INFLUENCE OF CHRONIC ACCELERATION UPON GROWTH AND BODY COMPOSITION*

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An important aspect of body composition is size—usually indicated in terms of weight, or one of its derivatives. Under natural conditions, increasing weight represents increased mass—resulting from development in immature animals or fattening in mature animals. However, weight also may be changed artificially through alterations in the ambient accelerative force, which is equivalent, physiologically, to a change in gravity†. After prolonged exposure to a different accelerative force, changes in growth and body composition may be anticipated as a result of changes in work requirements for tonus, locomotion, *etc.*, as well as more specific effects on individual organs.

In the past, investigations of the physiological effects of chronic acceleration would have been purely academic interest. However, with the coming of astronautics, prolonged exposure of man to a variety of accelerative forces may be anticipated—ranging from the weightlessness of space and artificial satellites, through the subgravity of smaller bodies (Moon, 0.17*G*; Mars, 0.38*G*)‡, to the supergravities of the larger planets (Neptune, 1.53*G*; Jupiter 2.65*G*). Since practically all biological research has been conducted at normal gravity (except for some studies of interest to aviation medicine, in which accelerative forces are applied for relatively brief periods), there is no significant background information in the area of chronic acceleration. Currently, at least five programs investigating the biological effects of chronic acceleration are in progress: at Cambridge University[3] and the London Hospital Medical College[4] in England; and at the University of Iowa,[5-10] Emory University,[11,12] and the University of California at Davis.[13-19] All of these programs utilize accelerative forces produced by cen-

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† According to Einstein's principle of equivalence, the effects of accelerative forces are indistinguishable, irrespective of their physical bases. A description of the phenomenon of gravity, and a comparison with centrifugal force is available,[1] as well as a discussion of the characteristics of the earth's gravity.[2]

‡ The symbol "*G*" denotes the strength of an accelerative force as multiples of the earth's gravitation (the latter designated as "*g*"). Unfortunately, "*G*" also represents the gravitational constant in the (Newton's) law of gravitation. A better symbolic notation for accelerative forces would be $W{:}M$ (*i.e.*, "weight to mass ratio"), however, this becomes cumbersome, especially conversationally. Moreover, this use of "*G*" has become conventional, and is readily understood, even by the general public. The term "gravitation" indicates specifically a property of matter (whereas "gravity," the ambient force, may also include centrifugal forces), and it is improper to use it to describe accelerative forces produced by motion.

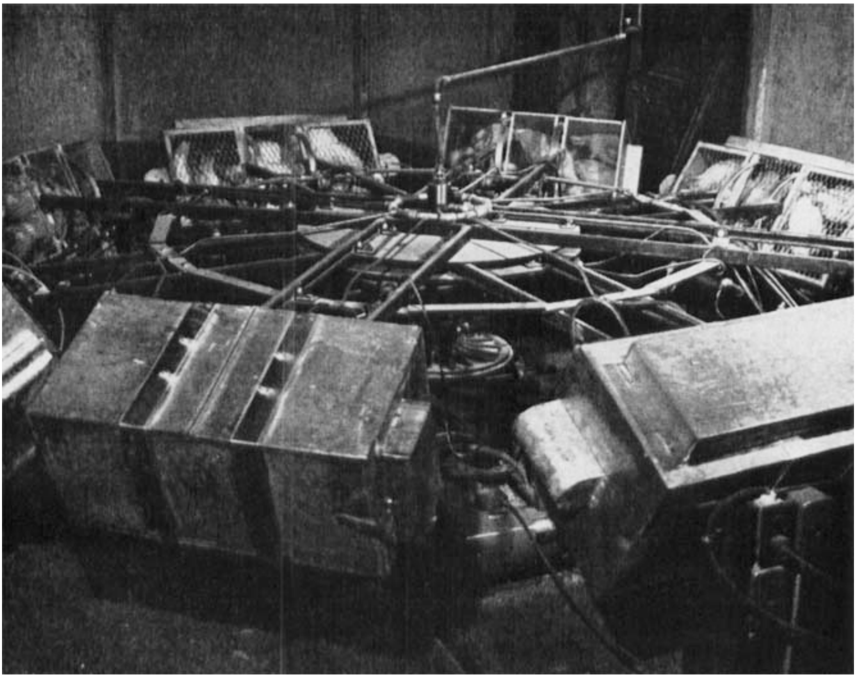

FIGURE 1. The animal centrifuge at Davis. The apparatus as shown here is operating at 1.5G. The cages are hinged, so that the accelerative force (the resultant of centrifugal force and gravity) is perpendicular to its floor. A detailed description of the structure and functional characteristics of this machine is available elsewhere.[14]

trifugation (a picture of our instrument is presented in FIGURE 1). Linear accelerations are necessarily restricted to relatively short periods—since an object accelerated linearly at 2.5G would go into orbit in 5.8 minutes, and escape the earth's gravity in 8.4 minutes.

Acceleration Biology

The effect of an accelerative force upon a restrained body (*i.e.*, one not moving under the influence of the force) is the phenomenon of weight: $w = m \times a$. The biological effects of changes in the weight:mass ratio can be divided into two categories: (1) whole animal effects, which are nonspecific and related to exercise; and (2) local or tissue effects, which are specific and result from changes in the "apparent density."* For ex-

* There is no specific term describing weight/volume (density = mass/volume, which is not affected by the ambient accelerative force). Consequently, one must use such complex terms as "apparent density" (since density usually is determined as weight/volume), or "weight density" to describe this parameter. The lack of a specific term for "w/v" is perhaps indicative of the general neglect of acceleration phenomena in biology. Undoubtedly there will be much need for such a term in the future since it is weight rather than mass, which largely determines the mechanical work done by a biological system.

ample, at 5G, the heart must handle a fluid with the normal apparent density of iron, thus specifically increasing the work done. Similar increased work requirements are placed on the gut and other organs with fluid contents.

The physiological effects of acute exposure (of seconds to minutes duration) have become well known, and several recent summaries are available.[20-22] Such exposure is most effective on the circulatory system, as a result of increased hydrostatic pressures in the vascular columns. For example, mean blood pressures in a seated man at normal gravity are: head, 70 mm. Hg; and foot, 140 mm. Hg. When subjected to an accelerative force of 3G (in a head to foot direction), the mean blood pressures become: head, 10 mm. Hg; and foot, 220 mm. Hg. The resulting diminished circulation to the brain leads rather rapidly to unconsciousness (the retina is most sensitive—due to the effect of the intra-ocular pressure—and "blackout" precedes unconsciousness). Resistance to acute acceleration is dependent upon physical accomodation, principally involving vasomotor mechanisms.

Chronic acceleration (of weeks to months duration) permits a great many more slowly induced changes (*e.g.*, metabolic, anatomic, *etc.*) to take place. If acute acceleration is considered as a biological stress, then

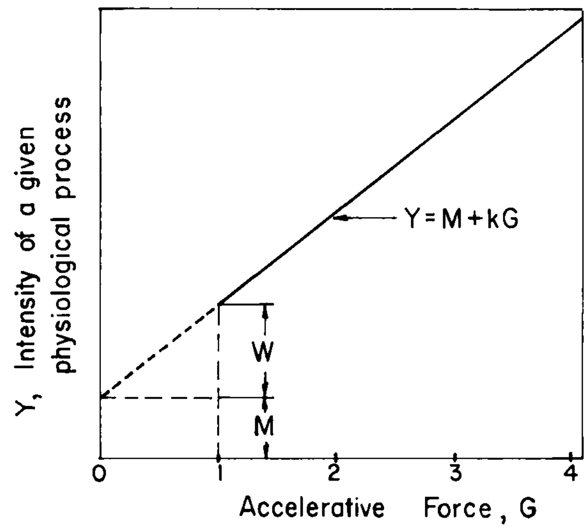

FIGURE 2. An example of mathematical relationships between intensity of physiological function and ambient accelerative force. When the physiological observations are plotted against corresponding accelerative forces, an equation may be derived in which the coefficient k relates these two parameters. When the equation is extrapolated to "Zero G," the invariant component (*i.e.*, that which mass-dependent, "M") is determined. Variatons in the intensity of the process at different accelerative forces are due to changes in the weight-dependent component, "W."

the chronically exposed animal represents a physiological adaptation to it.

The interpretation of the results of chronic acceleration experiments are of general interest. There are some indications that the physiological effects of subgravity, gravity and supergravity exposure present a continuous series, dependent only upon the ambient accelerative force.[23] Consequently, if the intensity of a physiological process (or size of an anatomic entity, including chemical composition) is determined for several accelerative forces, the "accelerative force–functional intensity" relationship can be described mathematically (FIGURE 2). The nature of this relationship would not necessarily be rectilinear—more complex relationships (for example: $Y = Me^{kG}$; or $Y = M + G^k$) are equally possible and resolvable. By such treatment of functional changes observed at increased accelerative forces in the neighborhood of normal gravity, physiological processes (or anatomic phenomena) can be resolved into two components: one, W, which is determined by weight; and the other, M, which is dependent only on mass, and is unaffected by the ambient accelerative force. Implicit in such an analysis is a prediction of the physiological and anatomic consequences of weightlessness. Without weight, processes would proceed at the intensity "M," and deviation from this principle would occur only if different control mechanisms exist above and below the acceleration of the earth's gravity. Since the ambient accelerative force, *i.e.*, the earth's gravity, has remained constant over the past thirty million years in which modern animals have evolved, it is difficult to conceive of the development of special controls for subgravity situations. Such predictions of the effects of weightlessness would have to be validated by actual satellite studies. However, initially such predictions should be of value in identifying potentially limiting biological factors in space travel. Later the supergravity observations would be of considerable value, as a "third point" (*i.e.*, in addition to weightless and normal gravity data) in interpreting satellite studies.

Effect of Chronic Acceleration upon Growth

One of the most consistently reported effects of chronic acceleration is a repression of growth.[4,6,10,11,12,16] In at least some cases, the rate of development—as indicated by the age of sexual maturation—also is slowed.[16] This effect is dependent on the intensity of the field, and perhaps other things: age, size, species, *etc.*

The results of our growth observations on chronic acceleration experiments have been variable and some of this undoubtedly is due to differences in acceleration schedules, animal characteristics, *etc.* Consequently, it has not been possible to reduce our growth data to a simple methematical statement. Several examples of growth rates (as a per cent difference in mass between centrifuged and control birds) are presented in FIGURES 3 and 4. In most cases the growth repression is marked, but where the accelerative force is quite low (*e.g.*, 1.5G), an enhanced growth appears to follow physiological adaptation (see trial N, FIGURE 3). A similar observa-

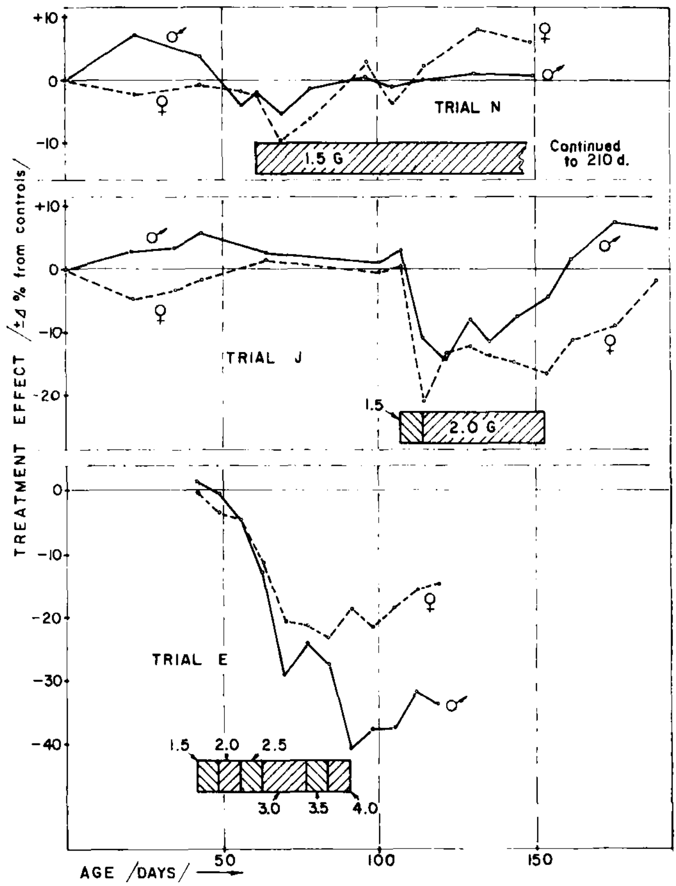

FIGURE 3. Repression of growth by chronic acceleration. Body masses of centrifuged White Leghorn Chickens (as per cent of difference from controls) are shown for several chronic acceleration experiments. Growth repression is enhanced by increased field strength. Other species (turkeys and New Hampshire chickens, which are much larger than Leghorns) are more susceptible to the effects of chronic acceleration. Older birds are generally more affected than younger ones by increases in the ambient accelerative force.

tion has been made with mice.[10] With long-term exposure to accelerative force, the growth effects appear to take place in stages (FIGURE 4).

The effect of chronic acceleration upon growth is quite likely not a matter of simple inanition or feed restriction at moderate field strengths (*i.e.*, less than 3G for chickens). Under these conditions, direct visual observation indicates that the birds' activities are normal—and there is no special tendency to seek feed and water when the centrifuge is momentarily stopped. At low intensity fields (1.5G), there is a marked drop in feed intake (—60 to —80 per cent) when the birds are returned to normal gravity, after several months exposure to acceleration (FIGURE 5).

At higher field strengths, or prior to physiological adaptation, the birds' movements appear to be restricted—and sometimes they are more or less immobilized. Under such circumstances feed and water deprivation may be a factor in response to chronic acceleration—but certainly not the only one. Where birds become sick from the treatment, death occurs in a few hours or days. However, acceleration-adapted birds deprived of feed and water survive 6.3 ± 0.4 days at 3G (similarly treated controls survive 12.8 ± 0.4 days at normal gravity).

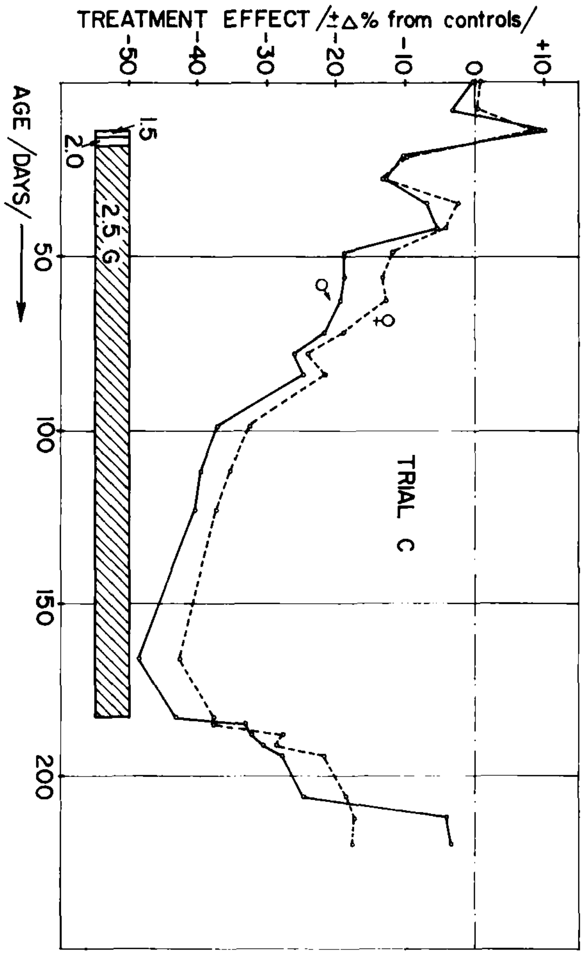

FIGURE 4. Effect of long-term centrifugation on body size. The body masses of White Leghorn—New Hampshire hybrid chickens are compared (as per cent difference) with those of controls during long-term centrifugation. The effect on growth appears to take place in stages. A steady-state, perhaps representing a more-or-less complete physiological adaptation, is obtained after 100 days centrifugation.

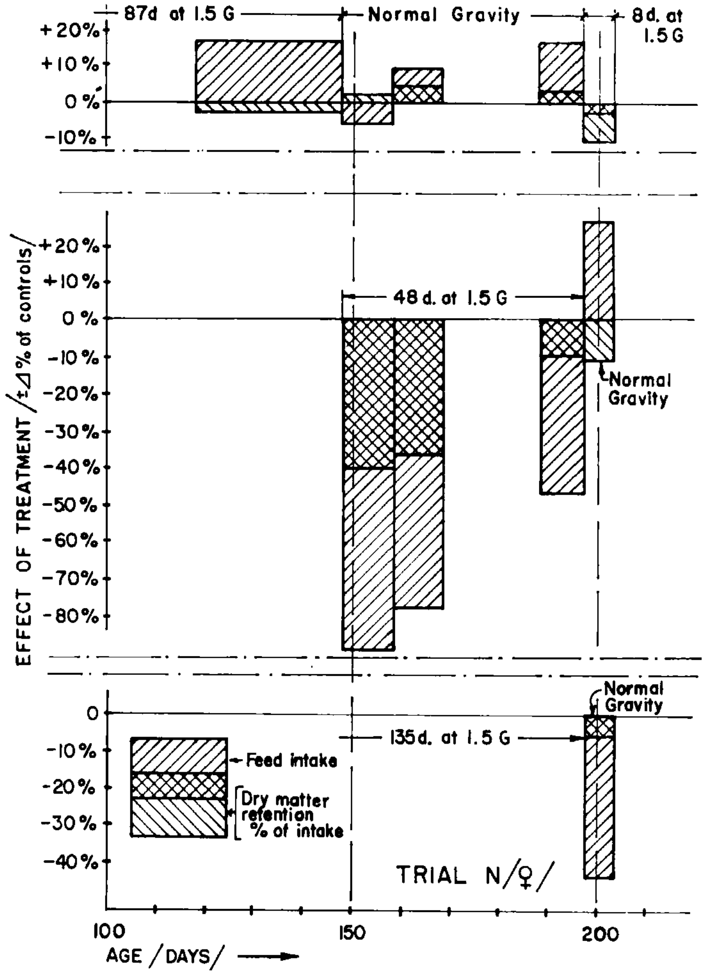

FIGURE 5. Changes in nutritional function accompanying moderate changes in the ambient accelerative force. Feed intake, and generally the relative retention of ingested dry matter are decreased by changes (±) in the ambient accelerative force. In birds adapted to 1.5G, the feed intake is increased about 15 per cent. If a rectilinear relation with accelerative force is asumed, this would indicate that about 70 per cent of the feed intake is determined by factors independent of weight.

Anatomic Effects of Chronic Acceleration

In several of our experiments, quantitative anatomic observations have been carried out—usually with the collaboration of the Department of Anatomy on this campus. The results of these experiments have been variable, and this may arise from difference in acceleration schedules and the relatively few numbers of birds involved. There are indications of

TABLE 1

QUANTITATIVE ANATOMY

	Females			Males		
	Centrifuged (x)	Control (c)	Treatment effect ($\pm \Delta$ %)	Centrifuged (x)	Control (c)	Treatment effect ($\pm \Delta$ %)
(No. of birds)	(6)	(6)		(6)	(6)	
Body mass (gm.)	711 ± 11	975 ± 28	−27.1%†	940 ± 38	1325 ± 27	−29.0%†
Shed blood	3.0 ± 0.3	2.6 ± 0.3	+15.4%	3.9 ± 0.2	3.3 ± 0.2	+18.2%
Head	3.4 ± 0.1	2.9 ± 0.1	+17.2%†	3.7 ± 0.1	4.7 ± 0.4	−21.3%*
Shanks	4.9 ± 0.1	3.5 ± 0.1	+40.0%†	5.8 ± 0.2	4.0 ± 0.1	+45.0%†
Skin (& feathers)	14.2 ± 0.4	20.0 ± 0.6	−29.0%†	11.9 ± 0.2	11.0 ± 0.8	+ 8.2%
Carcass	66.6 ± 2.2	66.7 ± 0.9	− 1.5%	69.6 ± 0.5	67.5 ± 0.5	+ 3.1%*
Carcass components:						
g-i tract	7.6 ± 0.3	7.4 ± 0.8	+ 2.7%	7.4 ± 0.2	5.8 ± 0.2	+27.6%†
Abdominal viscera	4.7 ± 0.4	4.2 ± 0.3	+11.3%	5.2 ± 0.5	4.8 ± 0.1	+ 8.4%
Soft tissue	39.8 ± 0.7	41.0 ± 1.2	− 2.9%	39.1 ± 0.5	41.3 ± 0.8	− 5.8%*
Skeleton	17.1 ± 0.3	14.0 ± 0.7	+22.1%†	17.9 ± 0.5	15.6 ± 0.2	+14.7%†
femur: % body wt.	0.42 ± 0.01	0.39 ± 0.01	+ 7.7%†	0.48 ± 0.02	0.44 ± 0.01	+ 9.1%
femur: % carcass bone	6.5 ± 0.5	5.9 ± 0.1	+10.2%	6.0 ± 0.01	5.9 ± 0.01	+ 1.7%
femur: length/width	9.4 ± 0.1	9.9 ± 0.1	− 5.1%*	8.3 ± 0.2	9.1 ± 0.3	− 8.8%
humerus: % body wt.	0.26 ± 0.01	0.22 ± 0.01	+18.2%*	0.28 ± 0.01	0.26 ± 0.01	+ 7.7%
humerus: % carcass bone	4.0 ± 0.2	3.2 ± 0.2	+25.0%†	4.3 ± 0.5	3.5 ± 0.1	+22.8%†
humerus: length/width	9.7 ± 0.2	10.1 ± 0.1	− 4.0%	9.7 ± 0.2	9.6 ± 0.3	+ 1.0%

Relative sizes of organs (as gm. per 100 gm. body mass) are summarized as the mean and its standard error for centrifuged (x) and control (c) groups. Treatment effects are calculated as the per cent difference between centrifuged and control birds: Treatment effect $= [(x-c)/c] \times 100$. These birds (from trial P) were 112 days of age and had been exposed to 1.5–3G for 75 days.

* Significant at the 5 per cent level.

† Significant at the 1 per cent level.

several types of reaction to chronic acceleration—at least as far as pathological changes are concerned—and these may be reflected in anatomic change. When the sample is small (*e.g.*, 5–20 birds) it is possible that one or another of such reaction-types may predominate. At our present level of understanding, we cannot differentiate between reaction-types in adapted birds—should they exist.

1. Major body parts. In one experiment (*P*), the more difficult parts of the body to dissect were removed: head (at the atlas); skin with feathers; blood which is readily shed through the severed neck immediately post-mortem; and the shanks (comprising the foot and nonmuscular portion of the leg, and which is homologous with the human foot). The remaining carcass approximates the edible portion of the bird. The effects of chronic acceleration on the relative sizes of these major body parts are presented in TABLE 1.

A significant and consistent (between sexes) change is noted only for relative shank mass, which increases about 40 per cent. The obvious interpretation that this is an adaptation to increased mechanical stress on the leg is not borne out by changes in individual bones: the humerus (which is a wing bone and consequently "nonloadbearing") increases in size (relative to carcass skeleton) more than does the femur—a major leg bone. The rather small increase in shank water content (TABLE 3) indicate that edema is not important in their increased size.

The decreases in relative head size in centrifuged males may represent a repression of comb and wattle development. At the time of sacrifice, these birds were approaching sexual maturity, which is accompanied by a marked increase in size of these cutaneous structures in males, and only to a much lesser extent in females.

2. Carcass anatomy. The carcass can be divided into: gastro-intestinal tract (intestines, gizzard, *etc.*); other abdominal viscera (heart, liver, lungs, *etc.*); soft tissue (including muscle, and other material which could be separated mechanically from the bones); and carcass skeleton. The principal changes noted in centrifuged birds were increases in the carcass skeleton and abdominal viscera; and decreases in "soft tissue" (TABLE 1).

When the individual organs are measured, there is observed generally an increase in size for all but the spleen and heart. Such changes (except for a decrease in the size of the g-i tract) have been reported by others[24] in birds which have been kept on a low plane of nutrition. However, as indicated earlier, it is not considered likely that the effects of centrifugation are merely a matter of feed restriction.

In many experiments, relative, as well as absolute, decreases in heart size have been observed frequently. It is possible that this may result from the special anatomy of the bird, in which the heart lies against the rather broad sternum, and is partly covered by the liver. When birds are subjected to long-term centrifugation, there is a tendency for a cavity to de-

TABLE 2

EFFECT OF CHRONIC ACCELERATION AND FEED RESTRICTION ON MUSCLE AND BONE SIZES

	Females			Males		
	x	c'	c	x	c'	c
(number of birds)	(15)	(15)	(18)	(10)	(15)	(20)
Body mass (kg.)	1.16 ± 0.03	1.25 ± 0.03	1.51 ± 0.04	1.45 ± 0.05	1.48 ± 0.03	1.87 ± 0.03
Leg muscle (% b.w.)	7.8 ± 0.2	6.2 ± 0.1	7.0 ± 0.01	8.4 ± 0.2	8.5 ± 0.4	9.3 ± 0.2
Leg bone/leg muscle	0.29 ± 0.01	0.31 ± 0.01	0.21 ± 0.01	0.29 ± 0.01	0.29 ± 0.01	0.20 ± 0.01
Pectoral muscle/leg muscle	0.55 ± 0.01	0.55 ± 0.02	0.49 ± 0.02	0.44 ± 0.03	0.44 ± 0.02	0.39 ± 0.01

Data are presented for centrifuged (x), feed restricted (c') and normal control (c) groups as means and standard errors. These birds from trial L) were 207 days of age, and had been exposed to 1.5–3.0G for 180 days.

velop in the sternum, and this is occupied by the heart. In rats, exercise leads to a 16 per cent increase in relative heart size.[25]

The development of muscle, particularly in the leg, has been of interest because of the obvious exercise aspects of chronic acceleration. The leg mass from the hock to hip is a large tissue, well defined and readily separated, and consists essentially of rather lean muscle and bone. The relative leg muscle mass has been measured several times, but the results have been variable. The differences indicated in TABLE 2, where increases are evident for females, but not for males, is just as frequently reversed. The relative amounts of bone and muscle in the leg rather consistently show increases in the bone/muscle ratio for centrifuged birds. The ratio pectoral muscle/leg muscle also is usually greater in centrifuged birds. However, these ratios between muscles and bone may be a result of the smaller size of centrifuged animals. In one experiment, an additional set of controls was maintained at about the same size as the centrifuged birds by means of feed restriction. When these are compared with the centrifuged birds (TABLE 2) few differences remain. This is somewhat different from the situation reported for exercised and feed restricted rats,[26] in which relative organ size, as well as body composition, was most similar between exercised and sedentary control animals.

Effects of Chronic Acceleration on Body Composition

The concentration of dry matter and fat in tissues of some centrifuged and control birds is presented in TABLE 3. Centrifuged birds have less dry matter than do controls—and this difference applies generally to all organs and tissues with exceptions noted for blood and for the head. Centrifuged birds generally have higher hematocrits, which would account for the greater dry matter content of the blood. The basis for the lesser hydration of heads from centrifuged birds is not readily explained—perhaps this may be involved with a lesser vascularity in the comb and wattles.

The concentration of fat in the viscera and other soft tissues of the carcass is markedly decreased in centrifuged birds. This difference was more evident (and subject to greater variation) in the soft carcass tissues than in the viscera, and also was more pronounced (and variable) in females. The greater variability of fat content in females may arise from differences in degree of sexual maturity, since the estrogens produced at that time greatly affect fattening. Centrifuged animals, in which attainment of sexual maturity is delayed, would be more uniform in degree of fattening. These differences in fattening are even more evident in the composition of the entire carcass, which is presented in TABLE 4.

Conclusions

From work done at our laboratory and at others it appears that a great amount of useful information can be obtained from studies involving

TABLE 3

COMPOSITION OF TISSUES

	Females				Males			
	Centrifuged		Control		Centrifuged		Control	
	dry matter (%)	fat (%)	dry matter (%)	fat (%)	dry matter (%)	fat (%)	dry matter (%)	fat (%)
Whole body	32.7 ± 1.8		39.3 ± 1.9		32.4 ± 0.4		37.6 ± 1.3	
Shed blood	17.2 ± 0.3		16.1 ± 0.3		19.5 ± 0.8		17.0 ± 0.7	
Head	29.2 ± 1.0		29.1 ± 0.8		28.1 ± 0.5		24.6 ± 1.0	
Shanks	44.4 ± 1.2		46.4 ± 1.3		43.4 ± 0.9		47.9 ± 1.6	
Skin (and feathers)	49.3 ± 2.0		53.5 ± 2.1		49.8 ± 1.1		55.0 ± 1.1	
Viscera	24.2 ± 0.5	3.14 ± 0.41	31.6 ± 2.9	13.76 ± 3.45	24.1 ± 0.4	2.56 ± 0.34	27.0 ± 0.6	7.73 ± 0.60
Soft tissue	24.5 ± 0.5	1.95 ± 0.36	32.6 ± 2.7	12.12 ± 3.34	24.5 ± 0.3	2.25 ± 0.68	30.3 ± 1.5	8.80 ± 1.81
Bones	43.5 ± 0.6		48.0 ± 1.1		44.4 ± 0.7		48.3 ± 1.4	

Treatment effect (± Δ % from controls)

	Females		Males	
	% d.m.	% fat	% d.m.	% fat
Whole body	−16.8*		−13.8*	
Shed blood	+ 3.6		+14.7	
Head	+ 0.3		+14.2*	
Shanks	− 4.3		− 9.5	
Skin (and feathers)	− 7.7		− 9.5*	
Viscera	−23.2*	−77.2*	−10.7†	−66.9†
Soft tissue	−24.8*	−83.9*	−19.1*	−74.5*
Bones	− 9.4*		− 8.1*	

Dry matter and fat concentrations are summarized as means and standard errors for some tissues. Treatment effects for centrifuged birds are calculated as the per cent difference from controls. These birds were from trial *P* (TABLE 1).

* Significant at the 5 per cent level.

† Significant at the 1 per cent level.

TABLE 4

CARCASS COMPOSITION

	Females		Males	
	Centrifuged	Control	Centrifuged	Control
Carcass (gm.)	489 ± 10 gm.	649 ± 20 gm.	654 ± 18 gm.	894 ± 15 gm.
Carcass composition (% of carcass weight)				
Water	71.3 ± 0.7%	64.4 ± 2.1%	10.6 ± 0.3%	65.7 ± 1.2%
Soft tissue: Fat	1.7 ± 0.3%	9.4 ± 2.2%	1.7 ± 0.5%	6.7 ± 1.0%
Soft tissue: Fat-free	16.7 ± 0.2%	16.2 ± 1.1%	16.6 ± 0.3%	16.1 ± 0.1%
Bone	10.6 ± 0.2%	10.0 ± 0.3%	11.4 ± 0.2%	11.1 ± 0.1%

Treatment effect (± Δ % from controls)

	Females	Males
Carcass weight	−24.7%†	−38.0%†
Water	+10.7%†	+ 7.5%†
Soft tissue: Fat	−82.0%*	−74.7%
Soft tissue: Fat-free	+ 3.3%	+ 3.1%
Bone	+ 6.0%	+ 2.7%

The carcass compositions are summarized as means and their standard errors. Treatment effects for centrifuged birds are calculated as the per cent difference from controls. These birds were from trial *P* (see TABLE 1).

* Significant at the 5 per cent level.

† Significant at the 1 per cent level.

chronic acceleration. Perhaps most physiological phenomena could be investigated profitably to determine their weight-dependent aspects.

The present understanding of the physiological effects of chronic acceleration is primitive—and only a few of the principles are apparent. Undoubtedly increased exercise is involved, and many of the anatomic effects resemble those of fasting. There probably are metabolic aspects of the adaptation to chronic acceleration, the capacity to convert chemical energy to mechanical work should be important. The factors which permit this adaptation are heritable, and a six-fold resistance to chronic centrifugation can be obtained by several generations of selection.[15] The pathology of birds which do not survive centrifugation (to be described elsewhere) gives an impression of a general metabolic derangement. It is quite likely that these altered physiological processes lead to many changes in body composition beyond those reported herein.

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