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Piersma, T; Lindström, Åke

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Rapid reversible changes in organ size as a component of adaptive behaviour

Theunis Piersma and Åke Lindström

Many studies in comparative ecophysiology have been carried out as if vertebrates, once fully grown, are anatomically and physiologically constant over time. If this were correct, physiological adaptation could be deduced from comparative analyses based on 'species-specific' data points from taxa with different life styles, so long as phylogenetic biases are suitably accounted for¹. Evidence is rapidly accumulating, however, that many traits examined in such studies²⁻⁴ show considerable variability dependent on environmental context and time of year. Organ sizes and derived physiological traits such as basal metabolic rate (BMR) vary between seasons⁵⁻⁸, and several studies indicate that similar changes occur over even shorter timescales⁹⁻¹³.

We review the multi-faceted evidence (from behavioural, ecological and physiological studies) for rapid changes in body composition, including organ size and organ function of reptiles, mammals and birds that face changing environments or changing tasks within a constant environment. This flexibility may be widespread, and is a critical part of the adaptive physiological repertoire of many animals. We also briefly review techniques used to ascertain such changes within individuals.

Variable and flexible bodies

There is, of course, always a fair degree of intraspecific variation in the external and internal morphology of animals, with most attention being paid to the adaptive significance of trait variation between genetically similar individuals (phenotypic plasticity, see Box 1). Yet, several morphological structures may show drastic changes in size and appearance within an individual's lifetime, often multiple times. Gonads, for example, are notoriously variable in size, with the testes and follicles of birds increasing 100-fold or more during each breeding season, declining to minute sizes in the long periods in between¹⁷.

It is folk wisdom that the mass of fat carried by many bird species varies enormously in relation to season and phase of migration. In spite of an early publication in English by Russian scientists¹⁸ that suggested otherwise, for a long time it has been assumed that individual avian migrants vary only in the amount of fat, the rest of the body remaining basically

Organ structures and correlated metabolic features (e.g. basal metabolic rate) have often been taken as fixed attributes of fully grown individual vertebrates. When measurements of these attributes became available they were often used as representative values for the species, disregarding the specific conditions during which the measurements were made.

Evidence is accumulating that the functional size of organs and aspects of the metabolic physiology of an individual may show great flexibility over timescales of weeks and even days depending on physiological status, environmental conditions and behavioural goals. This flexibility is a way for animals to cope successfully with a much wider range of conditions occurring during various life-cycle events than fixed metabolic machinery would allow. Such phenotypic flexibility is likely to be a common adaptive syndrome, typical of vertebrates living in variable environments.

Theunis Piersma is at the Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands (theunis@nioz.nl) and at the Centre for Ecological and Evolutionary Studies (CEES) of the University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands; Åke Lindström is at the Dept of Ecology-Animal Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden.

constant during migration^{19,20}. [Dolnik and Blyumental¹⁸ showed remarkable diurnal changes in the fat-free mass of the liver of migrating chaffinches (*Fringilla coelebs*), which they attributed to a variable glycogen content, and also strong decreases (40-50%) in the mass of the liver and the intestine with an increase in overall fat load before migratory departure.] In contrast, studies on mammals also carried out during the 1960s made it widely recognized that mammalian guts show rather massive changes in size in response to variations in food demand, for example, as a result of lactation²¹.

Over the past decade, there has been much renewed interest in temporary and reversible changes in internal morphology, especially the adaptive significance of changes in the size of the gut¹⁶ and adjacent organs, as biologists try to come to terms with the constraints on the physical performance of organisms^{3,22-26}. The emerging consensus among mammal and bird physiologists is that peak performances must be sustained by temporarily enlarged supporting organs, notably the alimentary tract but also the other organs in the belly cavity. The maintenance of such organs is energetically costly (as evidenced by increased BMR during many in-

stances of peak performance, discussed below), so that energy is saved by normally maintaining these organs at sub-maximal sizes.

Recent studies have highlighted the fact that it is not only the digestive machinery that varies in size in relation to performance. Other 'organs', such as various muscle blocks, also undergo dramatic adaptive changes. During the period when eared grebes (*Podiceps nigricollis*) renew all their flight feathers simultaneously, and flight is therefore impossible, their flight muscles are small. But in the two weeks before departure from the moulting areas, the grebes double the size of their flight muscles²⁷. Changes in breast muscle mass of similar magnitude have also been shown in migrant shorebirds that undergo large changes in body mass and fat load¹³. Interestingly, reversible changes in the fat-free part of the body are also implicated by the results of aviary experiments in which starlings (*Sturnus vulgaris*) were faced with different tasks and conditions²⁸. In another study, an experimental doubling of the physical efforts by starlings to remain in energy balance led to a reduction in overall energy expenditure

(L.M. Bautista *et al.*, unpublished). This was possible because the hard-working individuals lowered their body mass; they may have reduced the size of some costly organs. These starling studies illustrate the scope for study of the interplay between physical performance, energy balance and body composition – there is an urgent need for developing accurate non-terminal methods to study temporal changes in organ size in living animals.

Problems of repeated sampling

That intra-individual changes in organ size have been reported relatively rarely, let alone studied in conjunction with individual performance, stems from the problem of detecting and correctly estimating the size of such changes. Organ size is most accurately determined through the dissection of deceased animals. Even if the practical and ethical problems of sacrificing animals for scientific reasons are overcome, one ultimate problem for detecting changes in organ size remains: one cannot kill an animal twice. It follows that indirect methods have to be used, either terminal or non-terminal.

Animals that have died naturally are often not suitable for terminal measurements, since the causes of death may bias the analysis, and are sometimes not even known. Instead, the origin and status of dissected animals need to be properly controlled. Then, if certain requirements are fulfilled, the variation within a sample of dead animals may indeed reflect what happens within one individual^{20,29}. Most importantly, the animals need to be highly synchronized in their behaviour and correlated anatomical features.

There are several non-terminal methods that potentially allow the estimation of changes in overall body composition (e.g. fat content), and in some cases even organ size: ultrasound, body tomographic imaging techniques, external measurements, metabolic rates (standardized as BMR), closed energy budgets, digestion trials and total body electrical conductivity (TOBEC). All of these methods have two obvious drawbacks. First, they need to be validated against dead animals. Thus, they are not entirely 'non-terminal'. Second, estimates will be less accurate than those from terminal methods. Their main advantages are that individual animals can be measured repeatedly and that the time course of changes can thus be resolved.

Direct estimates of body composition and organ size

With ultrasound, magnetic resonance imaging (MRI) and x-ray computed tomography (CT), relevant organs can be studied in their exact position within the body. These techniques have already been used in medicine and in studies related to animal production for some time, but not yet to any great extent in ecophysiological studies of wild animals. Ultrasound has been used for assessing relatively large and conspicuous physiological features, like thickness of fat depots and large muscles³⁰, but studies of finer details may be within reach. The size of the flight muscles can be estimated by measuring the profile of the breast^{31,32}. However, few organs besides large superficial muscles can be measured in corresponding ways.

Indirect estimates of body composition and organ size

There are several indirect ways to see if changes in lean body composition and organ size do occur at all, even though the exact origin of these changes cannot be revealed. BMR is generally described as the energy turnover rate (heat production) at thermoneutral conditions during their inactive phase of the day of non-active, post-absorptive, normothermic animals that are not producing body feathers (moult) or eggs. Several studies have shown how sets of body organs are

Box 1. Terminology of intraspecific variation in design

A capacity for change or transformation within genetically uniform organisms in response to different environmental conditions is widely known under the term **phenotypic plasticity**^{14,15}. Although rarely specified, most authors use this term quite loosely to indicate a response (a reaction norm) to a continuum of varying environments. Such phenotypic responses, triggered by particular sets of environmental conditions, are usually irreversible. If the environment experienced by an individual shows drastic (and sometimes predictable, for example, seasonally mediated) changes during its lifetime, organisms may show the capacity for flexible, reversible transformations. Usually, such phenotypic transformations have simply been included under the banner of phenotypic plasticity, but then this term is often used interchangeably with **flexibility**¹⁴ or **morphological flexibility**¹⁶.

The special category of reversible changes in individual phenotypes comprising flexible responses to changing tasks should be indicated by the term **phenotypic flexibility**. Perfectly predictable seasonal changes in outward appearance, such as the alteration of breeding and non-breeding plumages of birds, should be regarded as a single phenotypic adaptation to a seasonal environment, with variations in the timing and extent of plumage changes of genetically similar individuals representing true phenotypic plasticity. Note that another category of seasonal phenotypic plasticity, that of (individually irreversible) changes in the phenotype of successive generations of insects and other organisms within a season, is called **seasonal polyphenism**.

correlated with BMR^{3,7,13}. This is not surprising since many vital organs (kidneys, heart, liver and intestines) have high mass-specific metabolic rates and make up a significant part of an animal's BMR^{33,34}. Consequently, repeated measurements of BMR may reveal short-term changes of organ size. However, surprisingly few studies of intra-individual changes in BMR have been published^{5,6,10}.

Organs may, but do not necessarily have to, change in connection with the build-up of stores of fat. As long as the animal also changes in overall body mass, food balance trials provide a good method to determine the substrate type comprising the body mass changes. Four principal substrates may be involved, and they differ in energy density. Water contains no available energy at all. Fat, which is usually deposited with a small amount of water (c. 5%, T. Piersma, unpublished) has 38 kJ·g⁻¹ of energy, whereas protein and glycogen both have about 5.5 kJ·g⁻¹ wet mass. By measuring the metabolizable energy intake (gross energy intake minus energy lost in excrements), as well as the energy expenditure (through indirect calorimetry, that is, respirometry), it is possible to estimate the energy density of changes in body mass, and the relative contribution of various substrates. This method has been used to assess the occurrence of protein deposition along with fat in birds preparing for migration^{10,35}. A similar budget can be made for nitrogen turnover³⁶. The drawbacks of these methods are, as with metabolic rates, that the exact location of organ size changes cannot be determined, that parallel increases and decreases in the size of various organs may go undetected, and that relatively large body mass changes must be involved.

With the measurement of Total Body Electrical Conductivity (TOBEC) it is possible to estimate the lean mass of a live animal³⁷. Read-outs from the measuring device can be compared with a calibration curve deduced from dissected animals. Several validation studies have been carried out, but it is debated whether this method significantly improves the accuracy of predictions compared with those made from body mass, visible fat scoring and morphometrics alone³⁸. A particular problem is that various levels of dehydration, not uncommon among experimental animals, may lead to serious errors in the estimates.

Instructive examples

Snake guts

Not surprisingly, the best evidence for the extent of phenotypic flexibility comes from studies in which successive

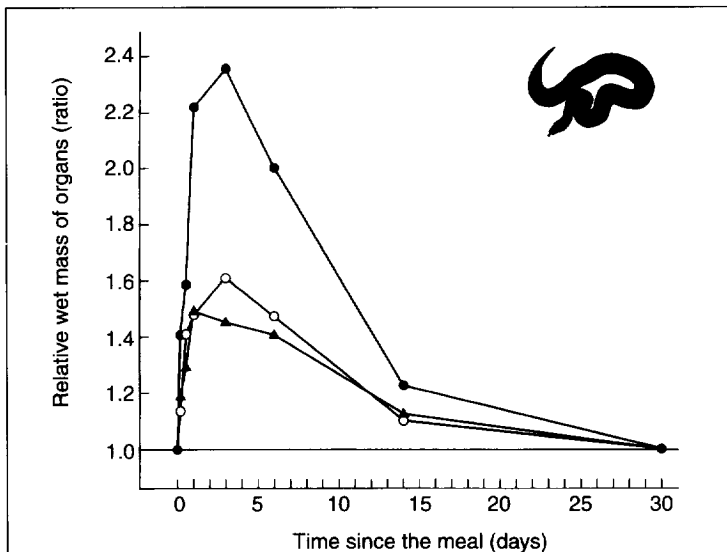


Fig. 1. Rapid changes in the digestive system of burmese pythons (*Python molurus*) after a big meal, as illustrated by the relative changes of wet masses of the anterior part of the small intestine (closed dots), the liver (open circles) and the kidneys (triangles). At time = 0, the snakes were fed rats or mice weighing the equivalent of 25% of their body mass. Each data point represents an average of the organ masses of three dissected snakes taken from an homogeneous experimental group, divided by the average organ masses of three other snakes at the start of the experiment. Data from Ref. 12.

samples of experimental animals were sacrificed and compositionally analysed. A particularly exciting example of the massive changes that some organs routinely undergo as a response to a physical challenge, and one in which the time course of such changes was especially well resolved, is provided by the studies of Secor and co-workers on changes in digestive organ structure after feeding in viperid and pythonid snakes^{11,12}. Such sit-and-wait foraging snakes forego eating for several weeks to several months before consuming an enormous meal. Then they spend a long time digesting it.

Within 24 hours after eating such a big meal, burmese pythons (*Python molurus*) showed a more than twofold increase in small intestinal mass, and 45% increases in the masses of kidneys and liver (Fig. 1). Other organs, such as the stomach, lungs and heart, increased in mass as well. The

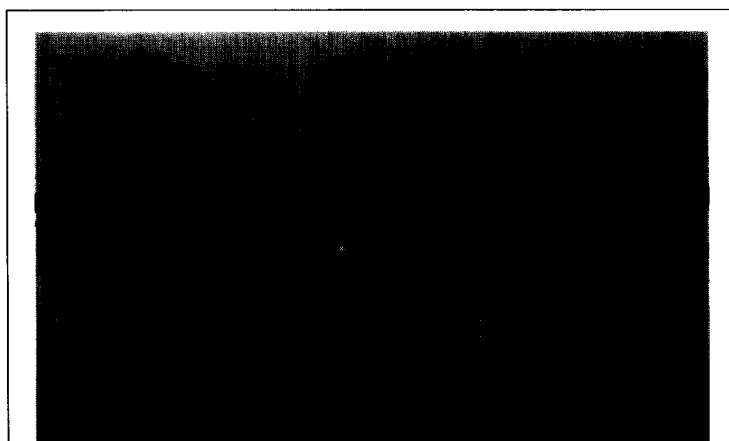


Fig. 2. A visual impression of the changes in the size of the subcutaneous fat deposits, the breast muscles and the belly cavity of red knots (*Calidris canutus*) over the three weeks when they stop over in Iceland to refuel for a further northward flight to the arctic breeding grounds. These birds not only show storage of fat, but significant and often complementary changes in the fat-free mass of several organs (including the gut, liver and flight muscles) as well. Example from G.A. Gudmundsson, T. Piersma and K. Lilliendahl, unpublished.

morphological changes during the first day post-feeding were accompanied by a sevenfold increase in metabolic rate and a similar increase in intestinal absorption rates. Because the build-up of all the organs occurred before food reached the intestine to be absorbed, the general hypertrophy must be fuelled by, as yet unknown, body stores. Even though the organ hypertrophy is estimated to consume no less than a third of the energy yield of an ingested meal, organ flexibility is nevertheless likely to lead to significant cost reductions relative to a sustained maintenance of all the energetically costly organs.

Organ adjustments in reproducing, small mammals

Lactation represents the period when the energy and nutritional drain on female mammals is largest. A well-known response is to increase temporarily the size and capacity of the intestine²¹. Recent work has shown that a further increase of the energy burden of lactating mother mice (*Mus musculus*) with large litters, by exposing them to subzero air temperatures, leads to even further increases in intestinal size and activity²³. Not only did the intestine show hypertrophy, other organs involved in metabolic processes such as the liver and kidneys increased as well^{23,26}. In lactating females each of these organs almost doubled or in some cases even tripled in size compared with when the experimental animals were still virgin. This general hypertrophy took place over four weeks, much longer than the single day required by snakes after a sudden meal. Since the studies on pregnant and lactating mice were not designed to resolve the time course of changes in organ size, it cannot be excluded that small mammals are also capable of significant organ mass increases or decreases within a few days.

Migration-related avian body flexibility

Large increases in gut size in response to energetic and nutritional challenges are not unique to reptiles and mammals, occurring also in birds^{16,22}. When house wrens (*Troglodytes aedon*), tiny passerine birds weighing only about 10 g, were challenged by forced exercise and exposure to subzero temperatures, their body mass showed very little change, but the mass of their stomach and intestine increased by 10% and 35%, respectively²². Changes of comparable or larger magnitude in response to variations in energy demand or food quality are reported for gut size of a much larger number of avian species^{16,39}, the most dramatic changes being shown by mollusc-eating shorebirds in the course of their seasonal long-distance migrations³⁹.

To fuel the 2000–5000 km long flights between suitable stopover areas, on their way to high arctic breeding grounds, red knots (*Calidris canutus*) and other shorebirds store huge subcutaneous fat deposits (Fig. 2), thereby almost doubling in body mass in the course of 3–4 weeks. Detailed body composition analyses of sequentially sampled birds demonstrated that stomach size shows rather large changes as well, decreasing by half in one example (Fig. 3). This is of a comparable magnitude to the gut changes of the burmese pythons, even though the time course is rather longer. Another shorebird, the bar-tailed godwit (*Limosa lapponica*), was studied at a stopover site, and showed a 30% increase in stomach mass in the first half of a three-week refuelling period, and a 20% decrease in the second half (Fig. 3). Both species thus started their long-distance flights with reduced stomach masses. In the case of the red knot, which specializes on hard shelled-mollusc prey and therefore carries a relatively heavy stomach (10% of lean body mass), a 50% reduction of stomach mass leads to a 5% decrease in fat-free mass.

Comparable compositional changes (especially with respect to the digestive machinery) occur in long-distance migrating passerine birds such as garden warblers (*Sylvia borin*)^{10,40} and thrush nightingales (*Luscinia luscinia*)³⁵. These studies additionally indicate that changes in organ size and BMR of avian migrants may take place in the course of days rather than weeks.

Functional significance

An avian migrant that manages to reduce the mass of the organs in the abdominal cavity before take-off does so at a time when these organs are temporarily non-functional and therefore relatively costly to maintain, owing to the costs of carrying them around during long-distance flight. Additionally, the bird that can delay the hypertrophy of its flight muscles until the enlarged muscles are actually fully needed, makes even larger energy savings. Similar arguments can be put forward for most examples of organ flexibility listed above. Organs are metabolically active and therefore costly to maintain. In addition, they may be costly to carry, or they may be costly because they take up space in a body cavity that is already filled with other functional parts.

Although the argument that energy savings can be made by adjusting specific organ sizes to required performance is a likely and straightforward one, no studies have hitherto come up with detailed budgets of the energy gains and losses of such organ changes. The organ hypertrophy enabling burmese pythons to digest their meal has been estimated to cost about a third of the assimilated energy of that meal¹², but the energy savings of carrying a much smaller digestive machinery during the long periods of fasting have still to be determined.

A smaller gut may reduce energy expenditure but this also has drawbacks. Bar-tailed godwits that have small stomachs restricted their diet to relatively soft food items³⁹, prey types which may not be as profitable as hard-shelled ones. Red knots that have small stomachs may be similarly restricted to feeding on relatively unprofitable soft foods and/or at suboptimal feeding areas (T. Piersma, J. van Gils and M.W. Dietz, unpublished). In general, organ flexibility will lead to time costs when adjustments have to be made to cope with changing environmental or physiological challenges.

Even though we understand very little of the way in which energetic and other trade-off functions determine specific organ sizes, it is clear that phenotypic flexibility at the organ level allows animals to perform successfully and survive environmental conditions that, by and large, are outside their 'normal' range. Mice and house wrens survive the cold, and the mice manage to feed their large litters by increasing the size and capacity of their guts. Similarly, many species of avian migrants may only be able to reach the corners of the Earth by virtue of their remarkable body flexibility.

Prospects

Experimental studies on mammals and birds have shown that unexercised muscles show serious atrophy within a few days, but that hypertrophy also occurs rapidly when the workload is increased^{41,42}. Indeed, in many cases of organ flexibility a 'use/disuse' mechanism can be implicated, but sometimes this is evidently not the whole story. For example, in the sit-and-wait foraging snakes that undergo a rapid hypertrophy of the digestive machinery immediately upon eating a meal, it is unclear which neural or hormonal signals warn the intestine that food has reached the stomach¹¹. In shorebirds that show a decrease of the size of their alimentary tract during a time when they are still storing fat at fast

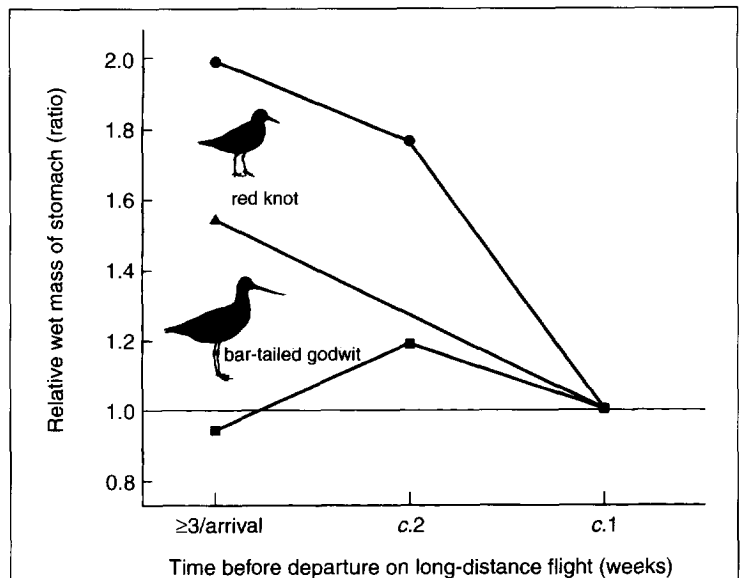


Fig. 3. Changes in the relative wet mass of the empty stomach in two shorebird species (red knot, *Calidris canutus* and bar-tailed godwit, *Limosa lapponica*) relative to the time of departure on 3000–5000 km migratory flights to arctic breeding areas. Stomach masses are scaled to overall average mass before departure. The dots refer to red knots preparing for the flight from West Africa to Europe, the triangle refers to red knots that fly from Europe to Greenland and/or arctic Canada, and the squares refer to bar-tailed godwits that fly from Europe to central arctic Siberia. The red knots were sampled long before and just before departure, but the bar-tailed godwits were also sampled in their normal emaciated state just after arrival from a previous long-distance flight, before regaining the stores for onward migration. Data from Ref. 39.

rates, neural or endocrine regulatory mechanisms are also implicated³⁹. This is a wide-open field of enquiry.

The general finding that physiological traits are variable, even within individuals, and dependent on behaviour and environmental context suggests that comparative analyses using species-specific values⁴ are bound to be biased unless all parameter values are obtained under standardized conditions²⁵. At the same time, the existence of phenotypic flexibility opens up alternative avenues to do comparative studies of organismic adaptation, at the level of the individual.

Currently, studies of phenotypic flexibility at the organ level are seriously constrained by the practical limitations of monitoring organ size in live reptiles, mammals and birds. If these problems were solved in satisfactory ways, the study of rapid anatomical and physiological adjustments to changes in behavioural goal and in environmental context is likely to become an important and exciting new field of adaptational biology.

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