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Use of the Metabolisable Energy Coefficient in Bird Studies: Statistical Power in Taxa and Food Comparisons

Ian van Tets[A] *and Gordon Sanson*

Department of Ecology and Evolutionary Biology, Monash University,
Clayton, Vic. 3168, Australia.
[A]Present address: Department of Biological Sciences, University of Wollongong,
Northfields Ave, Wollongong, NSW 2522, Australia.

Abstract

A widely cited review of the digestive efficiency of birds concluded that the apparent Metabolisable Energy Coefficient (*MEC), a measure of the efficiency of energy assimilation, did not vary between bird orders. To test whether this result was due to the variation between the experimental methods of the studies chosen for the review, the *MEC was measured for four species (two galliforms and two columbiforms) fed a variety of seeds. The *MEC of the birds did not vary in any consistent manner when fed identical diets, thus supporting the review's result. However, the *MEC of each species varied consistently with change in diet. These findings can be explained by the statistical power of the *MEC comparisons. Comparisons of *MEC between bird species are less powerful than comparisons between diets.

Introduction

The amount of energy an animal extracts from a particular kind of food within a given time is dependent on the rate at which the food is consumed and the efficiency with which the energy of that food is assimilated during digestion. Variations in either of these factors have been shown to have a marked effect on energy flow (Weins and Innes 1974).

The second variable is generally measured by dividing the difference between the energy in the food eaten by an animal and the energy it excretes as faeces or urine by the energy in the food eaten. This measurement is called the apparent Metabolisable Energy Coefficient, *MEC, of the animal (Karasov 1990). It is also known as the animal's Energy Assimilation Efficiency (Castro *et al.* 1989). The energy in the food eaten is usually referred to as the Gross Energy Intake and the energy excreted as the Gross Energy Output.

The *MEC has been used for a variety of studies which can be divided into two major types. One type assesses the relative energy value of different foods to a particular species (e.g. Krebs and Avery 1984; Robel and Arruda 1986) and the other assesses the relative efficiency with which different species assimilate energy from a particular food source (e.g. Penny and Bailey 1970). Some studies have investigated both of these areas (Miller 1984).

In 1989, a review of *MEC research was published (Castro *et al.* 1989). Although significant differences were present between the efficiencies with which different food types were digested,

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Castro *et al.* (1989) found no significant differences in apparent *MEC between bird orders, and concluded that

> '. . . bird digestive chemistries are not adapted to feed on specific food types, at least with respect to assimilation efficiency. Different orders are apparently equally capable of extracting energy from a given food type. This is in contrast with the fact that bird digestive systems are well differentiated depending on their diet.' (Castro *et al.* 1989, p. 275).

The study only compared birds that naturally ate similar diets so this claim is limited to such birds. However, this conclusion is still surprising because if avian digestive systems have differentiated with respect to diet, one expects that the efficiency with which different bird taxa extract energy from similar foods would vary. Castro *et al.* (1989) attempted to explain this apparent contradiction by suggesting that the differences in digestive physiology and morphology were related to the digestion and assimilation of specific nutrients rather than energy itself. However, the variation in methodology between the studies reviewed prevented firm conclusions being drawn.

The apparent Metabolisable Energy Coefficient may vary with changes in body mass (Robinson *et al.* 1983; Demment and van Soest 1985). Smaller birds require more energy per gram of body mass (Robinson *et al.* 1983) and may, therefore, have greater *MECs than large birds on similar diets. Alternatively, larger birds may have greater *MEC values because they have a greater ratio of gut capacity to metabolic requirements (Demment and van Soest 1985). This is particularly likely for fibrous foods (Hume 1994). However, in the comparison by Castro *et al.* (1989) of granivorous bird orders, size was not controlled. Eight passerines, all weighing less than 60 g, were compared with one 200-g quail and three species of duck ranging from 700 to 1200 g. No other seed-eating orders, such as parrots or pigeons, were studied.

Ambient temperature may also affect metabolic rate, particularly if birds tested at temperatures below their thermal neutral zone are compared with those kept within it. However, the temperatures used in the experiments reviewed varied considerably. Some were conducted in unheated laboratories (Hoffman and Bookhout 1985), some at 1°C or lower (Willson and Harmeson 1973; Robel *et al.* 1979*a*, 1979*b*), some between 21 and 25°C (Brenner 1966) and some at 32°C (Cain 1976).

A number of other factors varied between experiments: photoperiod, cage size and the duration of the trials. It is difficult to draw firm conclusions on variation in energy assimilation between the digestive systems of bird orders from the evidence presented in the review.

Therefore, we are left with three possibilities:

(1) that the review's conclusion was incorrect and *MEC does vary between bird taxa,

(2) that the results of the review were correct but the interpretation was wrong (e.g. no significant differences existed in the value of *MEC between bird orders because of the statistical power of the comparisons used, rather than because of similarities in the taxa's digestive efficiencies) or

(3) that the review was correct and the efficiency with which birds obtain energy from a given food does not differ between taxa.

The aim of this study was, therefore, to determine which of these was the case. This was to be achieved through a comparison of the *MEC of birds from two different orders held in comparable conditions and feeding on a series of identical diets.

Two orders of granivorous birds were chosen for our study, as Castro *et al.* (1989) treated this group of birds with less consistency than most other groups. Furthermore, another review comparing the *MECs of birds eating different food types (Karasov 1990) found differences in energy assimilation between passerines and non-passerines when they were fed wild seeds.

Materials and Methods

The birds selected for this study were the feral pigeon, *Columba livia*, and the peaceful dove, *Geopelia placida* (order Columbiformes), and the bantam chicken, *Gallus gallus*, and the king quail, *Coturnix chinensis* (order Galliformes). The mean body mass of the peaceful doves and the king quail were 47 and 51 g respectively. The mean body mass of the pigeons was 300 g and that of the bantams 670 g.

All birds were held in outdoor aviaries (four aviaries, each 3 m × 2 m × 2 m). Prior to trials the smaller birds were fed a seed mix composed of oats, white millet (*Panicum miliaceum*), red panicum (*Panicum* sp.), Japanese millet (*Echinochloa crusgalli*) and plain canary (*Phalaris canariensis*). The larger birds were fed a seed mix of corn, wheat, oats, sorghum (*Sorghum vulgare*), dunn peas (*Pisum sativum* var.), maple peas (*Pisum sativum* var.), and safflower seed (*Carthamus tinctorius*). Fresh feed, shell grit and water were provided at approximately 0830 hours daily.

For feeding trials, six birds of the same species were placed in individual metabolism cages (52 cm × 38 cm × 38 cm). Photoperiod was set at 14 h light : 10 h dark during the experiment. The temperature was maintained at 25°C (± 2°C). The lower critical temperature, T_{lc}, of the lightest species, the peaceful dove, was estimated to be 22°C using the equation $T_{lc} = 13{\cdot}5\ (\text{mass})^{0{\cdot}181}$ (derived from the non-passerine equation in Kendeigh *et al.* 1977 by Peters 1983). As T_{lc} decreases with increasing body size (Peters 1983) the T_{lc} of the remaining birds was assumed to be slightly less than this value; 25°C could therefore be expected to fall within the thermal neutral zone of all four species.

Trials lasted five days, with the first three days being used to familiarise the birds with the experimental diet and conditions. During the trial the birds were provided with shell grit, water and one of the following seed species: sorghum, wheat, red panicum and plain canary.

The seeds were oven dried for 24 h at 60°C and weighed before being provided to the birds. This was found to be sufficient for the seed to reach constant mass. On a daily basis 80 g of seed were provided daily for the pigeons and bantams and 20 g for the king quail and peaceful doves. The mean mass of the individual seeds was 34 mg for sorghum, 30 mg for wheat, 6 mg for red panicum and 3 mg for plain canary.

The birds were weighed daily and, on completion of a trial, they were returned to the aviaries and rested for at least five days. When birds lost more than 2% of their body weight they were removed from the trial. The faeces and uneaten seed from the final 48 h of each trial were collected, oven dried at 60°C for 24 h, separated and weighed. Excess and spilled food was examined to determine whether the bird removed the husks from the seeds prior to ingestion. A micrometer was used to obtain an estimate of husk thickness using the average of measurements taken at three points along the husk surface. Caecal length was also measured for six birds from each species.

Three samples of each seed type (each approximately 0·5 g) were weighed, ground and then burnt in a ballistic bomb calorimeter (Gallenkamp) and the energy content, in kilojoules per gram, was determined. Gross Energy Intake, GEI, for each bird was determined from the food intake (g) multiplied by the mean energy value of the diet (kJ g^{-1}). Three samples of faeces collected from each bird in each trial were collected and burnt in the calorimeter. Gross Energy Output , GEO, was determined from the dry weight of faeces (g) multiplied by the mean energy value of the faeces (kJ g^{-1}). Apparent Metabolisable Energy Coefficient, *MEC, was calculated by subtracting GEO from GEI and dividing the result by GEI.

An ANOVA (Zar 1984) was used to compare the mean efficiencies of the different bird species on each of the diets. The means were ranked in descending order and a Tukey's Honestly Significant Difference test (Tukey's HSD) (Zar 1984) was used to determine between which birds the significant differences lay. The same process was used to compare the mean efficiencies with which the different seeds were digested by each bird species.

Results

The results of the feeding trials are shown in Table 1. There were no consistent significant differences ($P < 0{\cdot}05$) in *MEC among bird species for any diet (Table 2). Furthermore, no significant differences in *MEC ($P < 0{\cdot}05$) were found between the two species of comparable body mass, the peaceful dove and the king quail (Table 2). There were, however, consistent differences (not always significant) in *MEC between the different seed types for each bird species (Table 3). Equal replicates were not taken for the wheat diet as four peaceful doves lost more than 10% of their body weight and were removed, while one quail excreted no faeces.

Plain canary had the thickest husk of the seeds used (mean thickness 0·070 mm, s.d. 0·01). Red panicum had a mean husk thickness of 0·049 mm (s.d. 0·016). The other two seeds lacked a husk. None of the test birds removed seed husks prior to ingestion.

Differences were observed in the feeding patterns of the birds when they were kept in the resting aviaries. Both galliform species captured and fed on a wide variety of invertebrates, while the columbiforms fed only on seeds. Also, the columbiforms tended to feed in two periods, the early morning and late afternoon, whereas the galliforms fed throughout the day.

Table 1. *MEC values (%) for four bird species fed various seed diets

Seed type	Pigeon mean ± s.d.	Peaceful dove mean ± s.d.	Bantam mean ± s.d.	King quail mean ± s.d.
Sorghum	85·8 ± 2·5	85·0 ± 0·8	88·9 ± 0·9	86·0 ± 1·1
Wheat	83·0 ± 3·8	54·3 ± 22^A	78·5 ± 11	81·9 ± 1·4^B
Red panicum	80·2 ± 12	81·6 ± 0·4	77·2 ± 2·4	78·2 ± 4·3
Plain canary	78·3 ± 1·1	75·2 ± 1·4	74·7 ± 0·8	74·2 ± 3·0

^{A} $n = 2$. ^{B} $n = 5$.

Table 2. ANOVA and Tukey's test results comparing the *MECs of the different birds for each seed

B, Bantam; Q, King quail; P, Pigeon; D, Peaceful dove. Means with linked underlinings are not different ($P < 0·05$)

Species	F-value	Tukey's HSD			
Sorghum	8·0^B	B	Q	P	D
Wheat^A	0·65	P	Q	B	
Red panicum	0·52	D	P	Q	B
Plain canary	6·1^B	P	D	B	Q

^{A}Peaceful doves excluded. ^{B}ANOVA significant at $P < 0·05$.

Table 3. ANOVA and Tukey's test results comparing the *MECs of the different seeds for each bird

S, Sorghum; W, Wheat; P, Panicum; C, Plain canary. Means with linked underlinings are not different ($P < 0·05$)

Species	F-value	Tukey's HSD			
Pigeon	1·4	S	W	P	C
Peaceful dove^A	66^B	S	P	C	
Bantam	7·2^B	S	W	P	C
King quail	19^B	S	W	P	C

^{A}Wheat excluded. ^{B}ANOVA significant at $P < 0·05$.

Caecal lengths were greater in the galliforms than the columbiforms. The bantam and the king quail had mean caecal lengths of 96 mm (s.d. 20) and 33 mm (s.d. 3), respectively, while the mean caecal lengths for the pigeon and the peaceful dove were 4·0 mm (s.d. 1) and 1·3 mm (s.d. 0·1).

Discussion

The results confirm the result of Castro *et al.* (1989), as no consistent significant difference was found between the bird species for *MEC (Table 2). The birds did, however, differ in terms of their digestive morphology and their feeding behaviour in ways that would be expected to affect their *MEC. Karasov (1990) suggested that avian caeca are involved in fibre digestion. If this were the case, then their longer caeca should have raised the galliform's efficiency. If the two columbiforms are specialist granivores and the two galliforms more generalist, their assimilation efficiencies for a grain diet should differ (Karasov 1983). This apparent contradiction was probably due to the low statistical power of the *MEC comparisons.

The *MEC is expressed in terms of the Gross Energy Input, GEI, and the Gross Energy Output, GEO. Both these terms are composed of several components. GEI for a seed-eating bird has two main parts: the energy contained in the portion of the seed that is indigestible to all the bird species studied (in this case, most of the husk and a fraction of the endosperm), and the energy in the portion of the seed that the birds are potentially able to digest. The fractions of GEI made up by these two components vary between different seed types but not between different bird orders.

The GEO term is a subset of the GEI, excluding energy assimilated for heat, reproduction, maintenance, growth and storage. GEO includes the energy of the portion indigestible to all the birds, the undigested portion of the component potentially digestible to the birds, and the energy of endogenous material mixed with the excreta.

The proportion of the various components of the assimilated energy were not measured and may vary with such things as body size, digestive adaptations, the bird's condition, and the seed's composition. In the GEO, the proportion of energy contributed by the endogenous material and that fraction of the energy that granivorous birds are potentially able to digest, but that the bird in question has not digested, would also be affected by a similar range of factors. However, the proportion indigestible to all the birds would only vary with seed type. Therefore, if differences existed between the birds they would be obscured by the effects of the food studied, the body size and the environment. Thus, except where large differences in digestive efficiencies exist, large numbers of replicates would be required to detect differences in energy assimilation efficiency between birds.

Many of the experiments reviewed by Castro *et al.* (1989) used small numbers of replicates. Hoffman and Bookhout (1985) used 12 or fewer individuals for most of their trials, while Robel *et al.* (1979*a*, 1979*b*) used between 3 and 12 individuals for theirs. In this study six individuals of each species were used. As differences between taxa are likely to be quite small, the use of only a few individuals increases the probability that variation between individual birds would obscure variation between taxa. A power analysis (Zar 1984) was carried out on our red panicum feeding trials and revealed a power of less than 14% for the experiment. Generally, for statistical tests a power of 80% or greater is desirable (Zar 1984). On the basis of the results of the panicum trial, 43 birds of each species would have had to have been used to attain a power of 80%. For many researchers this number of animals is prohibitive.

However, *MEC comparisons by Castro *et al.* (1989) and Karasov (1990) have found significant differences in studies of the efficiency with which birds extract energy from different foods. This, in view of the *MEC equation, is not surprising.

The composition of the GEI term is related entirely to the composition of the food type. The GEO term is also strongly influenced by food type, particularly when the fraction indigestible to all the birds is large. Thus, while one expects differences between animal taxa to be slight, differences between food types would be, in general, larger. Therefore, the power of comparisons of the apparent *MEC for different foods and food groups is greater than the power of such comparisons between bird taxa.

The apparent effect of seed husk on *MEC provides a good example of this. Seed husks are composed largely of energy-rich fibre. With their relatively small caeca (see results), the columbiforms would have digested only a tiny fraction of this fibre, while the galliforms studied would have digested some fibre but not very efficiently (Karasov 1990). Therefore, the percentage of energy in the indigestible component of those seeds with husks would be high and *MEC values for birds eating those seeds low.

The results support this prediction. The two seeds with husks had lower *MEC values for all the birds than the seeds without husks. Furthermore, the seed with the thickest husk, plain canary, had a lower *MEC value for all the birds than the other husk-bearing seed, red panicum (Table 3).

We would also predict that removing seed husks prior to ingestion would raise *MEC for granivorous birds. Castro *et al.* (1989) and Karasov (1990) showed that passerine birds that dehusked seeds had high values for *MEC and that non-passerine birds that did not dehusk had relatively low values. It would be interesting to compare *MEC values for dehusking and non-dehusking birds within a taxonomic group.

It is plain, therefore, that comparisons between food types can detect differences in *MEC. Presumably, comparisons between *MEC values for bird groups can also detect differences, if sufficient replicates are taken. However, caution should be used before ascribing biological reasons for a lack of significant difference when the power of a comparison is low.

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