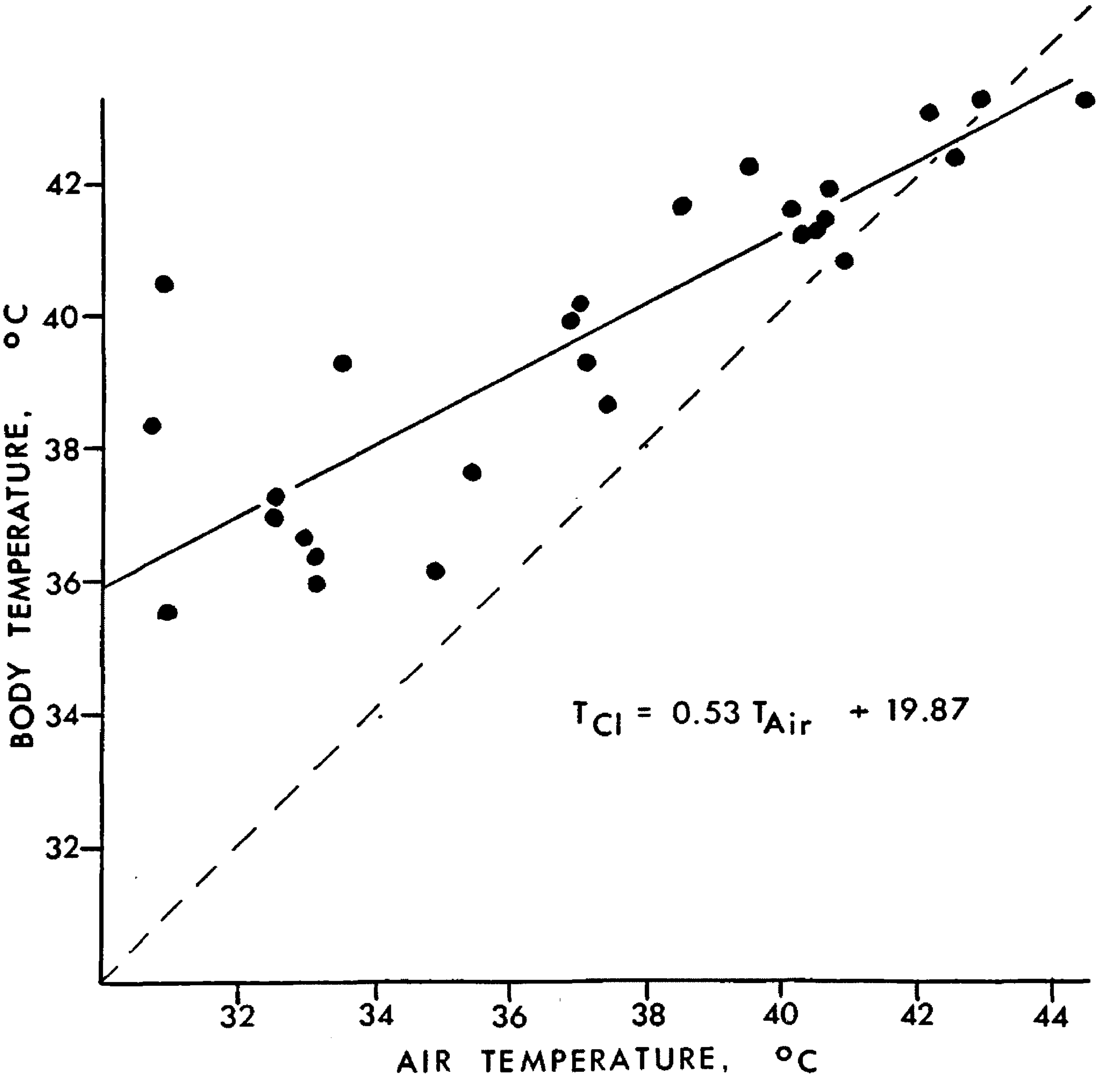
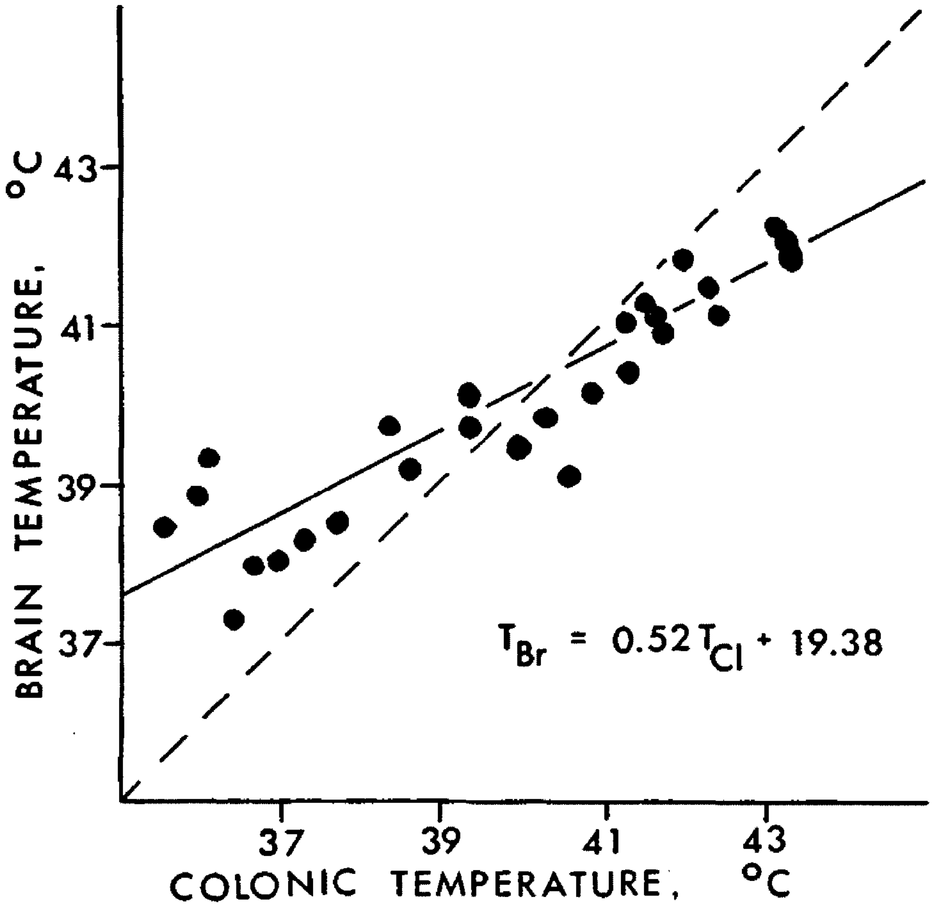

BODY TEMPERATURE, °C
42
40
38
36
34
32
32
34
36
38
40
42
44
AIR TEMPERATURE, °C
$T_{Cl} = 0.53\ T_{Air} + 19.87$

Figure 2. Relationship between brain and colonic temperature in the Calliope Hummingbird. The solid line represents the least-squares regression line fitted to the data. The dashed line is the isothermal line drawn for comparison. The least-square equation is inset.


BRAIN TEMPERATURE, °C
43
41
39
37
37
39
41
43
COLONIC TEMPERATURE, °C
$T_{Br} = 0.52 T_{Cl} + 19.38$

Hulbert 1970). Above a colonic temperature of 40.4°C body temperature is higher than brain temperature. The relationship between body and brain temperatures above 40.4°C is represented by the equation:

$$T_{Br} = 0.83T_{Cl} + 6.15 \quad (S_{Y\cdot X} = 0.47;\ r = 0.86)$$

The slope of the line (0.83) is not statistically different from unity. A test of the linear model indicated that this relationship between colonic and brain temperature at body temperatures in excess of 40.4°C is linear ($F=31$, $df=1,25$, $p \ll 0.001$).

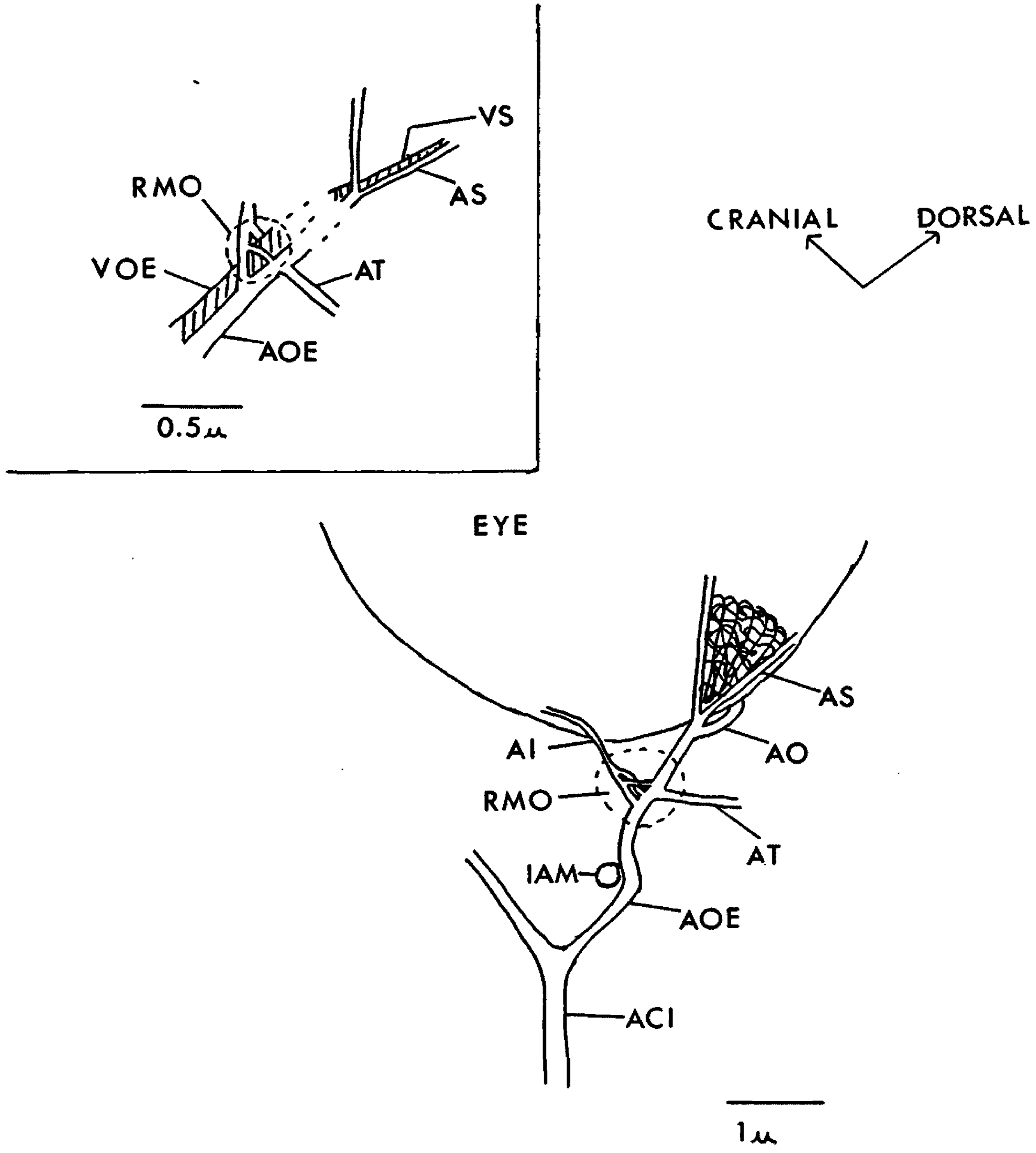
The mean body-to-brain temperature difference over the total range of colonic temperatures is -0.21°C while that above 40.4°C is 0.82°C, and below 40.4°C is -1.17°C.

VASCULAR ANATOMY

Dissection of the injected hummingbirds revealed the presence of a _rete mirabile ophthalmicum_. It is formed from branches of the A. ophthalmica externa and is situated extracranially between the posteroventral border of the orbit and the external acoustic meatus. The A. ophthalmica externa, which runs parallel to the V. ophthalmica externa for part of its length, passes dorsally over the external acoustic meatus, divides and forms the RMO. Proceeding dorsally, the first branch of the A. ophthalmica externa is the A. infraorbitalis. The A. infraorbitalis runs rostrally along the posteroventral border of the orbit. The RMO, which consists of 2 (possibly 4) arteries and 2 veins, lies between and possibly includes the A. ophthalmica externa and the A. infraorbitalis. The V. ophthalmica externa passes perpendicular to and between the rete arteries (Figure 3, inset). The

Figure 3. Diagram of the left arterial portion of the _rete mirabile ophthalmicum_ in the Calliope Hummingbird. The inset at the upper left is an enlargement of the major arterial and venous components of the RMO. The rete dorsal to the RMO and other vessels are not included.

Abbreviations: ACI, A. carotis interna; AI, A. infraorbitalis; AO, A. ophthalmotemporalis; AOE, A. ophthalmica externa; AS, A. supraorbitalis; AT, A. temporalis; IAM, Internal acoustic meatus; RMO, Rete mirabile ophthalmicum; VOE, V. ophthalmica externa; VS, V. supraorbitalis.


VS
RMO
AS
VOE
AT
AOE
0.5µ
CRANIAL
DORSAL
EYE
AS
AI
AO
RMO
AT
IAM
AOE
ACI
1µ

second branch off the A. ophthalmica externa is the A. temporalis which passes caudodorsally to the temporal muscles. The A. ophthalmica externa then branches forming the A. ophthalmotemporalis, which passes rostrally under the eye, the A. supraorbitalis, which runs dorsally along the posterior surface of the eye, and a third branch passing dorsally across the posterior superficial portion of the eye. The V. supraorbitalis runs parallel to the A. supraorbitalis for part of its length (Figure 3).

Dorsal to the RMO, on the posterior superficial portion of the eye, is a network of small arteries, veins, and capillaries. This network lies between the A. supraorbitalis and its branches (Figure 3). This network is separate from the RMO and should not be confused with it.

DISCUSSION

The Calliope Hummingbird, a species considerably smaller than the Zebra Finch, is capable of maintaining a cooler brain than body at high air, and therefore at high body, temperatures. The average body-to-brain temperature difference at body temperatures above 40.4°C is 0.82°C. This mean temperature difference falls within the range of body-to-brain temperature differences that have been observed in the other species of birds studied under similar conditions (Midtgård 1983; Appendix I: A).

The ecology of the hummingbird indicates that it is exposed to conditions in which brain cooling would occur. Calliope Hummingbirds cool their brains at body temperatures above 40.4°C. From Figures 1 and 2 it appears that body temperatures above 40.4°C occur in this bird at air temperatures above 38°C. The Calliope Hummingbird winters in the southern Mexican states of Michoacon, Mexico, and Guerrero, where temperatures above 29°C are rarily encountered (U.S. Environmental Data Service 1975a-1980a). However, in the bird's breeding range, which extends from southern British Columbia to California (American Ornithologist's Union 1982), air temperatures above 38°C are often encountered (U.S. Environmental Data Service 1975b-1979b). Under these environmental conditions it would be advantageous to always maintain a body temperature higher than the surrounding air temperature. In this way water may be conserved since a gradient for heat loss by non-evaporative means is preserved (Calder & King 1974; Kilgore et al. 1976; Weathers 1981), and brain cooling would allow the bird to maintain its brain within lethal limits.

The Calliope Hummingbird may also encounter elevated body temperatures during flight. Energy expended during flight exceeds that at rest by 16 times (from 4.0 ccO_2/gm hr at rest to 66.3 ccO_2/gm hr during activity; Lasiweski 1964). Of the energy expended 75 - 80% is probably converted to heat within the body contributing to a higher body temperature (Tucker 1968). This endogenous heat production would undoubtedly lead to a substantial increase in body temperature over resting levels. Data on body temperatures during exercise are not available for hummingbirds but are available for the Budgerigar(Melopsittacus undulatus), another relatively small bird. The body temperature of the Budgerigar, whose energy expenditure exceeds that at rest by only 8 times, rises from 41°C to 42°C during flight

(Aulie 1971).

Brain cooling is apparently accomplished by the RMO. The Calliope Hummingbird possesses a simple RMO of 2 - 4 arteries and 2 veins. The maximal number of arteries present in a bird this size as predicated by Midtgård´s allometric equations is 18.98 (1983; Appendix V: A). The number of arteries in the RMO of nonpasserines was found to be completely independent of body size (Midtgård 1983). It is unclear why the equation does not appear to predict well for the hummingbird. The results of this study indicate that the reduced cooling ability of the Zebra Finch is perhaps not due to the reduced number of vessels in the RMO as was suggested by Bech & Midtgård (1981). The Zebra Finch has an RMO of 6-7 arteries and 4-6 veins (Bech & Midtgård 1981) while the Calliope Hummingbird possesses a structure of fewer vessels and is still capable of cooling its brain.

In addition to the RMO itself there are two other areas where heat exchange may occur. The Arteria ophthalmica externa and the Vena ophthalmica externa run parallel with each other in close association for a short distance caudal to the RMO. Also there is an extensive network of vessls lying between the A. supraorbitalis and its branches. It is possible that this network may also function as a heat exchanger. Further research is necessary to determine if heat exchange is a functional possibility.

Midtgård (1983) examined the morphometry of and applied simple formulas for ideal heat exchangers to the RMO´s of forty species of birds ranging in size from 4 g to 100 kg. He found that the most important parameter for predicting exchange capabilities is the area available for countercurrent heat exchange, which characterizes the RMO better than the number of vessels involved. He used the morphometric data on the RMO to derive allometric equations predicting the magnitude of the body-to-brain temperature difference for passerines and nonpasserines. Based on these equations (Appendix V: B) the hummingbird should be capable of maintaining a 3.9°C difference between brain and body temperature, higher than what has been shown experimentally. Midtgård (1983) also found the theoretically deduced temperature differences to be larger than experimentally determined values. He suggested that the discrepancy could be due to the fact that the analysis is based on optimal conditions for countercurrent heat exchange, or it could be explained in terms of the mixing of arterial blood traveling from the RMO to the brain with blood traveling to the brain by a direct route. The theoretical analysis by Midtgård (1983) indicates that the RMO is capable of heat exchange, and with almost the same efficiency in all species studied regardless of the size of the bird. The present study supports Midtgård′s analysis by showing that a bird weighing only 2.5 g is capable of maintaining a cool brain with a body-to-brain temperature difference similar, with one exception, to that in all other species studied.

The relationship between body and brain temperature is not consistent over a range of colonic temperatures in the Calliope Hummingbird. At body temperatures below 40.4°C the hummingbird maintains a higher brain than body temperature. The average body-to-brain temperature difference at these lower body, and therefore air, temperatures is $-1.17^{\circ}C$. In most species of birds studied the relationship between body and brain temperature has yielded a regression line with a slope not statistically different from the isothermal line (Bech & Midtgård 1981; Bernstein et al. 1979a; Bernstein et al. 1979b; Crowe & Withers 1979; Kilgore et al. 1973; Kilgore et al. 1976; Kilgore et al. 1979; Kilgore et al. 1981; Schmidt & Simon 1979). The brain is cooled just as much at low body temperatures as at high body temperatures. Only in the American Kestrel does brain temperature increase more slowly than body temperature, producing a greater body-to-brain temperature difference at high air temperatures (Bernstein et al. 1979a).

Maintenance of the brain at a temperature higher than that of the body cannot be explained by heat exchange in the RMO. Cool arterial blood from the bird's core or cool venous blood from the buccopharyngeal areas, nares, beak, and eyes would only tend to lower the brain temperature to that of the body or below. Since the temperature of brain tissue is primarily controlled by its metabolic heat production and brain blood flow there are only several possible means by which the brain could be maintained at higher temperatures than core. Conductive losses of heat are probably minimal in birds since the brain is well insulated (Warncke & Stork 1977). One possible mechanism for maintaining a warmer brain than body temperature may be through an elevated endogenous heat generation by the brain (Midtgård 1983). The brain may generate more metabolic heat than other body tissues at lower body temperatures. Other vertebrates, notably Swordfish (Xiphias gladius), White marlin (Tetrapturus albidus), and Sailfish (Istiophorus platypterus) possess a "brain heater" (Carey 1982, p 1327), a mass of brown tissue, similar to mammalian brown fat, closely associated with the rete mirabile and the brain. This tissue has an highly developed blood supply, numerous mitochondria, and a high cytochrome C content, that indicate a high metabolic rate (Carey 1982). To my knowledge there is no structure in hummingbirds analogous to that found in these fish but an endogenous source of heat is at least a possibility. Decreased blood flow to the brain might also serve to maintain its temperature higher than core temperature since the brain may lose heat to circulating blood supplying the brain (Richards 1970). If blood flow to the brain were decreased at low body, and therefore air, temperatures less heat would be lost in general circulation to the body core. This mechanism would probably not operate at the same time as increased metabolic heat since increased metabolic rate requires an increased blood supply. An increased metabolic rate in conjunction with a decreased blood supply would accomplish little.

A more likely explanation for the higher brain than core temperature in the Calliope Hummingbird with low colonic temperatures is that colonic temperature underestimates core temperature. At low colonic temperatures, comparable to those measured in Calliope Hummingbirds, core (intracardiac) temperatures in chickens are several degrees higher than colonic (Missin 1977). This would not affect the interpretation that the hummingbird is capable of maintaining a cooler brain than body temperature at higher air, and therefore higher body, temperatures since colonic and core temperatures would both be equally high.

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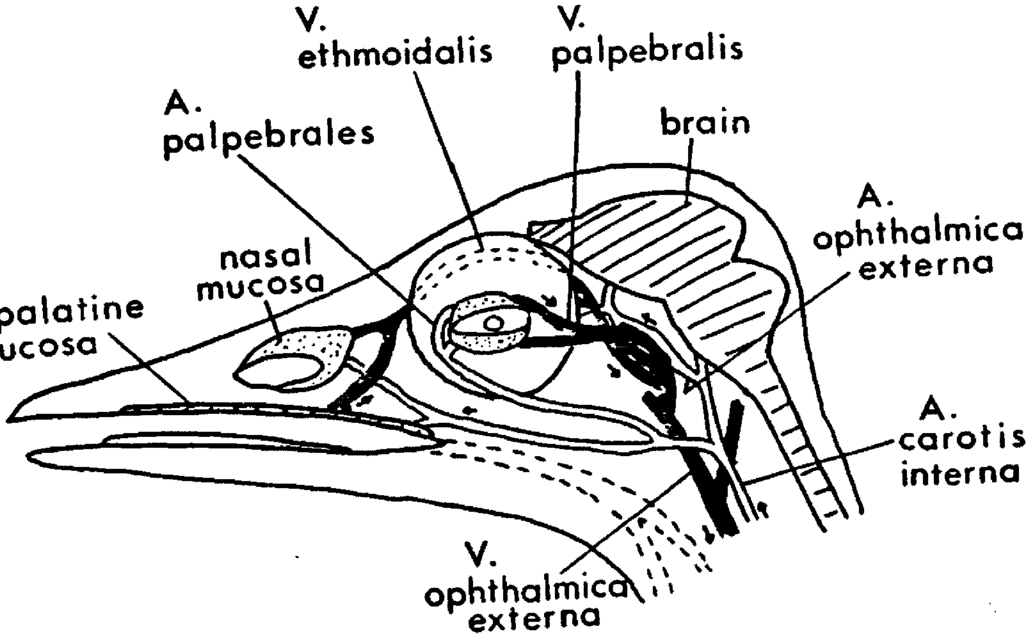
Appendix I: Miscellaneous Figures

A. Table of body to brain temperature differences in birds (from Bech & Midtgård 1981).

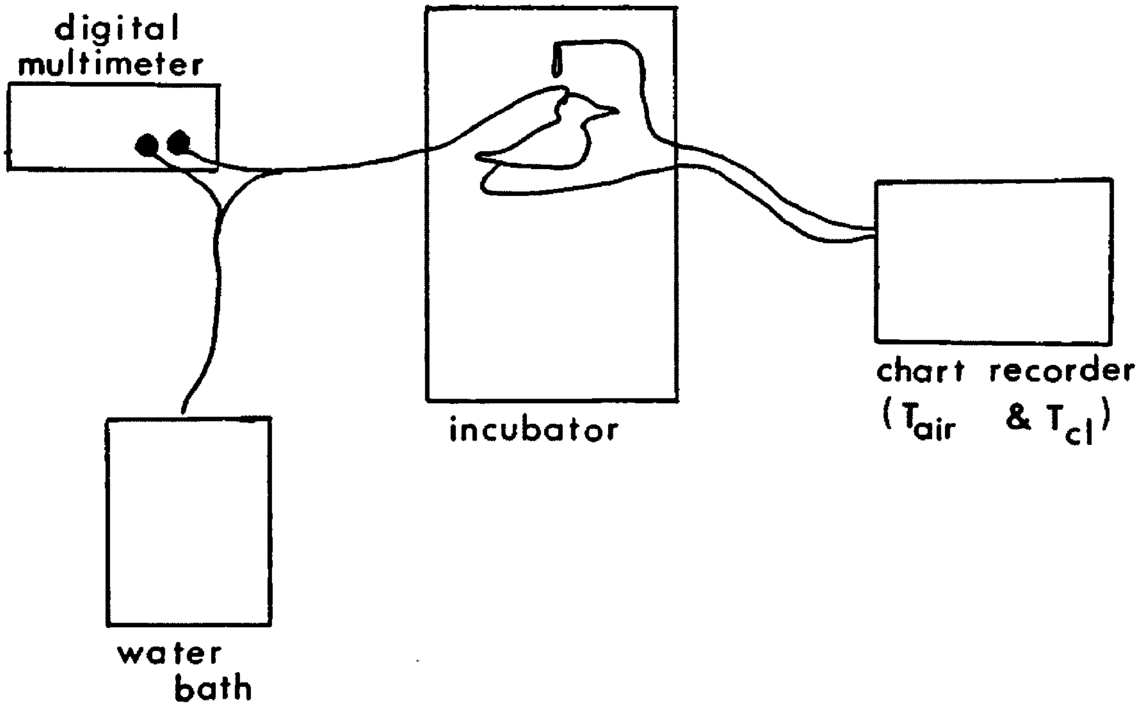
BODY TO BRAIN TEMPERATURE DIFFERENCES IN BIRDS

SPECIES	WEIGHT (KG)	$T_{Cl} - T_{Br}$ (°C)
Zebra finch (Poephila guttata)	0.013	0.18
Lesser nighthawk (Chordeiles acutipennis)	0.047	1.28
American kestrel (Falco sparverius)	0.119	0.70
Roadrunner (Geococcyx californianus)	0.251	0.80
Pigeon (Columbia livia)	0.361	1.06
Pigeon (Columbia livia)	0.377	1.03
White-necked raven (Corvus cryptoleucus)	0.385	0.92
Pigeon (Columbia livia)	0.430	1.08
Helmeted guineafowl (Numida meleagris)	1.130	2.13
Mallard (Anas platyrhynchos)	1.156	1.29
Fowl (Gallus domesticus)	2.300	0.70
Fowl (Gallus domesticus)	2.350	0.90
Fowl (Gallus domesticus)	-	1.00
Fowl (Gallus domesticus)	-	0.80
Pekin duck (Anas platyrhynchos domesticus)	2.650	1.03
Pekin duck (Anas platyrhynchos domesticus)	-	0.50
Rhea (Rhea americana)	30.900	1.00

B. Schematic representation of the *rete mirabile ophthalmicum* (redrawn from Midtgård 1983).


V. ethmoidalis
V. palpebralis
A. palpebrales
brain
A. ophthalmica externa
nasal mucosa
palatine mucosa
A. carotis interna
V. ophthalmica externa

C. Schematic representation of the experimental set up. Air and body temperature are recorded on a chart recorder. Brain temperature is measured as the voltage difference between a brain thermocouple and a reference thermocouple.


digital multimeter
incubator
chart recorder
(T_{air} & T_{cl})
water bath

Appendix II: Raw Data

Bird	Sex	Year	Wgt.	Air Temp.	Body Temp.	Brain Temp.
5C	F	1982	2.53	30.98	35.57	38.41
5C		1982		33.14	35.91	38.83
5C		1982		34.91	36.16	39.36
5C		1982		37.02	40.22	39.82
5C		1982		40.29	41.26	40.41
5C		1982		42.55	42.40	41.07
7C	F	1982	2.58	32.94	36.61	37.98
7C		1982		35.46	37.66	38.57
7C		1982		37.42	38.69	39.12
7C		1982		40.64	41.51	41.27
3C	F	1982	2.18	30.68	38.39	39.10
3C		1982		33.50	39.28	40.12
13C	F	1982	2.96	32.89	40.57	39.04
13C		1982		36.92	39.97	39.52
13C		1982		40.14	41.61	41.15
13C		1982		42.90	43.34	42.10
1NC	M	1983	2.55	33.08	36.41	37.29
3NC	M	1983	2.30	38.4	41.7	40.88
5NC	F	1983	2.40	39.54	42.32	41.49

6NC	M	1983	2.52	32.53	37.34	38.29
6NC		1983		32.48	36.95	38.03
7NC	M	1983	2.60	37.15	39.29	39.72
7NC		1983		40.73	41.95	41.82
7NC		1983		42.17	43.10	42.26
8NC	F	1983	2.67	40.53	41.25	41.06
10NC	F	1983	2.70	40.93	40.85	40.16

Appendix III: Capture and Maintenance of Humminngbirds

Calliope Hummingbirds were captured in Missoula County using a nylon low visibility mist net, 21.3 m by 91.4 m, with a 2.54 cm mesh. A feeder was hung along a creek and filled with a clear solution of 33% sucrose. After birds were attending the feeder their flight paths were observed to determine where to set the net. The net was set in predawn twilight (between 0530 and 0615) and was attended constantly. After a bird was removed from the net it was "force" fed a 33% sucrose solution. A sharp probe was used to gently pry the bird's bill open. Using a 1 cc syringe (without a needle) a drop of the sugar solution was placed at the tip of the open bill. When the bird realized that food was available it usually ate for several minutes. The bird was then placed in a paper lined glass jar with a mesh cover. Due to the length of handling time at the lab, no more than four birds were caught at one time. There was never more than 45 minutes between the capture of the first bird and leaving the capture site. If more time was allowed to elapse, at least one birds appeared to enter a torpor-like state. In some instances this led to death.

Upon return to the lab, the birds were individually fed and caged. If a bird appeared to be torpid it was hand warmed and fed until it became alert. Birds were individually caged in metal cages (60 cm by 45 cm by 40 cm) with 0.6 cm mesh. Three or four small dowels were provided for perching. An ordinary water bottle was used for the daily diet and fresh water was available in a bowl on the floor of the cage. Each cage was covered with inexpensive bridal veiling to make it *Drosophila*-tight.

For the first several days after capture a rounded piece of red acetate was placed over the tip of the water feeder. This helped the birds discover the food source more quickly.

Birds were fed a concentrate obtained from Biotropic-Verlag GmbH[1]. The concentrate was a mixture of amino acids, vitamins, and minerals. It was added to a combination of sucrose and dextrose and mixed with cold water. This solution was fed 5 days a week and was changed every day. The birds received a 33% sucrose solution on weekends. *Drosophila* were also given to the birds.

To reduce cost another possible recipe, given below, was provided by Dr. Lee Gass at the University of British Columbia.

600 ml cold water

3/4 cup sucrose

15 drops Linatone (commercial vitamin for birds)

9 drops Avitron (commercial vitamin for birds)

3 drops wheat germ oil

[2]1 teaspoon "Slimdown" protein powder

[1] Biotropic-Verlag GmbH, Blochmatt 7, D-7570 Baden-Baden 11, West Germany

[2] Produced by C.E.Jamieson & Co. (DOM) Limited, 519-969-7630

Appendix IV: Ketamine Hydrochloride as an Anesthetic

Finding a safe and reliable dose of anesthetic to produce the desired surgical plane can be difficult in birds and particularly so in small birds. In general birds tolerate less anesthetic between the planes of surgical anesthesia and death than do mammals. Problems of dosage are further complicated by the rapid reduction in temperature caused by most anesthetics. The problem is particularly severe in small birds where the body temperature can drop several degrees in only a few minutes (Fedde 1978).

I needed to produce a surgical plane of medium depth in hummingbirds to totally restrain them so that thermocouples could be implanted in the brain. An intravenous anesthetic was not practical due to the extremely small size of the bird´s blood vessels. An inhalation anesthetic was not used due to methods of pre- and post- surgical restraint. The restraint methods made close monitoring of the bird´s respiration very difficult. Of the parenteral anesthetics ketamine hydrochloride seemed best suited for our needs.

Ketamine hydrochloride has been used in a variety of birds ranging in size from 30 g to 3000 g (Fedde 1978). It has been found to be a safe anesthetic for parakeets at doses ranging from 0.05 - 0.10 mg/g body weight (Kirkby 1980, Fedde 1978, Mandelker 1972). There is a large safety factor associated with ketamine, the lethal dose being 0.5 mg/g body weight in a bird the size of a parakeet. Since dose rates varies inversely with the body weight of the bird, (Kirkby 1980), I tried an initial dose of 0.10 mg/g body weight.

Eleven Calliope Hummingbirds, 6 males and 5 females, weighing an average of 2.7 g were anesthetized. Ketamine hydrochloride (10 mg/cc) was injected into the pectoral muscle using a microliter syringe. A slide warming tray, set at 40°C, was used to maintain body temperature. This dose produced a medium anesthetic plane within one to five minutes. In this plane voluntary movement was characteristically absent, palpebral reflexes were absent, pedal reflexes were slow or intermittant and breathing was slow, deep, and regular. The anesthetic plane lasted between 15 and 25 minutes. Total recovery took an additional 3 to 4 hours. During this time the bird drifted in and out of consciousness. During the first half hour of this period some involuntary muscle movements occurred. The bird was restrained during and after surgery, using a flannel jacket, so was not able to damage itself during these involuntary muscle movements.

Due to the delicate nature of the hummingbirds and their need to feed very frequently, birds were not fasted before or after surgery. Vomiting occurred in only one case. Birds were fed a 33% sucrose solution during the recovery period. Care must be taken not to feed the birds too early. They exhibit swallowing movement before totally alert and will choke if fed when not alert.

Appendix V: Equations Used in Heat Exchange Calculations

In all equations M equals the mass of the bird. In this case M equals 2.5 grams.

A. Number of arteries = $16.1\ M^{0.18}$

B.
$$\Delta T = \frac{T_a - T_v}{1 + 0.015M^{0.32}}$$

where T_a is the temperature at the arterial inlet (equal to deep body temperature), and T_b is the temperature at the venous inlet (equal to the temperature at the surface of the eye).