Beyond the classic thermoneutral zone
Including thermal comfort

Boris RM Kingma1,2,*, Arjan JH Frijns2, Lisje Schellen1,3, and Wouter D van Marken Lichtenbelt1

1Department of Human Biology; NUTRIM School for Nutrition, Toxicology and Metabolism of Maastricht University Medical Center+; Maastricht, The Netherlands; 2Department of Mechanical Engineering: Eindhoven University of Technology; Eindhoven, The Netherlands; 3School of Built Environment and Infrastructure; Avans University of Applied Sciences; Tilburg, The Netherlands

Keywords: mathematical model; metabolism; theoretical biology; thermal behaviour; thermoregulation

Abbreviations: BMR, basal metabolic rate; PMV, predicted mean vote; PPD, percentage people dissatisfied; NST, category label indicating body heat deficit relative to basal metabolic rate cold induced thermogenesis by shivering and non-shivering is required to maintain thermal balance; SH+NST, category label indicating body heat deficit relative to basal metabolic rate cold induced thermogenesis by shivering and non-shivering is required to maintain thermal balance; SWEAT, category label indicating a body heat surplus increased evaporation is required to maintain thermal balance; TCZ, thermal comfort zone; TNZ, thermoneutral zone; TNZ category label indicating body heat loss is balanced relative to metabolic rate this definition of the thermoneutral zone incorporates the combination of mean skin temperature and ambient temperature; TNZ classical, TNZ referring to the classic definition of the thermoneutral zone which only defines the ambient temperature range; TNZ functional, TNZ referring to the classic definition of the thermoneutral zone taking into account clothing insulation and metabolic heat production associated with light office work; air, referring to the human body; body core; clothed, referring to the human body; clothing; convective; evaporative; respiratory; skin or mean skin; α, fraction of metabolic heat production that is accounted for by respiratory heat loss; A (m²), body surface area; ϕ, relative humidity; Fpel, permeation efficiency factor for water vapor evaporated from the skin surface through clothing to the ambient air; γ (mmHg Pa⁻¹), conversion factor from Pascal to mmHg; h (W m⁻² °C⁻¹), heat transfer coefficient; I (m²°CW⁻¹), insulation; λ (°C mmHg⁻¹), Lewis relation; M (W), Metabolic rate; P (mmHg), saturated vapor pressure; T (°C), Temperature; Q (W), heat loss; v (m s⁻¹), velocity; w, skin wetness fraction; ΔT (°C), Indicating a temperature range

The thermoneutral zone is defined as the range of ambient temperatures where the body can maintain its core temperature solely through regulating dry heat loss, i.e. skin blood flow. A living body can only maintain its core temperature when heat production and heat loss are balanced. That means that heat transport from body core to skin must equal heat transport from skin to the environment. This study focuses on what combinations of core and skin temperature satisfy the biophysical requirements of being in the thermoneutral zone for humans. Moreover, consequences are considered of changes in insulation and adding restrictions such as thermal comfort (i.e. driver for thermal behavior). A biophysical model was developed that calculates heat transport within a body, taking into account metabolic heat production, tissue insulation, and heat distribution by blood flow and equates that to heat loss to the environment, considering skin temperature, ambient temperature and other physical parameters. The biophysical analysis shows that the steady-state ambient temperature range associated with the thermoneutral zone does not guarantee that the body is in thermal balance at basal metabolic rate per se. Instead, depending on the combination of core temperature, mean skin temperature and ambient temperature, the body may require significant increases in heat production or heat loss to maintain stable core temperature. Therefore, the definition of the thermoneutral zone might need to be reformulated. Furthermore, after adding restrictions on skin temperature for thermal comfort, the ambient temperature range associated with thermal comfort is smaller than the thermoneutral zone. This, assuming animals seek thermal comfort, suggests that thermal behavior may be initiated already before the boundaries of the thermoneutral zone are reached.

Introduction

The thermoneutral zone (TNZ) is defined as: ‘the range of ambient temperature at which temperature regulation is achieved only by control of sensible (dry) heat loss, i.e. without regulatory changes in metabolic heat production or evaporative heat loss.’ One remarkable feature of the classical TNZ definition is that it only considers autonomic thermoregulatory mechanisms, and omits the influence of thermal behavior. Nevertheless, thermal behavior is considered as the major influencing factor of body
Temperature

The thermal comfort zone (TCZ) is defined in terms of perception and qualifies as the state of mind that expresses satisfaction with the thermal environment. Furthermore the TCZ is suggested to relate to positive anticipations of the current thermal environment. In other words, thermal discomfort (i.e., negative anticipation) drives a human being to counteract the thermal environment accordingly.

According to their definitions the TNZ and the TCZ are not directly related to each other. However, physiologically, both zones share a common source of information, namely skin and core temperature. Furthermore, functionally, they may share a common goal, that is to preserve body temperature. A living body can only maintain a stable core temperature when heat production and heat loss are balanced. That means that heat transport from body core to the skin must equal heat transport from skin to the environment.

This study investigates what combinations of body core, skin and ambient temperature satisfy the biophysical requirements of being in the TNZ for humans. Nevertheless concepts apply to other animals as well. Moreover, we study the consequence of changes in insulation and adding restrictions such as thermal comfort (i.e., derive TCZ). By comparing the ambient temperature ranges associated with the TNZ and the TCZ, the aim is to better understand the link between the two, and discuss practical implications with respect to metabolic research and the built environment.

Methods

This section describes the biophysical model that is used to analyze what combinations of body core temperature (T_c), mean skin temperature (T_s) and ambient temperature (T_a) satisfy the requirements of thermal balance. The section is structured as follows: first the effect size of autonomic and behavioral thermoregulatory mechanisms are described, second the biophysical model is introduced, third the ranges of biological and physical model parameters for 2 scenarios are given, fourthly the equations for T_c and T_s are given. Fifthly, 4 categories are defined that indicate what thermoregulatory action is required to maintain thermal balance. Sixthly, the derivation of T_a ranges associated with the TNZ and TCZ is described.

Thermoregulation within the TNZ: effect size

With respect to mechanisms of thermoregulation within the TNZ, we only consider mechanisms that influence insulation, and do not result in changes in metabolic heat production. With this restriction, the body is able to change total body tissue insulation by changes in blood flow from 0.124 m^2°C/W (i.e., maximal vasoconstriction) to 0.031 m^2°C/W (i.e., maximal vasodilation respectively). Together, through behavioral regulation clothing insulation can be changed from 0 m^2°C/W (i.e., nude, 0 Clo) to 0.92 m^2°C/W (i.e., arctic clothing, 6 Clo), the airflow and thereby also insulation provided by air can be modified (e.g., draft or breeze) or T_a can be adjusted (e.g., thermostat in building), see Figure 1 for a schematic overview.

Biophysical thermal network model

A biophysical thermal network model was used to calculate T_c and T_s, taking into account metabolic heat production (M), dynamic body tissue insulation (I_body), static clothing insulation (I_cl), static air insulation (I_a) and evaporative heat loss, see Figure 2.

1) With the first model (Fig. 2, Body) the range of T_s that satisfy a steady-state thermoneutral condition is calculated for a range of T_c around T_c = 37 °C, a range of M corrected for respiratory heat loss (see Supplemental Material, A2), and a range of (I_body) associated with maximal vasoconstriction and maximal vasodilation. Specific ranges are defined below.

2) With the second model (Fig. 2, Nude or Clothed) steady-state T_c is calculated over a range of ambient temperatures
10°C ≤ T_s ≤ 40 °C and skin temperatures 20 °C ≤ T_s ≤ 40 °C, given low wind speed (air velocity = 0.1 m/s) air insulation, in nude and in clothed condition. I_body is calculated as a function of T_c.

Physiological insulation, anthropometry and metabolic rate
Total body insulation is defined by a passive part: tissue insulation, and an active part: regulation of skin blood flow. In case of total skin vasoconstriction, tissue insulation provided by muscle and fat is about I_body, min = 0.124 m^2°C/W for a man with 4 mm subcutaneous fat. In case of full skin vasodilation, passive tissue insulation is by-passed and reduces I_body, min = 0.031 m^2°C/W. Thus, I_body is inversely related to blood flow. Several experiments show a linear relation between T_s skin blood flow and I_body for a resting man. Therefore, we calculate body insulation as a linear function of skin temperature (see E1). The modeled T_s, s.m., results from the minimal skin temperature (T_s, s.m.) that satisfies steady-state thermoneutral condition with T_c = 36 °C. Likewise, modeled T_s, f.s.m., results from the maximal skin temperature T_s, f.s.m. that satisfies steady-state thermoneutral condition with T_c = 38 °C. Thus the equation for I_body is given by (E1):

I_body = I_body, max + \left(\frac{I_body, max - I_body, min}{T_s, min - T_s, max}\right) (T_s - T_s, min)

Where T_s, min ≤ T_s ≤ T_s, max.

Heat loss from skin to environment scales linearly with body surface area (A). For this study, body surface area is set to correspond to an average man A = 1.86 m^2. The minimum amount of heat production to sustain life is referred to as the basal metabolic rate (BMR). In literature, BMR for an average man is reported as BMR ≈ 86 W or BMR ≈ 46 W/m^2. BMR is significantly related to age, gender, length and height. To account for these influences, we consider a 5% range 82 W ≤ BMR ≤ 90 W in this paper. BMR is often measured in physiological laboratory experiments. During such experiments, volunteers are quasi-nude and in supine position. Nevertheless, under daily living conditions, e.g., in office conditions, humans operate seldom in this state. Changes in posture, arousal and activity increase M significantly. For a sitting male, performing office work M ≈ 112 W or M ≈ 60 W/m^2. Similar to the BMR, a range of M is considered in this paper 106 W ≤ M ≤ 118 W.

To model both laboratory and office conditions, 2 scenarios are considered:
1) Classical TNZ: a nude person in supine position at BMR and
2) Functional TNZ: a clothed person in sitting condition at M associated with office work. The insulation provided by clothing is I_cl = 1Clo = 0.155 W/m^2°C.

Here, the classical scenario refers to the TNZ as defined in the glossary of terms for thermal physiology; the functional scenario is analogous to the definition of ‘TNZ classical’ with the difference that clothing is worn and M > BMR.

Equations for minimum and maximum T_s as a function of T_c, M, I_body and A
Heat balance between M and heat transport from core to skin minus respiratory heat loss is satisfied when

(1-α)M = A \left(\frac{T_s, max - T_s}{I_body}\right)

Here, α = 0.08 is the fraction of M that is accounted for respiratory heat loss (see Supplemental Material, A2 for more details).12

Minimum M for which M and body heat transport is balanced corresponds to the state where T_s is minimal and M and I_body are maximal and vice versa for maximal T_s. Hence the feasible steady-state T_c range is defined as (E2):

T_c = \frac{T_s, min - (1-α)M, min I_body, min A}{(1-α)(M, max + M, nst)}

Equation of T_c as a function of T_s and other heat transfer parameters
The equation for T_c below follows the scheme where M corrected for respiratory heat loss equals heat loss by radiation and convection (Q_r+c) plus evaporative heat loss (Q_e). For brevity, only the final equation for T_c is given in this section, see Supplemental Material for full derivation (E3).

T_c = \frac{T_s - (1-α)M, max I_body, max A}{(1-α)(M, min + M, air)} + Q_e + Q_r+c + Q_a

Here T_c is ambient temperature in °C, I_air, is air insulation in m^2°C/W, I_body refers to body insulation in m^2°C/W, I_air is clothing insulation in m^2°C/W and Q/A is evaporative heat loss in W/m^2.

Heat balance categories
Solutions for which T_c and T_s remain in steady-state are calculated for 10 °C ≤ T_s ≤ 40 °C, and skin temperature 20 °C ≤ T_s ≤ 40 °C. Constellations of T_c and T_s (solutions) that do not satisfy (36 °C ≤ T_s ≤ 38 °C) are filtered out. Until now, no restrictions on heat flow, other than (1-α)M = Q_r+c + Q_e, are defined; only temperatures are calculated that satisfy heat flow balance with the environment. Categories of body heat deficit, body heat surplus or body heat balance are defined by calculating the actual heat flow for each of the solutions and comparing that to the metabolic rate corrected for respiratory heat loss. The 4 categories are defined as follows:
1) TNZ body: heat loss is balanced relative to metabolic rate: (1-α)M, min ≤ Q_r+c + Q_e ≤ (1-α)M, max,
2) SWEAT: there is a heat surplus and evaporation is required to maintain thermal balance: Q_r+c + Q_e ≤ (1-α)M, min,
3) NST: there is a heat deficit and cold induced thermogenesis by non-shivering (M, nst) = 0.12M is sufficient to maintain thermal balance: (1-α)M, max ≤ Q_r+c + Q_e ≤ (1-α)(M, max + M, nst),13
4) SH+NST: there is a heat deficit and cold induced thermogenesis by shivering and non-shivering is required to maintain thermal balance: 

\[(1-\alpha)(M_{\text{max}} + M_{\text{sh}}) \leq Q_{\text{out}} + Q_{\text{s}} \leq (M_{\text{sh}} + M_{\text{nv}}),\]

Here maximal heat production through shivering and non-shivering is capped at \(M_{\text{sh}} + M_{\text{nv}} = 372\, \text{W}\), which is the empirical maximum cold-induced heat production in humans.  

**Finding \(T_a\) associated with TNZ and TCZ**

This section describes how the set of solutions described above (i.e., combinations of \(T_s\) and \(T_a\)) are further filtered to define the \(T_a\) range for the TNZ and the TCZ.

For the TNZ, the \(T_a\) range is defined by the subset of solutions for which corresponding \(T_s\) satisfy that body heat transport equals \(M\), i.e., \(T_{a_{\text{min}}} \leq T_a \leq T_{a_{\text{max}}}\).

To find the TCZ the same method is applied, however, the values for \(T_{s_{\text{min}}}\) and \(T_{s_{\text{max}}}\) are different. In this study the main comfortable skin temperature range used is \(31.5°C \leq T_s \leq 35.5°C\) as reported by Gagge et al.  

Moreover, a more conservative range \(32.8°C \leq T_s \leq 33.8°C\) as reported for man in supine position by Weiwei et al. is also considered.  

**Results**

The results section is structured as follows: first the TNZ is presented for the classical condition (i.e., not clothed and at basal metabolic rate) and the functional condition (i.e., clothed in business suit and at office work metabolic rate), second the TCZ is presented for both conditions.

**Classical TNZ: nude and basal metabolic rate**

The steady-state \(T_a\) range for the TNZ for a person in a nude condition and heat production at BMR as calculated by the model are shown in **Figure 3**. Each band in **Figure 3** depicts for a given \(T_a\) the range of \(T_s\) in which the equation constraints are satisfied for each category, e.g., ‘TNZ body’, ‘SWEAT’, ‘NST’, ‘SH+NST’. The band labeled ‘TNZ body’ depicts that thermal balance is satisfied and heat loss equals BMR. Thus, ‘TNZ body’ indicates for which \(T_a\) the ‘TNZ classical’ is supported from the perspective of human body internal heat transport.

Steady-state skin temperature ranges between \(30.5°C \leq T_s \leq 36.8°C\). Where \(T_a = 30.5°C\) corresponds to \(T_s = 36°C\) and \(I_{\text{body}} = 0.124\, \text{m}^2\text{°C}/\text{W}\) and \(M_{\text{min}} = 82\, \text{W}\). Vice versa \(T_a = 36.8°C\) corresponds to \(T_s = 38°C\), \(I_{\text{body}} = 0.031\, \text{m}^2\text{°C}/\text{W}\) and \(M_{\text{max}} = 90\, \text{W}\). Consequently, the slope of body insulation vs. skin temperature is \(-0.015\, \text{m}^2\text{°C}/\text{W}\) (used in Equation 1).

The area labeled ‘SH+NST’ is narrower than the area labeled ‘SWEAT’. This is explained by body insulation. In case of ‘SH+NST’ the body is at maximal insulation. This means the body can vary internal heat transport up to 30W, whereas in case of ‘SWEAT’ the body is at maximal conduction, in this case the body internal heat transport can vary up to 120 W. In between maximal vasoconstriction and maximal vasodilation the body gradually changes from an insulator to a conductor, and consequently, for each ambient temperature there is a wider range of skin temperatures that satisfy the steady-state solutions.

It is important to note that the steady-state ambient temperature range associated with the classical TNZ does not guarantee that the body is in thermal balance at basal metabolic rate per se. Instead, depending on the combination of \(T_a\) and \(T_s\), the body may require significant increases in heat production or may require significant decreases in heat production to maintain core temperature stable within the range \(36°C \leq T_a \leq 38°C\). In other words, TNZ body indicates for which \(T_a\) the ‘TNZ classical’ is supported from the perspective of human body internal heat transport.

**Functional TNZ: clothed and performing office work**

Relative to the nude case, clothing insulation and increased M shift the TNZ to lower \(T_a\) and cause the solution areas to be wider. That is, for each \(T_a\) in ‘TNZ functional’ there is a wider range of \(T_s\) for which the body can support required heat transport than in ‘TNZ classical’.

---

**Figure 3.** The classical thermoneutral zone (denoted by ‘classical TNZ’), is defined as the range of ambient temperature at which temperature regulation is achieved only by control of sensible (dry) heat loss, i.e., without regulatory changes in metabolic heat production or evaporative heat loss. Each band depicts for a given ambient temperature the range of mean skin temperature in which the equation constraints are satisfied for each category, e.g., ‘TNZ body’, ‘SWEAT’, ‘NST’, ‘SH+NST’. The light gray area labeled TNZ body depicts solutions that satisfy that internal body heat transport equals external heat loss and core temperature ranges between \(36°C \leq T_c \leq 38°C\). In other words, TNZ body indicates where the classical thermoneutral zone is supported from the perspective of the human body. NST: solutions for which steady-state heat loss is between \(83\, \text{W} \leq Q \leq 88\, \text{W}\). The body can achieve thermal balance by non-shivering thermogenesis. Shiver+NST: solutions for which steady-state heat loss is between \(88\, \text{W} \leq Q \leq 372\, \text{W}\). The body can achieve thermal balance by shivering thermogenesis. SWEAT: solutions for which steady-state heat loss is \(Q \leq 83\, \text{W}\). The body can achieve thermal balance by increased evaporation.

---

www.landesbioscience.com Temperature 145
The TNZ for a clothed person is \((14.8 \, ^\circ\text{C} \leq T_s \leq 24.5 \, ^\circ\text{C})\), see Figure 4. The skin temperature ranges between \((28.8 \, ^\circ\text{C} \leq T_s \leq 36.4 \, ^\circ\text{C})\). The slope of body insulation vs. skin temperature is \(-0.012 \, \text{m}^2/\text{W}\) (used in Equation 1). Core temperature and body insulation ranges are the same as in the laboratory case, however \(M_{\min} = 106 \, \text{W}\) and \(M_{\max} = 118 \, \text{W}\) and corresponds to the metabolic rate of a sedentary man performing office work.

**TCZ: nude and basal metabolic rate**

Next we narrow the band of thermoneutral skin temperatures from \(30.5^\circ\text{C} \leq T_s \leq 36.8^\circ\text{C}\) to the comfortable skin temperature range as reported by Gagge et al. \((31.5 \, ^\circ\text{C} \leq T_s \leq 35.5 \, ^\circ\text{C})\). This narrows the ambient temperature range of the TNZ: \(25.9 \, ^\circ\text{C} \leq T_a \leq 33.3 \, ^\circ\text{C}\) to the TCZ: \(27.5 \, ^\circ\text{C} \leq T_a \leq 32.3 \, ^\circ\text{C}\), see Figure 5. Hence the laboratory steady-state TCZ is narrower than the steady-state thermoneutral zone (\(\Delta T_{s,\text{tnz}} = 6.9^\circ\text{C}\) vs. \(\Delta T_{s,\text{tcz}} = 4.8^\circ\text{C}\)). Constraining the comfortable skin temperature range even further to a conservative \(32.8^\circ\text{C} \leq T_s \leq 33.8^\circ\text{C}\) as reported by WeiWei et al., the conservative comfortable ambient temperature range is restricted to \(29.0^\circ\text{C} \leq T_a \leq 30.4^\circ\text{C}\). Interestingly, even the conservative ambient thermal comfort range includes solutions where the body would need to either produce or lose more heat to maintain thermal balance, see Figure 5 areas ‘NST’ and ‘Sweat’ within the dashed lines.

**TCZ: clothed and at resting metabolic rate**

As with the laboratory case, the comfortable mean skin temperature range \(31.5 \, ^\circ\text{C} \leq T_s \leq 35.5 \, ^\circ\text{C}\) narrows the ambient temperature range from TCZ\(_{\text{clothed}}\): \(14.5 \, ^\circ\text{C} \leq T_a \leq 24.5 \, ^\circ\text{C}\) to TCZ\(_{\text{clothed}}\): \(17.5 \, ^\circ\text{C} \leq T_a \leq 24.0 \, ^\circ\text{C}\), see Figure 6. Hence the laboratory steady-state thermal comfort zone is narrower than the steady-state thermoneutral zone (\(\Delta T_{s,\text{tnz}} = 9.7^\circ\text{C}\) vs. \(\Delta T_{s,\text{tcz}} = 6.5^\circ\text{C}\)). For the conservative comfortable mean skin temperature range \((32.8 \, ^\circ\text{C} \leq T_s \leq 33.8 \, ^\circ\text{C})\), the conservative comfortable ambient temperature range is narrowed down to \(19.5^\circ\text{C} \leq T_a \leq 21.9^\circ\text{C}\).

**Discussion**

This study describes what constellations of \(T_{c}, T_{s}, T_{a}\) satisfy the biophysical requirements of being in the thermoneutral zone for steady-state conditions. Furthermore, by constraining \(T_{s}\) to a temperature range associated with thermal comfort the thermal comfort zone is derived.

**Toward a more accurate definition of the TNZ**

The biophysical analysis in this study shows that depending on \(T_{s}\), the classical definition of the TNZ does not guarantee at all that the body is indeed in a thermoneutral state. As can be seen in Figure 3, only the light gray area denoted as ‘TNZ body’ supports a thermoneutral state. For instance, in the nude condition, when ambient temperature is \(T_{a} = 30^\circ\text{C}\), thermoneural mean skin temperature is bound to \(33.4 \, ^\circ\text{C} \leq T_{s} \leq 33.8 \, ^\circ\text{C}\). However, body processes other than temperature regulation (e.g., blood pressure regulation, circadian rhythm or disease) may influence skin temperature as well.\(^{17}\) If \(T_{s}\) exceeds the predefined bounds, increased heat production (in case of higher \(T_{a}\)) or evaporation (in case of lower \(T_{a}\)) is required to maintain heat loss balanced relative to the metabolic rate. In determining the thermoneural temperature ranges for rats the importance of skin temperature is already taken into account.\(^{18}\) Therefore, the current definition of the TNZ might require a revision. According to the authors a more accurate definition of the thermoneural zone would be: ‘the combinations of ambient temperature and mean skin temperature for a given core temperature at which temperature regulation is achieved only by control of sensible (dry) heat loss, i.e. without regulatory changes in metabolic heat production or evaporative heat loss’. This subtle difference has a significant impact on the design of metabolic studies that require a thermoneural condition, since controlling \(T_{s}\) alone is not sufficient.

**The TNZ and experiments**

The first study that describes the TNZ in air and in humans is by Hardy and Dubois.\(^{19}\) They report a lower critical ambient temperature \(T_{a,H&D} = 28.5 \, ^\circ\text{C}\) and corresponding skin temperature \(T_{s,H&D} = 33.5 \, ^\circ\text{C}\). At first glance, these values are considerably different than reported in this study \((T_{s} = 26.4 \, ^\circ\text{C} \text{ and } T_{a} = 30.5 \, ^\circ\text{C})\). However, Hardy and Dubois did not define where they measured skin temperature and their volunteers also had a lower \(M = 75 \, \text{W}\) and lower \(I_{body,\max} = 0.093 \, \text{m}^2/\text{W}\). Using these averaged parameters the biophysical model finds for the
lower bound $T_s = 29.2$ °C and $T_r = 32.5$ °C, which is more in line with the experimental findings. The example above stresses the importance of the $M$ and the capacity of the body to change $I_{body}$ in relation to the TNZ. Notably, if $M$ increases due to normal behavioral activity, the neutral ambient temperature range is considerably lowered compared with the resting state. This is especially relevant in housing of mice and small rodents for which the variable thermal insulation of the body itself. For clothed man ($1\text{Clo}$) performing office work ($112 \text{ W}$), as in the functional case targeted by the PMV given below $0.5$. Using the same value for mean skin temperature $T_{\text{body}} = 34.7$ °C and predicts the comfortable ambient temperature range ($\nu = 0.1 \text{ m/s}$) between $21.5$ °C ≤ $T_a$ ≤ $25.1$ °C, where $|\text{PMV}| \leq 0.5$. Using the same value for mean skin temperature the biophysical model returns $21.7$ °C ≤ $T_a$ ≤ $23.1$ °C, which is comparable for the lower part, yet the upper limit of the PMV model is $2$ °C higher than the upper limit of our biophysical model. This suggests that humans remain in thermal comfort even while limited increases in evaporation through sweating are required to maintain a stable body temperature.

*Thermal comfort and indoor environments*

The relation between the TNZ and TCZ is based on mean skin temperature ranges associated with thermal comfort. Two ranges are considered: a relatively wide range as reported by Gagge et al., and a more conservative, relatively narrow range as reported by WeiWei et al. Both skin temperature ranges associated with thermal comfort are narrower than the skin temperature range associated with the TNZ. Consequently, the derived $T_s$ range of the TCZ is narrower than the thermoneutral zone (compare Figs. 3 and 5). In this study mean skin temperature was considered in relation to thermal comfort in a uniform and steady-state environment. However, several studies show the importance of distal skin temperatures in relation to thermal comfort in non-uniform and transient environments.

Analysis of non-uniform and transient environments is outside the scope of this study, however, this may require attention in a future study. Likewise, $T_r$ is known to affect thermal comfort as well. For instance, relatively low core temperature ($T_c = 36$ °C), is shown to require relatively high mean skin temperature ($T_s \approx 35$ °C) to maintain thermal comfort. The model in this paper does not impose that extra restriction. Adding the restriction could possibly lead to further narrowing of the TCZ.

As thermal comfort is considered as the major driver for thermal behavior, results of this study suggest that thermal behavior is likely to be initiated before the bounds of the TNZ are reached. Putting this in perspective of thermal discomfort being the negative anticipation of the thermal environment there is a benefit to preserve the individual being by counteracting a potentially hazardous environment before any harm is done. Nevertheless, as a result of acclimatization (e.g., regular exposure to a thermal challenge), the body may learn that it is able to cope with that environment without harm, and as such, recognize the respective thermal environment as relatively comfortable. Indeed, an acclimation study from our laboratory shows that already after 10 d of regular exposure to a discomfortable cold environment and outside the thermoneutral zone, thermal comfort increases from ‘uncomfortable’ to ‘just comfortable’. Thus, the TCZ may be more flexible than the TNZ and, after acclimation, may be extended outside the TNZ.

Current indoor thermal environment design for thermal comfort is primarily based on PMV (Predicted Mean Vote) criteria, calculated by the PMV/PPD model developed by Fanger. The PMV is expressed on a 7-point Thermal Sensation Scale ranging from cold (-3) to hot (+3). This vote can be linked to thermal comfort through the PPD, i.e., the percentage of people who will be dissatisfied with the thermal environment. The PMV/PPD model incorporates clothing, metabolic heat production and heat loss for a person at comfortable skin temperature. This is comparable to the current study approach, except that this study includes the variable thermal insulation of the body itself. For clothed man (1Clo) performing office work (112 W), as in the functional case covered in this study, Fanger assumes as mean skin temperature $T_{\text{body}} = 34.7$ °C and predicts the comfortable ambient temperature range ($\nu = 0.1 \text{ m/s}$) between $21.5$ °C ≤ $T_a$ ≤ $25.1$ °C, where $|\text{PMV}| \leq 0.5$. Using the same value for mean skin temperature the biophysical model returns $21.7$ °C ≤ $T_a$ ≤ $23.1$ °C, which is comparable for the lower part, yet the upper limit of the PMV model is $2$ °C higher than the upper limit of our biophysical model. This suggests that humans remain in thermal comfort even while limited increases in evaporation through sweating are required to maintain a stable body temperature.

Although the PMV/PPD model is designed for static thermal environments only, experiments show that the PMV/PPD model can also be applied during small thermal transients. This can be explained with the physiological aspect of the model described in this paper, that is during a small thermal transient the body may adjust body insulation or skin temperature and remain in the ‘TNZ body’ area (see Fig. 6), and thus does not require increased evaporation, metabolic heat production or any form of thermal behavior in order to preserve body temperature. However, perhaps more interesting, even within the $T_a$ and $T_r$ ranges associated with thermal comfort areas marked as ‘NST’ and ‘SWEAT’ are found. This suggests that a significant increase in metabolic heat production may be possible without losing thermal comfort.
which in turn may be beneficial to prevent or counteract metabolic diseases such as obesity and diabetes.

**Considerations and limitations**

Several model parameters in this biophysical model study were chosen to reflect a human in a resting condition. In this section consequences and limitations of these model choices are considered. Furthermore, it should be noted that although the model parameter values are retrieved from empirical studies, the exercise performed in this manuscript is not an in vivo experiment and thus requires an independent study to validate the finds, both for the TNZ and the TCZ.

First, on physiological parameters, the M was chosen as BMR and that during daily office work, which is slightly higher than the BMR. Increased activity would significantly increase M. As a result the TNZ would become wider (see equation E2) and shift to cooler $T_a$. Furthermore, values for $I_{body}$ were obtained from studies on healthy lean male subjects; in case of obesity it is reasonable to assume higher body tissue insulation. Besides M and $I_{body}$, body core temperature range used ($36 \, ^\circ C \leq T_c \leq 38 \, ^\circ C$) might not be sufficient to justify the entire range of body tissue insulation in resting man, i.e., there is evidence that maximal vasodilation and minimal tissue insulation are expected at body core temperature above $38 \, ^\circ C$.27 Second, on physical and boundary parameters, skin wetness was considered 6% of total skin surface area as proposed for resting man by Gagge et al.28 In case of greater skin wetness, evaporative heat loss would be greater and consequently shift the TNZ to warmer $T_a$. In contrast, higher relative humidity ($\varphi > 50\%$) would make it harder to evaporate sweat and shift the thermoneutral zone to lower $T_a$. Furthermore, air velocity was set relatively low ($v_{air} = 0.1 \, m/s$). In case of draft or a breeze convective heat loss would increase and shift the TNZ to lower ambient temperatures.

**Conclusion**

This study describes what constellations of body core, skin and ambient temperature satisfy the biophysical requirements of being in the thermoneutral zone for steady-state conditions. Furthermore, by constraining mean skin temperature to a temperature range associated with thermal comfort the thermal comfort zone is derived. The biophysical analysis shows that the steady-state ambient temperature range associated with the thermoneutral zone does not guarantee that the body is in thermal balance at basal metabolic rate per se. Instead, depending on the constellation of core temperature, mean skin temperature and ambient temperature, the body may require significant increases in heat production or heat loss to maintain stable core temperature. Therefore, the definition of the thermoneutral zone requires a revision to include core and skin temperature as well. Furthermore, after adding restrictions on skin temperature for thermal comfort, the ambient temperature range associated with thermal comfort is smaller than the thermoneutral zone. This, assuming animals seek thermal comfort, suggests that thermal behavior may be initiated already before the boundaries of the thermoneutral zone are reached.

**Disclosure of Potential Conflicts of Interest**

No potential conflicts of interest are disclosed

**Acknowledgments**

This work was supported by grants from AgentschapNL (INTEWON: EOSLT10033), TKI Energo and TKI Solar Energy (TEGB|13023).

**Supplemental Materials**

Supplemental Materials may be found here: www.landesbioscience.com/journals/temperature/article/29702

---

**Figure 6.** Steady-state ambient temperature range of the thermal comfort zone for a person dressed in a business suit and heat production at resting metabolic rate. Each band depicts for a given ambient temperature the range of mean skin temperature in which the equation constraints are satisfied for each category, e.g., ‘TNZ body’, ‘SWEAT’, ‘NST’, ‘SH’+NST. The light gray area labeled TNZ body depicts solutions that satisfy that internal body heat transport equals external heat loss and core temperature ranges between $36 \, ^\circ C \leq T_c \leq 38 \, ^\circ C$. Comfortable mean skin temperature is as reported by Gagge et al.15 The dashed lines indicate a more conservative range of comfortable mean skin temperature range as reported by Weiwei et al.16
References

1. IUPS TC. Glossary of terms for thermal physiology. Third edition. Revised by The Commission for Thermal Physiology of the International Union of Physiological Sciences (IUPS Thermal Commission). The Japanese Journal of Physiology 2001; 51:245-80.

2. Romanovsky AA. Thermoregulation: some concepts have changed. Functional architecture of the thermoregulatory system. Am J Physiol Regul Integr Comp Physiol 2007; 292:R37-46; PMID:17008453; http://dx.doi.org/10.1152/ajpregu.00074.2006

3. Schlader ZJ, Simmons SE, Stannard SR, Mündel T. The independent roles of temperature and thermal perception in the control of human thermoregulatory behavior. Physiol Behav 2011; 103:217-24; PMID:2135099; http://dx.doi.org/10.1016/j.physbeh.2011.02.002

4. ASHRAE. Thermal Environmental Conditions for Human Occupancy. ASHRAE standard 55-2004.

5. Frank SM, Raja SN, Bulcao CF, Goldstein DS. The relative overlooking of human thermoregulation for a wide range of environmental conditions: the passive system. J Appl Physiol (1985) 1999; 86:1588-93; PMID:10233122

6. Schlader ZJ. The relative overlooking of human behavioral temperature regulation. Temperature 2014; 1:1-2; http://dx.doi.org/10.4161/emp.29235

7. Burton AC, Edholm OG. Man in a cold environment. London: Edward Arnold (Publishers) LTD., 1955.

8. Veitesteinas A, Ferretti G, Rennie DW. Superficial shell insulation in resting and exercising men in cold water. J Appl Physiol Respir Environ Exerc Physiol 1982; 52:1557-64; PMID:7107465

9. Ducharme MB, Tikuisis P. In vivo thermal conductivity of the human forearm tissues. J Appl Physiol (1985) 1991; 70:2682-90; PMID:185465

10. Fiala D, Lomas KJ, Stohrer M. A computer model of human thermoregulation for a wide range of environmental conditions: the passive system. J Appl Physiol (1985) 1999; 87:1957-72; PMID:10562642

11. Harris JA, Benedict FG. A Biometric Study of Human Basal Metabolism. Proc Natl Acad Sci U S A 1918; 4:370-3; PMID:16576330; http://dx.doi.org/10.1073/pnas.4.12.370

12. Degroot DW, Kenney WL. Impaired defense of core temperature in aged humans during mild cold stress. Am J Physiol Regul Integr Comp Physiol 2007; 292:R103-8; PMID:17197640; http://dx.doi.org/10.1152/ajpregu.00074.2006

13. van Oosjen AM, van Marken Lichtenbelt WD, van Steenhoven AA, Westerterp KR. Cold-induced heat production preceding shivering. Br J Nutr 2005; 93:387-91; PMID:15877879; http://dx.doi.org/10.1079/BJN20041362

14. Tikuisis P. Predicting survival time for cold exposure. Int J Biometeorol 1995; 39:94-102; PMID:8530210; http://dx.doi.org/10.1007/BF00121587

15. Baghe AP, Snijwik JA, Hardy JD. Comfort and thermal sensations and associated physiological responses at various ambient temperatures. Environ Res 1967; 1:1-20; PMID:5614624; http://dx.doi.org/10.1001/0001-9517-90002-3

16. Wever L, Zhiwei L, Qihong D. Use of mean skin temperature in evaluation of individual thermal comfort for a person in a sleeping posture under steady thermal environment. Indoor Built Environ 2014; 0:1-11

17. Johnson JM, Bengelmann GL, Hales JR, Vanhouwe PM, Wenger CB. Regulation of the cutaneous circulation. Fed Proc 1986; 45:2841-50; PMID:3780992

18. Romanovsky AA, Ivanov AI, Shimansky YP. Selected contribution: ambient temperature for experiments in rats: a new method for determining the zone of thermal neutrality. J Appl Physiol (1985) 2002; 92:2667-79; PMID:1205388

19. Hardy JD, Dubois EF. Regulation of Heat Loss from the Human Body. Proc Natl Acad Sci U S A 1937; 23:624-31; PMID:16577831; http://dx.doi.org/10.1073/pnas.23.12.624

20. Speakman JR, Keijer J. Not so hot: Optimal housing temperatures for mice to mimic the thermal environment of humans. Mol Metab 2012; 2:5-9; PMID:24024125; http://dx.doi.org/10.1016/j.molmet.2012.10.002

21. Zhang H, Arena E, Huizenga C, Han T. Thermal sensation and comfort models for non-uniform and transient environments, part III: Whole-body sensation and comfort. Build Environ 2010; 45:399-410; http://dx.doi.org/10.1016/j.buildenv.2009.06.020

22. Schellen L, Loomans MG, de Wit MH, Olesen BW, van Marken Lichtenbelt WD. The influence of local effects on thermal sensation under non-uniform environmental conditions--gender differences in thermophysiology, thermal comfort and productivity during convective and radiant cooling. Physiol Behav 2012; 107:252-61; PMID:22877870; http://dx.doi.org/10.1016/j.physbeh.2012.07.008

23. Artia M. Thermal pleasantness and temperature regulation in man. Neurosci Biobehav Rev 1984; 8:335-42; PMID:6504416; http://dx.doi.org/10.1016/0149-7634(84)90056-3

24. van der Lans AA, Hoeks B, Brans B, Vijgen GH, Visser MG, Vosselman MJ, Hansen J, Jørgensen JA, Wu J, Mortaghy FM, et al. Cold acclimation recruits human brown fat and increases nonshivering thermogenesis. J Clin Invest 2013; 123:3935-403; PMID:23867626; http://dx.doi.org/10.1172/JCI68993

25. Lichtenbelt W, Kingma B, van der Lans A, Schellen L. Cold exposure--an approach to increasing energy expenditure in humans. Trends Endocrinol Metab 2014; 25:165-7; PMID:24462079; http://dx.doi.org/10.1016/j.tem.2014.01.001

26. Fanger PO. Assessment of man’s thermal comfort in practice. Br J Ind Med 1973; 30:313-24; PMID:4584989

27. González-Alonso J, Crandall CG, Johnson JM. The cardiovascular challenge of exercising in the heat. J Physiol 2008; 586:45-53; PMID:17855754; http://dx.doi.org/10.1113/jphysiol.2007.142158

28. Baghe AP. Rational temperature indices of man’s thermal environment and their use with a 2-node thermal comfort and productivity model of his thermal regulation. Fed Proc 1973; 32:1572-82; PMID:4705203