# *Short Communications and Commentaries*

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## Metabolism and Temperature Regulation of Kiwis (Apterygidae)

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One of the most distinctive group of birds is the ratites, a group that includes the Ostrich (*Struthio camelus*), rheas (*Rhea* spp.), cassowaries (*Casuarius* spp.), Emu (*Dromaius novaehollandiae*), kiwis (*Apteryx* spp.), and possibly tinamous (Tinamidae) among living birds, and elephant birds (Aepyornithidae) and moas (Dinornithidae) among extinct species. At various times this group was considered to be natural (i.e. monophyletic), and at other times the result of convergence on large size and flightlessness (i.e. polyphyletic). Recent work on the biochemical taxonomy of ratites (Sibley et al. 1988, Cooper et. al. 1992) favors a monophyletic origin and places them, including tinamous, in the Parvclass Ratitae. The position of the tinamous, however, is such that they may be considered a sister taxon to a more narrowly defined group of ratites (Cracraft 1974).

Although most ratites (sensu stricto) are large (>20 kg) and have omnivorous to vegetarian diets, kiwis (Apterygidae) are characterized by a mass of 1 to 4 kg and by feeding principally on soil invertebrates. Kiwis are collectively confined in distribution to the three major islands of New Zealand and are an autochthonous element of New Zealand's fauna. Robertson (1985) has summarized the contemporary distribution of kiwis in New Zealand. The Brown Kiwi (*Apteryx australis*) is found on North, South, and Stewart islands. The Little Spotted Kiwi (*A. owenii*) was found in the mountains of North Island, as well as on South Island, but today is limited to Fjordland on South Island and to some offshore island refuges (such as Kapiti Island) to which it was transported. The Great Spotted Kiwi (*A. haastii*) is limited to western and northwestern regions of South Island.

The unique origin and distinctive habits of ratites make them worthy of extensive study, but because of their large size and distribution in the Southern Hemisphere, they have been the subject of few studies, especially in terms of experimental biology. Furthermore, few kiwis are held in captivity outside New Zealand. Therefore, few data are available on kiwi physiology. They include Farner's (1956) measurements of body temperature in Brown Kiwis, and Calder and Dawson's (1978) measurements of metabolism. Calder and Dawson reported 11 measurements collectively made on the three species, which are not enough to define clearly the energy expenditure of any of these species. Here, I report 104 measurements of the rate of metabolism and body temperature as a function of ambient temperature in three species of kiwis. These data are compared with those available on other ratites.

*Methods.*—Kiwis were studied at the Kiwi House that is operated by the Otorohanga Zoological Society at Otorohanga, North Island, New Zealand (38°S, 173°E). I measured body temperature and rate of oxygen consumption in three (one female and two males) North Island Brown Kiwis (*A. australis mantelli*), two (one of each sex) Little Spotted Kiwis, and two (one of each sex) Great Spotted Kiwis. Kiwis were placed individually in a 230-L chamber that had hollow walls through which temperature-controlled water was pumped from a water bath. The rate of metabolism was estimated in terms of oxygen consumption by sucking room air through the chamber at rates between 5.1 and 8.8 L/min, which was sufficient to assure adequate mixing of air in the chamber, as was shown by the independence of the calculated rate of oxygen consumption from flow rate. The air leaving the chamber was sent in sequence to a tube to remove $CO_2$, to another tube to remove water, to a flow meter to measure flow rate, and finally to an Applied Electrochemistry oxygen analyzer, which sent an electrical signal of the oxygen content of the air stream to a stripchart recorder.

One kiwi was used in a day, during which it was exposed to three or four temperatures, each experiment lasting 2 to 3 h. Before each experiment the kiwi was weighed, and after each experiment its cloacal temperature was measured and its mass determined. After an experiment the bird either was returned to the chamber and exposed to another temperature, or it was returned to an outside holding pen and fed. As a result of this schedule, the kiwis were postabsorptive at the beginning of each day, and the measurements were made during daytime when kiwis are normally inactive. Kiwis usually remained very inactive in the chamber unless the temperature was near 30°C, the highest temperature used. Thermal con-

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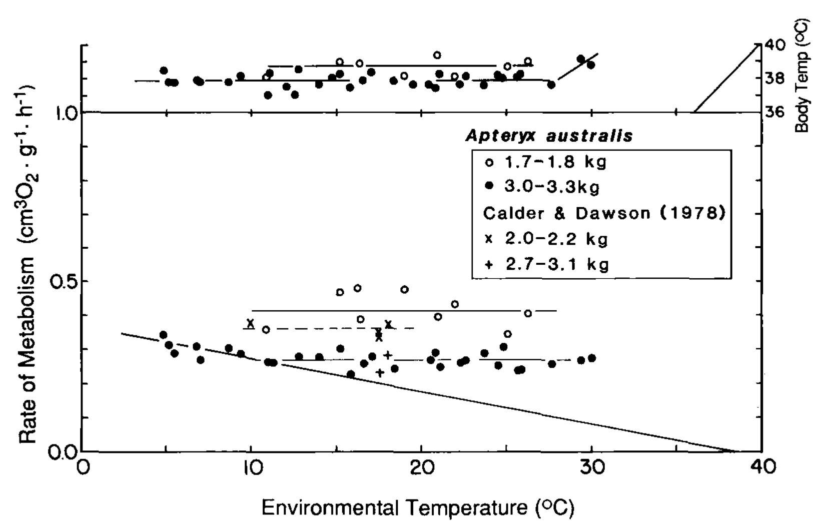

Fig. 1. Rate of metabolism and body temperature as function of environmental temperature in one female and two male North Island Brown Kiwis. Data are segregated by body size, the two larger bids (one male and one female) indicated by solid circles and the one smaller male by hollow circles. The zone of thermoneutrality is indicated in the metabolism data by the horizontal line for each size class. The sloping line in the metabolism data represents an estimate of minimal thermal conductance. Additional data from Calder and Dawson (1978).

ductances were estimated as recommended by McNab (1980). Data are presented as $\bar{x}$ ± SE (*n*, number of measurements).

*Results.*—Of the three Brown Kiwis used, a male and a female were large (3,137 ± 23.4 g [35]), and a second male was small (1,750 ± 8.6 g [11]). The mass of the large female (3,022 ± 16.1 g [13]) is within the range of masses found in the wild (2,060 to 3,850 g), but that for the large male (3,238 ± 7.3 g [20]) is greater than in the wild (1,720 to 2,730 g; Colbourne and Kleinpaste 1983). The large male's mass probably included appreciable fat deposits. The two large kiwis had a slightly lower body temperature (37.9 ± 0.07°C [31]) and a lower mass-specific basal rate (0.267 ± 0.0043 cm$^3$ O$_2$·g$^{-1}$·h$^{-1}$ [24]) than the small male (38.7 ± 0.16°C [8] and 0.417 ± 0.0170 cm$^3$ O$_2$·g$^{-1}$·h$^{-1}$ [9], respectively). Farner (1956) reported similar body temperatures at night to those reported here; the daytime measurements he recorded were lower, usually between 36.0 and 37.0°C. The basal rates reported here for the large kiwis include two values from Calder and Dawson (1978) on animals having the same mass. Basal rates are 59 and 78% for large and small kiwis, respectively, of the values expected from body mass by the nonpasserine equation of Aschoff and Pohl (1970). When data on the basal rate of the large kiwis are considered separately, the male had a basal rate equal to 0.261 ± 0.0038 cm$^3$ O$_2$·g$^{-1}$·h$^{-1}$ (36), and the female had a basal rate equal to 0.288 ± 0.0080 cm$^3$ O$_2$·g$^{-1}$·h$^{-1}$ (6), which in the male equals 58% and in the female 63% of the values expected from mass. The low basal rate in the large Brown Kiwis (relative to rate expected from mass) is unlikely to be due to the presumptive presence of body fat, because body fat has not been shown to influence basal rate (McNab 1968, Scott et al. 1972, Goyal et al. 1981) and because the female, which has an appropriate mass for females living under field conditions, has a basal rate similar to that seen in the large male. The higher basal rate in the smaller kiwi may be associated with its higher body temperature and, possibly, some activity. The best estimate of basal rate in this species, then, probably is 59 or 61% of the values expected from mass, depending on whether the data are combined or the individuals are averaged, respectively. The smaller Brown Kiwis studied by Calder and Dawson (1978) had an average mass of 2,075 ± 80.3 g (4) and a mean basal rate equal to 0.360 ± 0.0091 cm$^3$ O$_2$·g$^{-1}$·h$^{-1}$ (4), which is 71% of the rate expected from the birds' mass. This value leads to another suggestion, namely that smaller Brown Kiwis have higher basal rates (71 and 78%) than larger individuals (58 and 63%).

Brown Kiwis had a zone of thermoneutrality that extended at least from 30.0°C down to 10.0°C, but it may have extended down to 7 to 8°C (Fig. 1). Unfortunately, I could not expose the kiwis to ambient temperatures below 5°C, so the estimate of minimal thermal conductance is approximate. The best estimate available is 0.0098 ± 0.00025 cm$^3$ O$_2$·g$^{-1}$·h$^{-1}$·°C$^{-1}$ (7), which is obtained from measurements of rate of metabolism and body temperature at ambient temperatures between 5 and 10°C. This estimate is 65% of the value expected from the curve described for birds by Lasiewski et al. (1967).

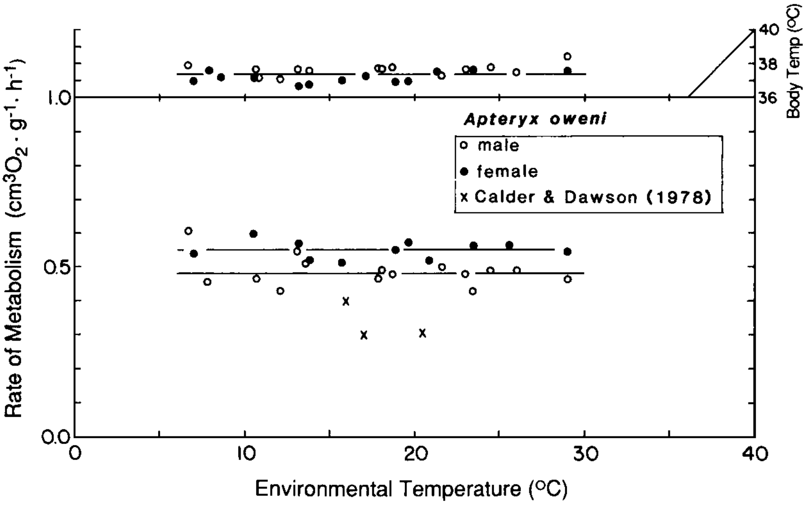

Fig. 2. Rate of metabolism and body temperature as function of environmental temperature in one male and one female Little Spotted Kiwis. Data are not combined because of difference in mass and basal rate of these individuals. The zone of thermoneutrality is indicated in the metabolism data by the horizontal line for both individuals. Additional data from Calder and Dawson (1978).

The female Little Spotted Kiwi had a larger mass (1,564 ± 4.6 g [15]) than the male (1,190 ± 5.3 g [15]). No significant difference existed in their mean body temperatures (pooled $T_b$ = 37.4 ± 0.07°C [27]), but the female, in spite of a larger mass, had a higher mass-specific basal rate (0.551 ± 0.0086 $cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$ [11]) than the male (0.478 ± 0.0001 $cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$ [15]). Consequently, the female had a much higher basal rate than the male relative to the rates expected from body mass (i.e. 100 vs. 81%, respectively). These measurements are appreciably greater than the three reported by Calder and Dawson (1978), which are not included in the calculations (Fig. 2).

The higher basal rate in the female deserves a comment. On the last day of measurement, a curator at the Kiwi House palpated the female and suggested she was forming an egg. Consequently, we stopped measuring her body temperature. A couple of months later I inquired whether the female had laid an and was told she had not. An egg, however, might have been resorbed as a result of handling, so that the high rate of metabolism in this individual might have reflected the cost of building an egg. I conclude that the best estimate for basal rate is that measured in the male.

The zone of thermoneutrality in the Little Spotted Kiwi extended from 6 to 29°C (Fig. 2). I detected no increase in rate of metabolism at low temperatures. Minimal thermal conductance, therefore, can be no greater than 0.017 $cm^3 O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$, which is 69% of the value expected from mass in the male.

The two Great Spotted Kiwis did not differ significantly in body mass (2,529 ± 32.9 g [28]), body temperature (38.4 ± 0.09°C [28]), or mass-specific basal rate of metabolism (0.375 ± 0.0046 $cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$ [25]). The basal rate in this species is 78% of the rate expected from mass. The two measurements of rate of metabolism in Great Spotted Kiwis by Calder and Dawson (1978) are lower than reported here and are not included in the calculations. The zone of thermoneutrality extends at least from 5 to 30°C (Fig. 3). As in the Little Spotted Kiwis, I found no evidence of an increase in rate of metabolism at low temperatures in the Great Spotted Kiwis. Minimal thermal conductance equals, or is less than, 0.011 $cm^3 O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$, which is 65% of the value expected from mass.

*Discussion.*-Kiwis have the lowest basal rates of metabolism compared with all avian standards, even by the lowest standard commonly used, the nonpasserine curve of Aschoff and Pohl (1970). By this standard, the Brown Kiwi has a basal rate that is 61%, the Little Spotted Kiwi 81% (excluding the female that may have been forming an egg), and the Great Spotted Kiwi 78% of predicted rates. These rates are even low (77 to 106%; $\bar{x}$ = 91%) by mammalian standards (McNab 1988). The low basal rates of kiwis may be related to their very small pectoral muscle masses (McNab 1994a), which in the North Island Brown Kiwi constitutes only 0.13% of total mass (P. R. Millener pers. comm.).

All kiwis do not have the same basal rates. First of all, their total basal rates are significantly correlated with body mass ($r^2$ = 0.813). Second, the two spotted kiwi species, which are more closely related to each other than either is to the Brown Kiwi (Cooper et al. 1992), appear to have higher basal rates compared with a mass standard than does the Brown Kiwi. The two species of spotted kiwis have basal rates that av-

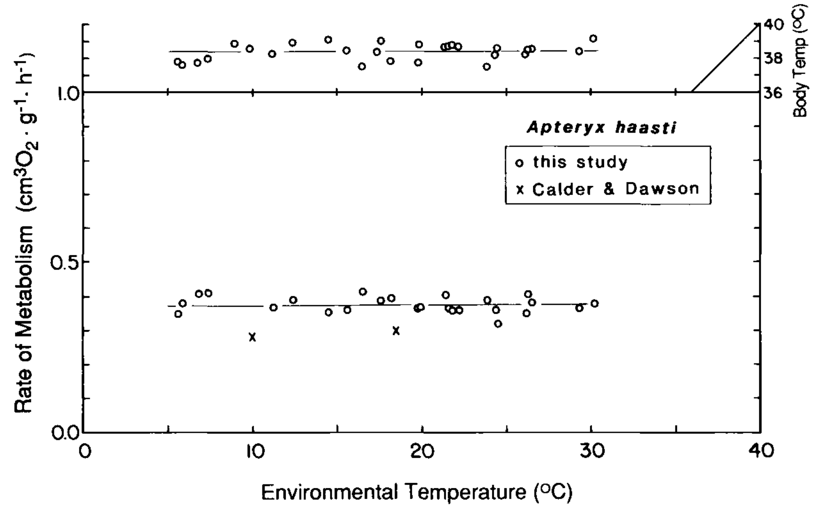

Fig. 3. Rate of metabolism and body temperature as function of environmental temperature in one male and one female Great Spotted Kiwis. Data are combined. The zone of thermoneutrality is indicated in the metabolism data by the horizontal line. Additional data from Calder and Dawson (1978).

erage 1.30 (i.e. [0.78 + 0.81]/[2 × 0.61]) times that of the Brown Kiwi after compensating for the effect of body mass. This difference might be associated with phylogeny or with geographic distribution. The spotted kiwis on South Island may be exposed to colder temperatures, especially in winter, than are encountered by North Island Brown Kiwis. South Island and Stewart Island Brown Kiwis have not been studied, but if the basal rate of kiwis reflects climate, then these populations would be expected to have higher basal rates than are found in North Island Brown Kiwis.

The basal rates of kiwis also can be compared with those of other ratites. This comparison, however, is limited by the scarcity of data on ratites and by the nonstandard conditions under which most of the measurements were made. For example, Withers (1983) reported much lower rates of metabolism in the Ostrich than was reported by Crawford and Schmidt-Nielsen (1967), a difference that may have reflected the time of measurement, nocturnal values in this diurnal species being appreciably lower than those obtained during the day. Similarly, the recent measurements on the Emu by Maloney and Dawson (1994) are under standard conditions and lower than those reported by Crawford and Lasiewski (1968). Measurements of rates of metabolism in rheas (Crawford and Lasiewski 1968) and a cassowary (Benedict and Fox 1927), which are similar to the values expected from the nonpasserine curve of Aschoff and Pohl (1970), probably were not made under standard conditions. In fact, the only ratite data that are under standard conditions probably are the rates reported here on kiwis, the Chilean Tinamou (*Notoprocta perdicaria;* Withers et al 1987), the Ostrich (Withers 1983), and the Emu (Maloney and Dawson 1994).

The data on these six species were examined by an analysis of covariance, with $\log_{10}$ basal rate as the dependent variable and $\log_{10}$ mass, food habits, and climate as independent variables. The only factor that had a significant influence on basal rate was body mass ($P < 0.001$, $r^2 = 0.993$), although highland species (i.e. the two spotted kiwis and the Chilean Tinamou) had higher basal rates than lowland species, compared with the Aschoff-Pohl nonpasserine standard. The reason why this difference did not appear statistically significant was because the highland species also were the smallest species, so that highland (i.e. cool climate) was statistically confounded by body size. Of special interest were the observations of Withers et al. (1987) that the Chilean Tinamou has the highest basal rate relative to values expected from mass (91%) in contrast to the lower rates found in kiwis (61 to 81%). This difference may have reflected the general correlation of basal rate with the proportion of body mass that is pectoral muscle (McNab 1994a). Thus, the Brown Kiwi has pectoral muscle masses that are only 0.13% of body mass, whereas tinamous have pectoral muscle masses that fall between 21.9 and 32.3% of body mass (Hartman 1961), although the Chilean Tinamou has not been investigated. Many more data on the energetics of ratites are required for a complete analysis of the factors influencing their basal rates.

The low basal rates found in kiwis are compatible with the view that the ancestors of kiwis were volant (Houde 1986, Stevens 1991, Cooper et al. 1992), flew to New Zealand after it had separated from the Australia-Antarctican remnant of Gondwanaland (Stevens 1991), and evolved flightlessness in the absence of mammalian predators. The driving force for this directional evolution likely was energy conservation in response to the limited resources found on New Zealand (McNab 1994b). The ancestors of kiwis appear to have responded to life on oceanic islands in a manner similar to that of the volant ancestors of flightless rails, namely, a reduction of energy expenditure accomplished by a radical reduction in pectoral muscle mass (McNab 1994a). Because mammalian predators were absent, this adaptation would have been uncontested by counter selection for the maintenance of flight.

Estimates of minimal thermal conductance in all kiwis are less than expected from body mass, being no greater than 65 to 69% of the values expected from mass. These low conductances facilitate energy conservation at cool to cold ambient temperatures and undoubtedly are derived from the distinctive, highly overlapping feather structure found in kiwis.

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# Pair-bond Dissolution in Mallards

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Mallards (*Anas platyrhynchos*) form seasonally monogamous pair bonds sometime during autumn migration, on wintering areas, or during spring migration (Rohwer and Anderson 1983); nearly all pair bonds are formed by the time of spring migration (McKinney 1975). Females appear selective in choosing a mate (Weidmann and Darley 1971), likely evaluating male attributes such as age, body size, dominance rank, experience, and plumage quality (Holmberg et al. 1989, Weidmann 1990). Some of these attributes may be important in enhancing the ability of males to defend their females from unpaired males that may attempt forced copulations, and to defend areas where the female can feed undisturbed (Goodburn 1984, McKinney 1985). Thus, because paired birds tend to dominate unpaired birds and to occupy better feeding habitats (Paulus 1983 on Gadwalls [*Anas strepera*]), pair bonding appears to benefit both sexes.

However, despite the vast amount of information published on Mallards, data on pair-bond duration remain scant due to the difficulty in observing marked pairs. Although a few observations of male Mallards accompanying females with broods have been reported (Dzubin 1955, Chura 1962), visual observations of marked birds have found that many pair bonds only lasted until the onset of incubation, and nearly all terminated by the second week of incubation (Dzubin 1955, Oring 1964, Titman 1983). Studies of radio-marked Mallard pairs in Minnesota found that of 15 pairs monitored, males remained with females an average of four days into incubation (Gilmer et al. 1977). However, a study of radio-marked Mallard pairs in Iowa found that pair bonds likely were maintained into midincubation and through more than one nesting attempt (Humburg et al. 1978). Specifically, of 22 marked females whose first nesting attempts were destroyed on days 10 to 17 of incubation, 11 were identified in remating sequences of which 8 remated with their original males. Elsewhere in Iowa, among 14 radio-marked Mallard pairs, 9 females rejoined original males after first nests were destroyed (Ohde et al. 1983). There also are at least two reports of a Mallard pair bond in the wild extending beyond a single breeding season (Dwyer et al. 1973, Blohm and Mackenzie 1994). In a population of resident Mallards in urban Norway, Mjelstad and Saetersdal (1990) reported on 10 of 12 color-banded pairs that remated during the second year of the study. Mjelstad and Saetersdal argued that re-uniting of Mallard pairs may be the rule rather than the exception in sedentary urban populations.

In this paper, we present data on duration and age composition of Mallard pair bonds, and causes of pair-bond dissolution in a small sample of radio-marked Mallard pairs. In addition, we report an unusual observation of a pair of Mallards remaining together on our study area for at least three consecutive years after marking. Our data were collected in northern New York within a large wetland complex in a highly forested and agricultural region of the St. Lawrence River Valley.

From late March through late April 1990 to 1992, 388 male and 128 female Mallards were captured with decoy traps (Sharp and Lokemoen 1987) and banded with U.S. Fish and Wildlife Service aluminum bands. Individuals were aged as second-year (SY) or after-second-year (ASY) birds following criteria of Krapu

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