

ENERGY REQUIREMENTS FOR EXISTENCE IN RELATION TO SIZE OF BIRD

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Standard metabolism is the energy requirement, usually measured over short periods, of an individual at complete rest and in a postabsorptive state and is of considerable importance to physiologists. Of greater ecological interest, however, is the energy requirement of normal activities under free-living conditions. This may be approximated (within about 13 per cent in the Blue-winged Teal, *Anas discors*; Owen 1968) by measuring the rate of food utilization over long periods of time of individuals confined in cages.

With caged birds, the caloric value of the excreta (*excretory energy*, including the wastes from both the alimentary tract and kidneys) subtracted from the *gross energy* (intake over a period of days) gives the *metabolized energy*. When the bird maintains a constant weight, the energy metabolized is sufficient just for existence. This *existence energy*, or *existence metabolism*, progressively increases with decrease in ambient temperature to a maximum at the lowest ambient temperature tolerated (Kendeigh 1949; 1969).

Existence metabolism includes the energy expended in standard metabolism, specific dynamic action, and locomotor activity within the cage. Cages vary in size, dependent on the species, to permit approximately the same amount of free movement, e.g., hopping but not flight (Martin 1967). The energy cost of free existence is greater than that of cage existence in proportion to the amount of locomotor activity involved. Existence energy requirements in cages, measured for 18 species weighing from 9 to 4300 g and belonging to three different orders, provide sufficient data to test variation with the size of the bird and to correlate existence metabolism with standard metabolism.

The equations for existence metabolism (M), as a function of temperature (t), are given for the significant ($P < 0.05$) linear regressions in order to be comparable for the various species (table 1). Quadratic, cubic, quartic, or even quintic regressions describe the relationship in some species significantly better than does the linear regression, and such equations are available in the original citations. No zone of

thermal neutrality is demonstrated in existence metabolism for any species, as there frequently is with standard metabolism, although curvilinear regressions often slope more gradually at the higher ambient temperatures.

The a values in the generalized equation $M = a - bt$ represent existence metabolism at 0°C and in some species are significantly, but not proportionately higher in birds under a long rather than a short photoperiod. The b values, representing the slopes of the regression lines or the temperature coefficients, do not differ consistently between the two photoperiods. When existence energy is plotted against species weight separately for the long and short photoperiods, the two regression lines have the same slope and the difference between their elevations is not statistically significant. The means of the two photoperiods have therefore been used to represent all species. Where there are significant differences in existence metabolism between sexes correlated with weight, the data are analyzed separately. The number of data points entering into the regressions is therefore greater than the number of species. Separate regression lines for passerine and non-passerine species at 30°C do not differ in slope but are significantly different in elevation; they do not differ at 0°C and hence the data have been combined to give one regression line at this temperature (fig. 1).

The logarithmic forms of the allometric equations representing the variation at 30°C of existence metabolism as a function of weight are, for passerine species ($N = 15$):

$$\log M = 0.1965 + 0.6210 \log W \pm 0.0633$$

and for non-passerine species ($N = 9$):

$$\log M = -0.2673 + 0.7545 \log W \pm 0.0630$$

when $M = \text{kcal/bird-day}$, $W = \text{weight in grams}$, and the \pm value represents the standard error of the estimate of $\log M$. At 0°C the equation for all species ($N = 24$) is:

$$\log M = 0.6372 + 0.5300 \log W \pm 0.0613.$$

The allometric equations of this and other logarithmic transformations given in the text are shown in figure 1 and tables 1 and 2.

TABLE 1. Equations for the regression of existence metabolism ($M = \text{kcal/bird-day}$) on ambient temperature ($t = ^\circ\text{C}$, below about 35°C).

Species	Weight (g)	Photoperiod		Authority
		10 \pm hr	15-hr	
Passerine				
Yellow-bellied Seedeater, <i>Sporophila nigricollis</i>	9.3	14.21 - 0.262 t^c	17.97 - 0.401 t^c	Cox 1961
Blue-black Grassquit, <i>Volatinia jacarina</i>	9.4	13.88 - 0.259 t^c	16.32 - 0.324 t^c	Cox 1961
Variable Seedeater, <i>Sporophila aurita</i>	10.7	15.99 - 0.282 t^c	18.00 - 0.340 t^c	Cox 1961
Zebra Finch, <i>Taeniopygia castanotis</i>	12.1	18.04 - 0.380 t^c	—	El-Wailly 1966
Field Sparrow, <i>Spizella pusilla</i>	13.2 ♀	14.69 - 0.261 t	16.21 - 0.288 t	Olson 1965
	13.9 ♂	15.59 - 0.285 t	16.64 - 0.295 t	Olson 1965
Common Redpoll, <i>Acanthis flammea</i>	14.0	15.59 - 0.215 t^d	—	Brooks 1968
Hoary Redpoll, <i>Acanthis hornemanni</i>	15.0	15.62 - 0.255 t^d	—	Brooks 1968
Tree Sparrow, <i>Spizella arborea</i>	19.0	18.57 - 0.247 t	22.57 - 0.366 t	West 1960
House Sparrow, <i>Passer domesticus</i>	25.2	24.69 - 0.272 t	25.70 - 0.320 t	Kendeigh 1949; Davis 1955
White-throated Sparrow, <i>Zonotrichia albicollis</i>	27.4	23.05 - 0.38 t	—	Kontogiannis 1968
Dickcissel, <i>Spiza americana</i>	29.6 ♀	24.37 - 0.518 t	29.18 - 0.545 t	Zimmerman 1965
	31.6 ♂	25.90 - 0.537 t	28.54 - 0.517 t	Zimmerman 1965
Green-backed Sparrow, <i>Arremonops conirostris</i>	37.0	29.39 - 0.554 t^c	30.45 - 0.555 t^c	Cox 1961
Evening Grosbeak, <i>Hesperiphona vespertina</i>	54.5	37.24 - 0.612 t^c	—	West and Hart 1966
	57.0	—	40.52 - 0.540 t^f	Williams pers. comm.
Non-passerine				
Blue-winged Teal, <i>Anas discors</i>	309 ♀	106.89 - 1.952 t^c	—	Owen 1968
	363 ♂	116.81 - 2.212 t^c	—	Owen 1968
Japanese Green Pheasant, <i>Phasianus versicolor</i>	800 ♀ ^a	116.77 - 1.831 t^b	160.11 - 2.646 t^c	Moore 1961
	1100 ♂ ^a	172.46 - 2.738 t^b	181.47 - 2.457 t^c	Moore 1961
Ring-necked Pheasant (hybrid), <i>Phasianus colchicus</i>	800 ♀	105.41 - 0.632 t^b	137.31 - 1.971 t^c	Seibert pers. comm.
	1400 ♂	143.01 - 0.567 t^b	162.87 - 2.187 t^c	Seibert pers. comm.
Reeves Pheasant, <i>Syrnaticus reevesii</i>	1000 ♀	131.84 - 1.134 t^b	151.95 - 2.565 t^c	Seibert 1963
	1300 ♂	205.76 - 2.576 t^b	206.34 - 2.484 t	Seibert 1963
Canada Goose, <i>Branta canadensis</i>	4300 ♂	506.58 - 5.392 t	515.54 - 4.574 t	Williams 1965

^a Weights approximate only.^b 9-hour photoperiod.^c 12-hour photoperiod.^d 7-hour photoperiod.^e Varying photoperiod.^f 18-hour photoperiod.^{*} Differences between photoperiods significant.

The slopes of the regression lines for existence energy at 30°C in figure 1 and standard metabolism in the zone of thermal neutrality are not significantly different statistically, but the elevations are. In some species, 30°C may be slightly below the lower critical temperature of the zone of thermal neutrality, but in most species it is well above it. The average increase of existence metabolism at 30°C over standard metabolism is 31 and 26 per cent in passerine and non-passerine species, respectively. The somewhat greater energy cost of cage existence in passerine than in non-passerine species may be a reflection of their greater activity.

The flatter slope of the regression line for existence energy as a function of weight at

0°C than at 30°C indicates that small species within each group are compelled to increase their heat production for body temperature regulation to a greater relative extent than are large species (Kendeigh 1969). The temperature of 0°C is approximately the lower limit of ambient temperature tolerance of many small tropical and migrant passerine species (Cox 1961; Zimmerman 1965; El-Wailly 1966). The relation of metabolic rate to size of animal has long been of interest to physiologists. The "law of surface areas" (Rubner 1883; Richet 1885) maintains that the rate of heat production at the level of standard metabolism in the zone of thermal neutrality is controlled by the rate at which it is lost from the body and hence is proportional, not to body weight

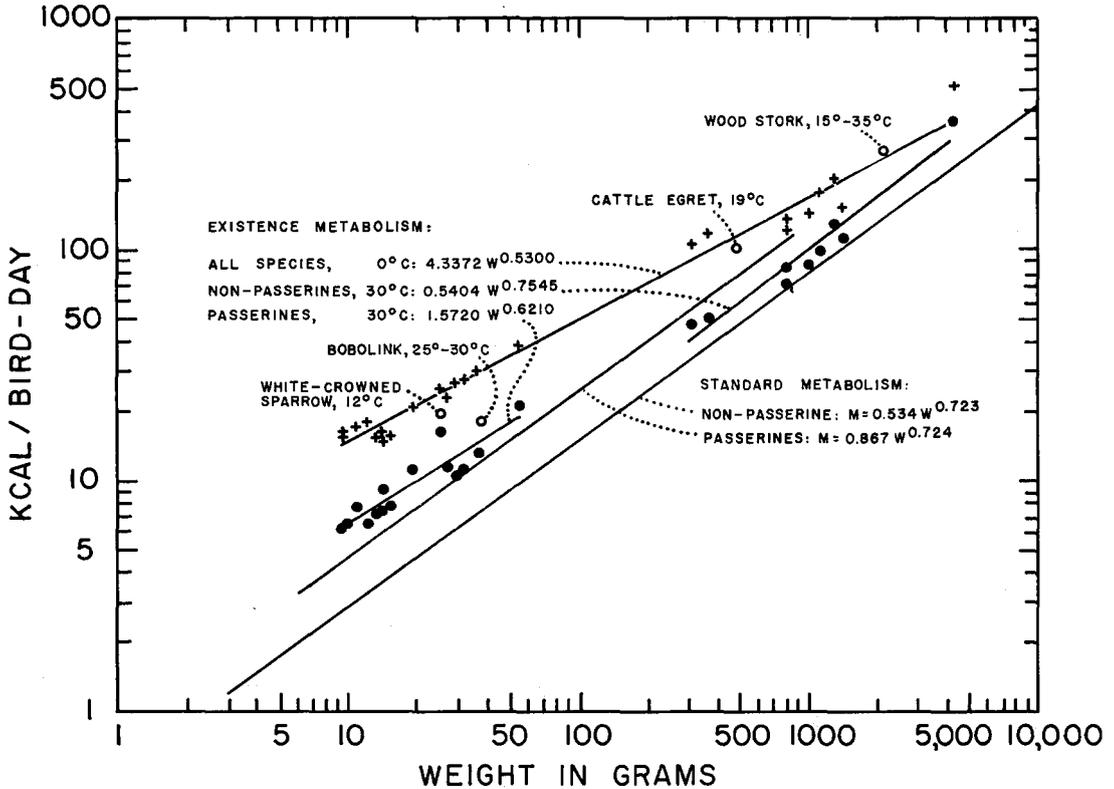


FIGURE 1. Relation of existence metabolism and standard metabolism to weight in birds. The regression lines for existence metabolism are drawn from the logarithmic form (see text) of the allometric equations shown in the figure. The regression lines for standard metabolism are from Lasiewski and Dawson (1967) with the allometric equations expressed for $W = g$ instead of kg. The solid circles and crosses are calculated from the equations given in table 1; the open circles are additional data for other species at particular temperatures as follows: Cattle Egret, *Bubulcus ibis* (Siegfried 1969); Wood Stork, *Mycteria americana* (Kahl 1964); White-crowned Sparrow, *Zonotrichia leucophrys gambelii* (King 1961); and Bobolink, *Dolichonyx oryzivorus* (Gifford and Odum 1965).

($W^{1.0}$), but to the external surface area ($W^{0.667}$). The metabolic rate is relatively greater in small than in large animals because of the greater ratio of surface area, concerned with heat loss, to body mass, concerned with heat production. There is much controversy about this "law," and it is now evident that factors other than external surface area may be involved, such as internal surfaces for absorption of food and oxygen in digestive and respiratory tracts, rate of oxygen transport in the blood, concentration of cellular enzymes and mitochondria, and proportion of body organs with high energy requirements to the total body mass (Kleiber 1961). Several of these factors, however, may be adaptations or adjustments for maintaining different rates of metabolism rather than a direct cause of the rates themselves.

In view of these criticisms, any relation between external surface area, rate of heat loss, and rate of heat production is of special

interest. Although the body is covered with feathers, the insulative properties of this coat of feathers may vary in birds of different sizes. Heating engineers have long known that a given thickness of insulative material is less effective in protecting small as compared with large steam pipes. Dilla et al. (1949), in studying the science of clothing, derived the following equation for the insulative value of fabrics on spheres of different sizes:

$$I = \frac{r}{K} \times \frac{x}{r+x}$$

where I = insulation index ($^{\circ}\text{C}/\text{cal-sec-cm}^2$), r = radius of the sphere, x = thickness of the insulation, and K = conductivity of the fabric.

Assuming that the body of a bird approaches a sphere, that the conductivity of feathers is a constant so that K is removed from the equation, and that the specific gravity of birds is 1, then the insulation index of a 100-g bird with a plumage thickness of 1.0 cm is 0.74. The

TABLE 2. Comparison of thermal conductance and plumage in passerine species of different size.

Weight (g)	10	25	50	100	500
Surface area (cm ²)	46	86	136	215	630
10 W ^{0.667}					
Thermal conductance					
kcal/bird-hr-°C (× 10 ⁻²)	1.26	1.98	2.80	3.90	8.50
kcal/g-hr-°C (× 10 ⁻³)	1.26	0.79	0.56	0.39	0.17
4.07 W ^{-0.508} a b					
kcal/cm ² -hr-°C (× 10 ⁻⁴)	2.74	2.30	2.06	1.81	1.35
Number of feathers					
No./bird	1418	1672	1896	2147	2868
937 W ^{0.178} b					
No./g	142	67	38	21	6
No./cm ²	31	19	14	10	4.6
Weight of plumage					
g/bird	0.6	1.5	2.9	5.6	26.3
0.068 W ^{0.959} b					
mg/g	62	60	58	56	53
mg/cm ²	13	17	21	26	42

^a Adapted from Lasiewski et al. (1967) using 1 cm² O₂ = 4.8 gcal.

^b Log-log transformations of these allometric equations are available in the text.

same thickness of plumage on a 10-g bird would give an insulation index of only 0.57. For the 10-g bird to have the same insulation index as the 100-g bird, the plumage would need to have a thickness of 1.65 cm. Obviously this does not occur; large birds have a thicker plumage than smaller birds, although few actual measurements have been made.

Scholander et al. (1950) have shown by direct measurement that heat transmission through mammalian fur decreases, and therefore its insulation value increases, proportional to its thickness, at least up to a certain maximum. Probably the same relation holds with bird plumages. In order to determine the relation of heat flow to the size of the bird and to the characteristics of the plumage, consideration will be given to "thermal conductance" and the density and mass of the feathers.

Thermal conductance is commonly calculated by dividing the rate of standard metabolism by the difference between core and ambient temperatures and is usually minimal at or below the lower critical temperature of the zone of thermal neutrality. This is a general term, as heat is transferred from the core of the body to the skin and the surface of the plumage partly by conduction and partly by blood flow and is then lost to the surroundings by conduction, convection, evaporative cooling, and radiation. Evaporative cooling, principally through the mouth and respiratory system, is most important at high ambient temperatures; radiation generally is most important at medium and low temperatures.

Lasiewski et al. (1967) have calculated a regression equation for thermal conductance, based on data for 35 passerine and non-

passerine species, which in a modified form is

$$\log C = 1.6096 - 0.508 \log W$$

where C is kcal/gram-hour-°C and W is weight in grams. A very similar equation is given by Herreid and Kessel (1967). An analysis of the data for 18 non-passerine and 17 passerine species presented by Lasiewski et al. (1967) indicates that regression lines for thermal conductance as a function of species weight for these two groups are not significantly different.

Regression equations for number and weight of feathers, as functions of body weight, have been calculated from data given by Wetmore (1936) for 62 passerine species. Number of feathers (F_n = number per bird) varies as

$$\log F_n = 2.9718 + 0.1779 \log W \pm 0.0496.$$

Weight of feathers (F_w = g per bird) varies as

$$\log F_w = -1.1677 + 0.9591 \log W \pm 0.0956.$$

The slope (0.9591) is not statistically different from 1.0 and the equation is very similar to the one given by Turcek (1966). Palmgren (1944) and Brody (1945) have also shown the almost direct relation of weight of feathers to weight of birds.

The total heat flow from the bird to the environment is, of course, greater in large than in small birds (table 2) but of greater significance is that, per unit weight or surface area, it varies inversely with size. Insulation is the reciprocal of thermal conductance, and hence is poorer in small than in large species, in agreement with engineering concepts.

Hutt and Hall (1938) noted some years ago that the number of feathers per gram or square centimeter increases with a decrease in the size

of the bird, as shown in table 2. This would seem to give small birds better insulation than large birds. However, weight is probably a better index of the insulative properties of the plumage since weight integrates number, length, size, and specific gravity of the feathers and bears some relation to the thickness of the plumage. The weight of the plumage per unit surface area is less in small than in large species, which is in agreement with the greater thermal conductance and poorer insulation of small species.

This discussion should indicate that the relative size of the external surface is a factor affecting the rate of metabolism but in a more complex manner than envisaged by the early physiologists. It is not simply that smaller birds have a greater surface area for radiating heat in proportion to body mass for heat production, but that smaller birds, because of their size, are incapable of carrying as good insulation in the form of heavy plumage.

The equations for existence metabolism presented here should prove useful in predicting values for other species where direct measurements are not convenient or practicable. Why the relation between existence metabolism, as well as standard metabolism, and weight should differ between passerine and non-passerine species at high ambient temperatures is not clear. There appears to be no difference between the two groups in thermal conductance, hence in the insulative characteristics of their plumages. The higher rate of metabolism in passerine species is, however, related to the generally higher body temperatures found in passerine species (Wetmore 1921). In a recent compilation, to be published elsewhere, median core or body temperatures of birds at rest range from 37.1° to 41.4°C in 16 non-passerine orders, including 138 species. The median core temperature of 49 species of Passeriformes is 42.0°C. However, the higher body temperatures of passerine species is probably the result, and not the cause, of their higher metabolism. The cause of the higher rate of metabolism in Passeriformes must be sought elsewhere.

SUMMARY

Energy requirements for existence of birds maintaining constant weight in cages have been calculated as the difference between gross energy intake as food and energy loss in excreta. Equations are presented for the relationship of existence metabolism to temperature for each of 18 species, and for the variation of existence metabolism of all species as a function of weight at 30° and at 0°C. The

cost of cage existence is calculated as the difference in existence metabolism at 30°C and standard metabolism in the zone of thermal neutrality, and is equivalent to 31 and 26 per cent of standard metabolism in passerine and non-passerine species, respectively. The relatively higher rates of metabolism and greater sensitivity to cold in small species are related to their less effective feather insulation.

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LITERATURE CITED

- BRODY, S. 1945. Bioenergetics and growth. Reinhold Pub. Co., New York.
- BROOKS, W. S. 1968. Comparative adaptations of the Alaskan Redpolls to the Arctic environment. *Wilson Bull.* 80:253-280.
- COX, G. W. 1961. The relation of energy requirements of tropical finches to distribution and migration. *Ecology* 42:253-266.
- DAVIS, E. A., JR. 1955. Seasonal changes in the energy balance of the English Sparrow. *Auk* 72:385-411.
- DILLA, M. VAN, R. DAY, AND P. A. SIPLE. 1949. Special problem of hands. p. 374-388. In L. M. Newburgh [ed.] *Physiology of heat regulation and the science of clothing*. W. B. Saunders, Philadelphia.
- EL-WAILLY, A. J. 1966. Energy requirements for egg-laying and incubation in the Zebra Finch, *Taeniopygia castanotis*. *Condor* 68:582-594.
- GIFFORD, C. E., AND E. P. ODUM. 1965. Bioenergetics of lipid deposition in the Bobolink, a trans-equatorial migrant. *Condor* 67:383-403.
- HERREID, CLYDE F. II, AND B. KESSEL. 1967. Thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* 21:405-414.
- HUTT, F. B., AND L. HALL. 1938. Number of feathers and body size in passerine birds. *Auk* 55:651-657.
- KAHL, M. P., JR. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecol. Monogr.* 34:97-117.
- KENDEIGH, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. *Auk* 66:113-127.
- KENDEIGH, S. C. 1969. Tolerance to cold and Bergmann's Rule. *Auk* 86:13-25.
- KENDEIGH, S. C. 1969. Energy responses of birds to their thermal environments. *Wilson Bull.* 81: In press.
- KING, J. R. 1961. On the regulation of vernal pre-migratory fattening in the White-crowned Sparrow. *Physiol. Zool.* 34:145-157.
- KLEIBER, M. 1961. *The fire of life*. John Wiley and Sons, New York.
- KONTOGIANNIS, J. E. 1968. Effect of temperature and exercise on energy intake and body weight of the White-throated Sparrow, *Zonotrichia albicollis*. *Physiol. Zool.* 41:54-64.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the Giant Hummingbird, *Patagona gigas*. *Comp. Biochem. Physiol.* 23:797-813.

- MARTIN, E. W. 1967. An improved cage design for experimentation with passeriform birds. *Wilson Bull.* 79:335-338.
- MOORE, DAVID J. 1961. Studies in the energy balance of the Versicolor Pheasant. M. S. thesis. Ohio University, Athens, Ohio.
- OLSON, J. B. 1965. Effect of temperature and season on the bioenergetics of the Eastern Field Sparrow, *Spizella pusilla pusilla*. Ph.D. thesis, University of Illinois.
- OWEN, R. B., JR. 1968. Energy requirements of Blue-winged Teal under free-living and captive conditions. Ph.D. thesis, University of Illinois.
- PALMGREN, P. 1944. Körpertemperatur und Wärmeschutz bei einigen finnischen Vögeln. *Ornis Fennica* 21:99-104.
- RICHET, C. 1885. Recherches de calorimetrie. *Arch. de Physiol.*, 3rd Ser., 6:237-291, 450-497.
- RUBNER, M. 1883. Ueber den Einfluss der Körpergröße auf Stoff- und Kraftwechsel. *Zeit. Biol.* 19: 535-562.
- SCHOLANDER, P. F., V. WALTERS, R. HOCK, AND L. IRVING. 1950. Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.* 99: 225-271.
- SEIBERT, H. C. 1963. Metabolizable energy in the Reeves Pheasant. *Game Res. Ohio* 2:185-200.
- SIEGFRIED, W. R. 1969. Energy metabolism of the Cattle Egret. *Zoologica Africana* 4:265-273.
- TURCEK, F. J. 1966. On plumage quantity in birds. *Ekol. Polska, Ser. A*, 14 (32):617-634.
- WEST, G. C. 1960. Seasonal variation in the energy balance of the Tree Sparrow in relation to migration. *Auk* 77:306-329.
- WEST, G. C., AND J. S. HART. 1966. Metabolic responses of Evening Grosbeaks to constant and to fluctuating temperatures. *Physiol. Zool.* 39:171-184.
- WETMORE, A. 1921. A study of the body temperature of birds. *Smithsonian Misc. Coll.* 72 (12): 1-52.
- WETMORE, A. 1936. The number of contour feathers in passeriform and related birds. *Auk* 53:159-169.
- WILLIAMS, J. E. 1965. Energy requirements of the Canada Goose in relation to distribution and migration. Ph.D. thesis, University of Illinois.
- ZIMMERMAN, J. L. 1965. Bioenergetics of the Dickcissel, *Spiza americana*. *Physiol. Zool.* 38:370-389.

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