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Extreme water efficiency of Cape gannet *Morus capensis* chicks as an adaptation to water scarcity and heat stress in the breeding colony

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ABSTRACT

Cape gannet *Morus capensis* chicks depend entirely on fish prey and metabolic water for water requirements during development. Water loss through evaporative cooling due to heat stress is substantial. We measured water flux and field metabolic rates (FMR) of Cape gannet chicks and adults to determine if gannets developed water saving strategies. The water economy index (WEI, g kJ^{-1}) decreased with chick age according to the model $\text{WEI} = 0.676 - 0.272 \times \log_{10}(t)$, indicating that water efficiency increased with age. At fledging, the WEI of chicks was at the level expected of adult desert birds. Desert birds maintain a low WEI by also having a low FMR, whereas Cape gannet chicks have FMR comparable to other seabird species' nestling requirements. We propose that maintaining low WEI is adaptive for Cape gannets because (1) chicks need to balance water loss through evaporative cooling, (2) fledglings need to overcome a period of up to a week when they cannot ingest any water and (3) adults spend extended periods in the breeding colony during which water can become a limiting factor. Understanding the physiological mechanism of maintaining low WEI will become increasingly important with future rising temperatures.

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Field metabolic rate; physiological adaptations; seabirds; water economy index (WEI); water flux

Introduction

Deserts are considered to be extreme environments, mainly due to their lack of water. In most deserts the problem of water scarcity is exacerbated by high temperatures, forcing animals to increase the amount of water used for thermoregulation (Tieleman and Williams 2000). Surprisingly, for some seabird species conditions in the marine environment can be similar; during the breeding season, drinking water can be a limiting factor and heat stress aggravates the lack of water. Adult seabirds are nest-bound for extended periods during incubation and chick guarding, while chicks are confined to nests in a colony where fresh drinking water is not available. In spite of the relatively cold seas surrounding their colonies,

Cape gannets (*Morus capensis*) are exposed to high temperatures and high solar radiation at their breeding islands and both chicks and adults experience heat stress (Hochscheid et al. 2002). Gular fluttering is used for evaporative cooling, but water loss can be substantial during this process (Schleucher et al. 1991; Ellis et al. 1995). Water is not only an essential nutrient but is also involved in many crucial physiological processes like transport, lubrication and temperature regulation (Karasov and del Rio 2007). Organisms require water in larger amounts than the body can produce, so maintaining a positive water balance will have important fitness consequences for a species that has no fresh water available in its breeding colony (Hochscheid et al. 2002).

Pelagic seabirds have no access to fresh drinking water, so requirements for water need to be met by ingesting seawater, the water in their food, plus metabolically produced water. Most seabirds have adapted to drinking seawater by secreting excess salt through salt glands (Schmidt-Nielsen 1960; Peaker and Linzell 1975). Nevertheless, many seabirds breed on hot and dry islands along the coastlines of the major upwelling regions (Nelson 1978) and during the breeding season they stay on these islands for prolonged periods without access to seawater. In contrast to their parents, seabird chicks do not have access to seawater. They spend their first few months on the breeding island and entirely depend on the water they receive from food delivered by their parents. Solar radiation on the breeding islands can be intense and requires substantial thermoregulatory investments of individuals to prevent overheating (Hochscheid et al. 2002). Hochscheid et al. (2002) showed that especially older Cape gannet chicks with a dark plumage suffer from heat stress; body temperature is about 1 °C higher and the temperature of dorsal feathers even 20 °C higher than adults (48 and 28 °C, respectively). Cape gannet chicks have limited behavioural responses to avoid dehydration and likely have physiological adaptations that help them deal with these conditions (Goldstein 2002; Hochscheid et al. 2002) potentially in a similar manner as for example desert birds (e.g. Tieleman and Williams 2000).

Nagy and Peterson (1988) introduced the concept of the water economy index (WEI, g kJ^{-1} water), which expresses water turnover relative to energy turnover and is determined by calculating water flux in relation to energy expenditure as a ratio. This index is independent of body size and reflects water conservation adaptations; the lower this ratio, the less water is used by animals for the same amount of energy output. Tieleman and Williams (2000) found that the WEI of desert birds (0.16 ± 0.061 , $n = 14$) was significantly lower than in non-desert birds (0.20 ± 0.089 , $n = 40$). Nagy (2004) also reported significant differences in mean WEI between desert (0.11 ± 0.015 , $n = 6$) and non-desert (0.20 ± 0.034 , $n = 6$) eutherian mammals, but no significant differences were found for desert vs. non-desert marsupial mammals and reptiles. Tieleman and Williams (2000) also found that birds from desert habitats have reduced basal and field metabolic rates compared to species that live in mesic areas and that the low energy expenditure of desert birds was accompanied by reduced rates of total evaporative water and water flux, resulting in a small WEI. These special adaptations increase water efficiency in an environment where water is scarce.

The objective of this study was to determine the water economy index of Cape gannets (adults and chicks) on the basis that they occupy a habitat where water may be limiting at critical times of the life cycle. The water stress of adults is somewhat lessened because they can ingest sea water and eliminate the excess salt through salt glands (Withers 1992). However, in the absence of drinking opportunities, all water requirements of chicks are solely met by pre-formed water in their diet and by metabolic water. We therefore predict

that Cape gannet chicks could have evolved water saving adaptations comparable to those reported for desert birds, i.e. relatively small values for the water economy index (Tieleman and Williams 2000; Nagy 2004).

Material and methods

This study was conducted at Malgas Island (33°03'S, 17°55'E), Saldanha Bay, South Africa. Isotopic measurements on Cape gannet chicks were carried out over two breeding seasons: 2002–2003 ($n = 10$) and 2003–2004 ($n = 7$). Measurements on adults were done during the breeding season of 2005–2006 ($n = 20$).

FMR, body water content and water flux

Nestling FMR was determined using the doubly labelled water (DLW) technique; details of the technique are described in Navarro et al. (2015) for chicks and in Mullers, Navarro, Daan, et al. (2009) for adults. In the case of chicks, we used the standard two-sample protocol (Speakman 1997), which allowed the calculation of the size of the water pool, rates of water influx and efflux, as well as rate of CO₂ production. Chicks were injected with DLW and after one hour an initial blood sample was taken. The final blood sample was collected 48 h after injection. In both breeding seasons we collected blood from four random chicks in the colony to assess the background isotope values. In adults, we used the single sample protocol (Speakman 1997) to minimise handling stress on the study subjects; this only allowed the calculation of rates of water efflux and CO₂ production. Adults were injected when they were about to leave for a foraging trip and the final blood sample was taken immediately after the parent returned on the nest. Isotopic data used for this analysis are the same obtained for chicks in Navarro et al. (2015) and the same obtained for adults in Mullers, Navarro, Daan, et al. (2009).

Estimates of total body water and rates of water flux were derived from isotope dilution in the DLW experiments. Total body water was calculated from the initial dilution of the ²H isotope, i.e. the difference between the initial blood sample and background measurements of ²H. These measurements were compared with those measured directly from carcass analysis (Navarro 1992). In summary, 21 chicks of variable ages, two fledglings and three adults were collected, under permit, between 1987 and 1989. Birds were dissected into four components; integument (skin plus down, feathers removed), viscera (all internal organs, stomach content removed), leg and pectoral muscles and carcass. Each body component was ground, homogenised and air-dried at 50 °C to constant mass. Wet and dry masses were determined and total body water was calculated as the difference between the two masses.

Water flux rates were calculated according to the methods and equations given by Visser et al. (2000) for animals not in a steady state with regard to body mass and size of the water pool. Water efflux rate, uncorrected for fractionation effects (Visser et al. 2000, eq. 5) was calculated as:

$$W_{\text{efflux uncorrected}} \cdot \text{g d}^{-1} = (\text{TBW}_f - \text{TBW}_i) \times \ln\left\{\frac{[(C_i - C_b) \times \text{TBW}_i]}{[(C_f - C_b) \times \text{TBW}_f]}\right\} / [\ln(\text{TBW}_f / \text{TBW}_i)] \times t$$

where TBW_i and TBW_f represent the total body water at the start and end of the measurement period, respectively (g). TBW_i was calculated on the basis of isotope dilution using the plateau method (see below). TBW_f was estimated by multiplying the final body mass by the ratio of the initial amount of body water to initial body mass, assuming that the percentage of body water did not change during the measurement period. C_b , C_i and C_f represent the measured $^2\text{H}/^1\text{H}$ isotope ratios of the background, initial and final samples, respectively (atom percent). The value t is the elapsed time interval (days) between the initial and final samples.

The following correction to water efflux was made for isotope fractionation effects due to evaporative water loss:

$$W_{\text{efflux}}, \text{ g d}^{-1} = W_{\text{efflux uncorrected}} / (Xf - 1 + X)$$

(Speakman 1997, eq. 7.6), where X represents the proportion of the water flux lost through evaporative pathways (taken as 0.25, as recommended by Visser et al. 2000) and f is the fractionation factor (taken as 0.94, as recommended by Speakman 1997, p. 107).

Water influx rates (W_{influx} ; g d^{-1}) corrected for fractionation effects were calculated according to:

$$W_{\text{efflux}} = W_{\text{efflux}} + (TBW_f - TBW_i)/t.$$

The size of the initial body water pool (TBW_i ; g) was calculated for each individual on the basis of the determination of the hydrogen dilution space by the plateau method described by Speakman (1997):

$$TBW_i = 18.02 \times Q_d \times (C_d - C_i) / (C_i - C_b)$$

where the quantity (Q_d ; mol) and the ^2H concentration (C_d ; atom percent) of the dose are known, as well as the ^2H concentration in the bird's body water pool (C_b ; atom percent) prior to the administration of the dose. C_b , for each experiment taken as the average value of the four birds sampled on each breeding season.

Rates of CO_2 production were calculated using equation 7.17 in Speakman (1997), namely: $r\text{CO}_2 = (N/2.078) \times (k_o - k_d) - 0.0062 k_d \times N$; where N is the size of the body water pool (ml), k_o is the turnover ratio of ^{18}O and k_d is the turnover ratio of deuterium. $r\text{CO}_2$ values were converted into energy expenditure (FMR; kJ/d) assuming an energy equivalent of $27.33 \text{ kJ l}^{-1} \text{ CO}_2$ for a fish-eating bird (Gessaman and Nagy 1988).

Water economy index

A measure of how animals conserve water is given by the water economy index (WEI, units throughout this paper: $\text{g kJ}^{-1} \text{ H}_2\text{O}$) introduced by Nagy and Peterson (1988), and calculated as the ratio of water flux ($\text{g d}^{-1} \text{ H}_2\text{O}$) and FMR (kJ d^{-1}). It is assumed that metabolic rates used to calculate WEI were obtained from animals in a steady-state regarding their water balance. This condition is often not directly measured, but it is assumed to exist when body mass remains constant during the measurement period (Nagy and Peterson 1988). In the present study, the steady-state water balance of chicks was established by comparing the

rates of water influx and efflux obtained from the DLW measurements. In the case of adults, this was assumed because the single sample DLW experiments preclude the simultaneous measurement of rates of water influx and efflux.

Statistical analyses

Computations and graphics were done using program R (2.10.0), Windows version (R Development Core Team 2014). Regression models, including ANCOVAs, were fitted with the *lm* (linear models) function, whereas fitting of Gompertz growth model was done with the *nls* (non-linear least squares) function. 95% confidence intervals of regression parameters were calculated using the adjusted bootstrap percentile method; bootstrapping was done with the package *boot* (Fox 2002). We examined the allometric scaling of physiological variables with body mass by log-transforming (base 10) the variables prior to fitting standard linear least-squared regression. Means are given ± 1 standard deviation.

Results

Total body water

Nestling total body water content (BW, g), as determined by ^2H dilution in the DLW experiments, increased with mass (m , g) according to $\text{BW}_{\text{DLW}} = 0.782 m - 5.70 \times 10^{-5} m^2$ ($r^2 = 0.999$, $n = 17$). Body water content derived from carcass analysis had a similar relationship to mass: $\text{BW}_{\text{carcass}} = 0.851 m - 7.68 \times 10^{-5} m^2$ ($r^2 = 0.998$, $n = 21$). A combined model revealed that both data-sets could be described with a common line and that the two methods of estimating water content gave the same results ($F_{2,34} = 1.8$, $p = 0.18$). The combined model (Figure 1(a)) was $\text{BW} = 0.823 m - 6.90 \times 10^{-5} m^2$ ($r^2 = 0.998$, $n = 38$). Bootstrap 95% confidence intervals of this model were 0.780–0.858 and -7.90×10^{-5} to -5.30×10^{-5} , for the first and second parameters, respectively.

The water index (WI), i.e. the percentage of nestling mass corresponding to water, decreased linearly with increasing age according to $\text{WI}_{\text{DLW}} = 79.735 - 0.258t$ ($r^2 = 0.806$, $n = 17$), where t is the chick's age in days. An almost identical model describes the water index for the carcass analysis: $\text{WI}_{\text{carcass}} = 79.98 - 0.268t$ ($r^2 = 0.824$, $n = 21$). These two models were not statistically different ($F_{1,34} = 0.06$, $p > 0.9$). The model for the combined data-sets (Figure 1(b)) was $\text{WI} = 79.83 - 0.262t$ ($r^2 = 0.834$, $n = 38$). Bootstrap 95% confidence intervals for the parameters of the combined model were 78.0–81.2 and -0.296 to -0.228 , for the intercept and slope, respectively.

Water flux

The rate of water influx (W_{influx} , g d^{-1}) in relation to chicks' body mass (m , g) was described by the allometric model: $W_{\text{influx}} = 3.839 \times m^{0.568}$, ($r^2 = 0.591$, $n = 17$). Similarly, the allometric model for the rate of water loss or efflux (W_{efflux} , g d^{-1}) in relation to chicks' body mass was: $W_{\text{efflux}} = 1.651 \times m^{0.687}$, ($r^2 = 0.800$, $n = 17$). Rates of water influx and efflux did not differ significantly from each other as revealed by an ANCOVA: the intercepts of the two models were not significantly different ($F_{1,28} = 0.07$, $p = 0.71$), and neither were the exponents ($F_{1,28} = 1.35$, $p = 0.252$). The allometric model for water flux was: $W_{\text{flux}} = 2.499 \times m^{0.628}$,

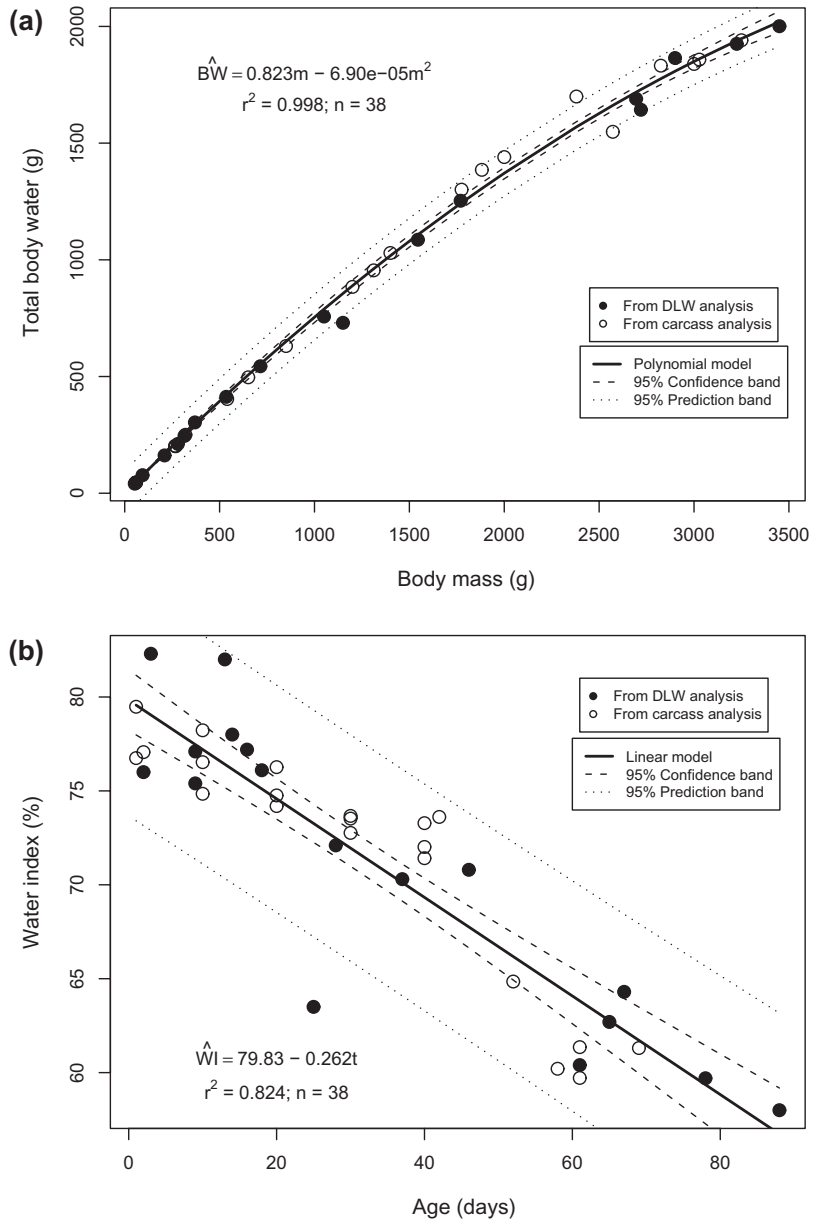


Figure 1. Body water of Cape gannet chicks at Malgas Island, over two breeding seasons 2002/2003 and 2003/2004; (a) total body water in relation to initial body mass, and (b) the fraction of nestling mass corresponding to water in relation to the chick's age.

Notes: Data corresponds to two different methods of quantifying the amount of body water: (1) from DLW experiments in which the amount of body water was calculated from the initial dilution of the ^2H isotope (solid circles); and (2) from carcass analysis (open circles) (Navarro 1992). In both panels, the models shown were fitted to the combined data-sets.

($r^2 = 0.718, n = 17$) (Figure 2). Bootstrap 95% confidence intervals for this model were 0.82–7.12 and 0.472–0.794 for the intercept and exponent, respectively.

Mean water flux of adults was $415 \pm 138 \text{ g d}^{-1}$ (range: 158.7–810, $n = 20$), and it was independent of body mass ($r^2 = 0.025, p = 0.763$).

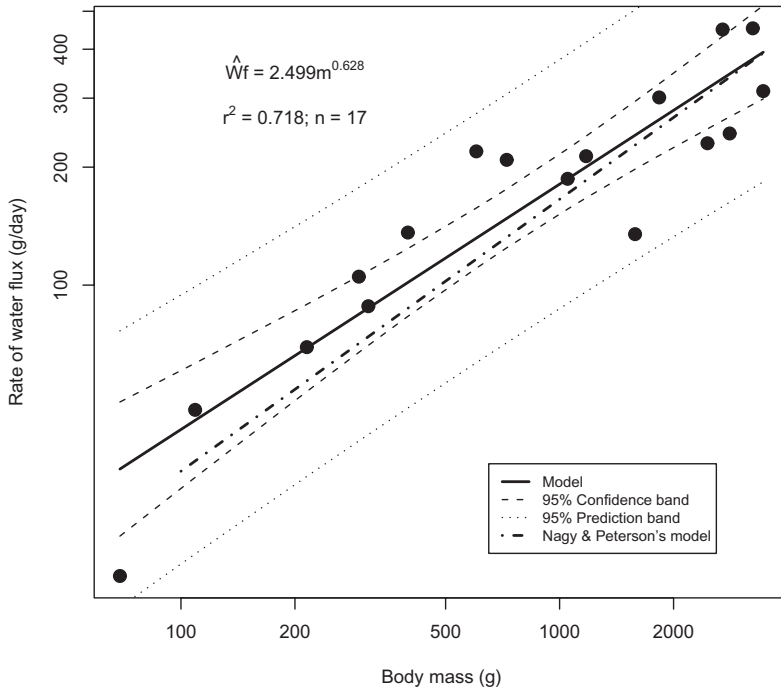


Figure 2. Rate of water flux (g/d) in relation to body mass (g) of Cape gannet chicks at Malgas Island, over two breeding seasons 2002/2003 and 2003/2004.

Notes: Water flux corresponds to the average rate of water influx and efflux measured in the DLW experiments. Body mass corresponds to the average between initial and final samples. The dot-and-dashed line corresponds to water flux predicted using the model by Nagy and Peterson (1988).

Field metabolic rate

The FMR (kJ d^{-1}) determined from DLW experiments in chicks was described by the model $\text{FMR} = 1.23 m^{0.923}$ ($r^2 = 0.944$, $n = 17$), where energy expenditure increased exponentially in relation to body mass (m ; g). The intercept's and exponent's bootstrap confidence intervals for the power model were 0.70–3.04 and 0.78–1.01, respectively. The mass-specific FMR ($\text{FMR}_{\text{ratio}}$), derived from dividing the FMR value by mass to the 3/4 power ratio (Weathers and Sullivan 1991), was independent of chick age ($r^2=0.05$, $p = 0.19$). The average $\text{FMR}_{\text{ratio}}$ was 4.11 ± 1.28 ($\text{kJ d}^{-1} \text{g}^{-3/4}$), $n = 17$.

Water economy index

WEI (g kJ^{-1}) decreased with chick age according to the model (Figure 3): $\text{WEI} = 0.676 - 0.272 \times \log_{10}(t)$, ($r^2 = 0.566$, $p < 0.01$), where t (days) is the age of the chick. Similarly, WEI decreased with chick's mass according to the model $\text{WEI} = 0.892 - 0.204 \times \log_{10}(m)$, ($r^2 = 0.538$, $p < 0.001$), where m (g) is the chick's mass. The mean WEI of adults was 0.13 ± 0.099 , $n = 20$.

Discussion

Cape gannet chicks spend the first 100–120 days of their life in the breeding colony without access to drinking water. The added effects of high levels of solar radiation put a high

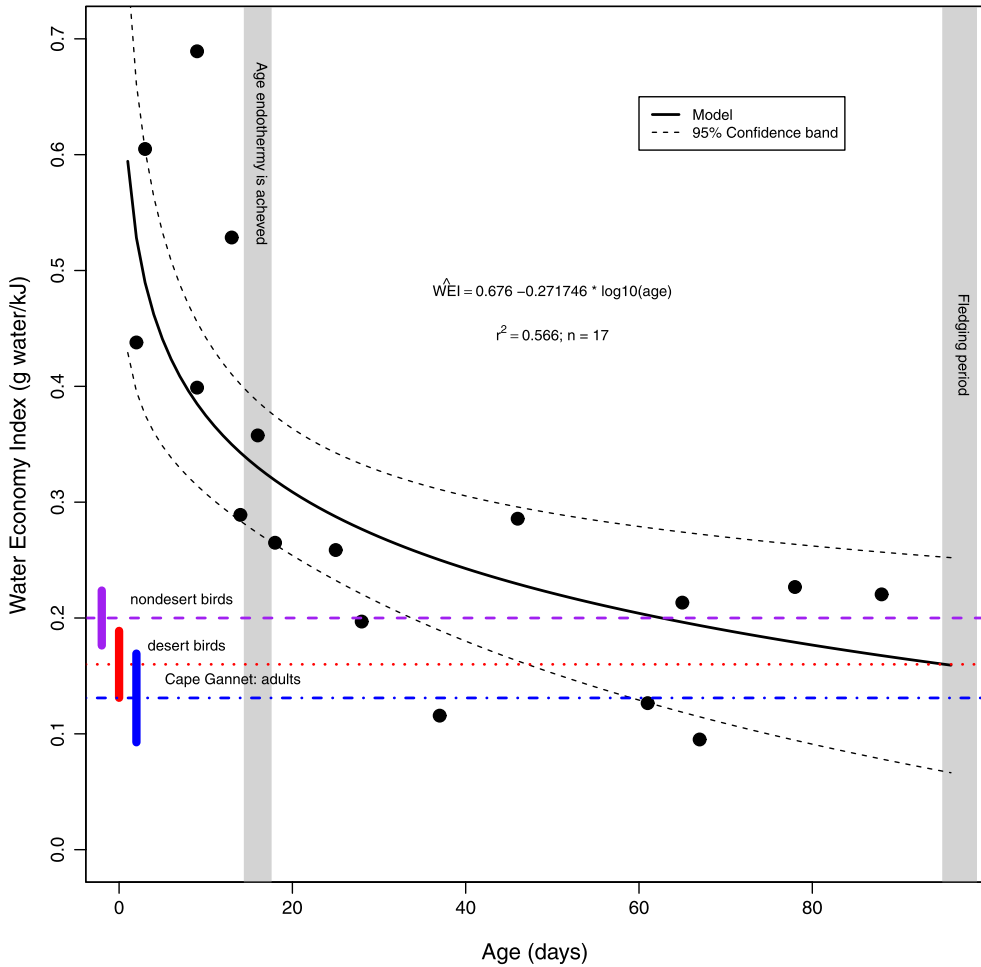


Figure 3. Water economy index (WEI, g H₂O/kJ) of Cape gannet chicks in relation to age, plus WEI for adults (blue line) at Malgas Island.

Notes: Value for desert (red line) and non-desert (purple line) birds are from Tieleman and Williams (2000). Vertical lines represent the 95% confidence interval. Estimate of age for achieving endothermy from Kirkham and Montevecchi (1982).

evaporative stress on chicks as well as adults (Hochscheid et al. 2002). In this field study, we demonstrate that Cape gannet chicks deal with both inaccessibility to water and heat stress in a similar manner as desert birds, by attaining low water efficiency index during growth. The WEI of chicks that were ready to fledge (0.14 g kJ⁻¹) was comparable to desert birds (0.16 g kJ⁻¹, Tieleman and Williams 2000). Maintaining a positive water balance is of crucial importance for juveniles, especially considering that juveniles are likely to spend several days to a week without food, and thus water, after leaving the nest and before catching their own food (Jarvis 1974; Navarro 1992). Desert birds maintain low WEI through decreased energy expenditure and reduced rates of evaporative water loss (Tieleman and Williams 2000). However, adult seabirds generally have high FMR (Ellis and Gabrielsen 2002) and FMR of Cape gannet chicks is within the range of nestling energy requirements of 30 bird species, mainly seabirds and passerines ranging from 9.7 to 3700 g (Navarro et al. 2015; see Weathers 1992; Table 1 for a list of the species included in this comparison). Additionally,

the total evaporative water loss through gular fluttering in Cape gannets is thought to be high (Hochscheid et al. 2002). How Cape gannets maintain a low WEI remains a fascinating subject for future studies, but the potential adaptive purpose will be discussed here.

Body water and field water flux

There was close agreement between the total body water of chicks measured by carcass drying (Navarro 1992) and that measured by isotope dilution. Although the carcass and DLW measurements were from two different sets of birds, the results validate the estimate of the size of the body water pool made by isotope dilution.

Rates of water flux in growing chicks of the Cape gannet were close to those predicted from Nagy and Peterson's (1988) model for a range of free living bird species. The predicted values lie within the 95% confidence interval of the gannet chick's model (Figure 2), and although Nagy and Peterson's model was formulated for adult birds, it could also be used for growing birds. The wide bootstrap range for the intercept in the model is due to the presence of an "influential observation" in the data-set, namely the lowest point in Figure 2. The inclusion or exclusion of this data point in the bootstrap samples has a great influence on the intercept estimate. However, the really important parameter in the model, the exponent, is not so greatly influenced by this data point. In this context, the intercept is a biologically meaningless concept as it represents the value of the response variable for a bird at mass zero. Data suggest that the rates of water flux between adults and juveniles or sub-adults are similar in dry environments (Williams et al. 1993; Tieleman et al. 2004; this study). The reduced water influx in areas with low water availability (Tieleman et al. 2004) might result in a potentially small buffer for variation in water fluxes, which could explain why water fluxes of chicks are comparable to adults. Also, the selection pressure on maintaining water balance would be the same for both adults and chicks (Tieleman et al. 2004). Rates of water influx and efflux of chicks were not significantly different, which is an indication that Cape gannet chicks were in a steady-state with regard to water balance during the measurements. Evaporative water loss was thus balanced with water content of prey delivered by the parents plus metabolic water. It is also evident that chicks are capable of maintaining water balance soon after hatching. Adams et al. (1991) measured rates of water flux in Cape gannet chicks and also did not find differences between influx and efflux rates. The mean water flux measured by Adams et al. (1991) was 6% below the value predicted by the combined water flux model in this study. Likely this was a consequence of the better-quality diet in their study compared to this study. The proportion of sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*) in the diet of Cape gannets was 66–84% during 1986–1988, but only 16–35% during 2003–2006 (Mullers, Navarro, Crawford, et al. 2009). Better-quality food (higher lipid content) likely resulted in less fish needed for growth and thus less water to get the same amount of energy. The lower water flux could potentially be compensated for by increased metabolic water derived from lipids during water stress (Marron et al. 2003). The water flux rates in adults show a large variation, which could be associated with variation in activity levels of the Cape gannets. Water flux increases with more time spent off the nest (Adams et al. 1991), and a large variability in foraging trip lengths (Mullers and Navarro 2010) might account for this variation between individuals. These differences in foraging effort likely explain why water flux was higher in this study compared to Adams et al. (1991). Cape gannets increase their trip durations when food

availability decreases (Mullers and Navarro 2010), which increases water flux. The decrease in availability of their preferred natural prey between the 1980s and the 2000s (Coetzee et al. 2008) would account for these patterns.

Water economy index

As tissues of growing Cape gannets mature, the proportion of body water decreases linearly with age. At the same time chicks become more efficient in their utilisation of water as the WEI also decreases with age. By the time chicks are ready to fledge their WEI was 0.14 g kJ^{-1} , which was within the 95% confidence interval of the adult WEI and also within the 95% CI for desert birds, but well below the 95% CI for non-desert birds (Figure 3).

WEI calculated for Cape gannet data from Adams et al. (1991) was $0.07 \text{ g kJ}^{-1} \text{ H}_2\text{O}$, within 1 SD of the mean value ($0.13 \text{ g kJ}^{-1} \text{ H}_2\text{O}$) in the present study. The low WEI in Adams' study was likely caused by the high-quality fish consumed by gannets in the 1980s (Mullers, Navarro, Crawford, et al. 2009), when less fish was needed to sustain energy output. Nagy et al. (1984) used DLW to measure FMR, including water flux, of breeding African penguins *Spheniscus demersus*. From data in their Table 1, we calculated WEI to be 0.14 ± 0.010 ($n = 10$), which is almost identical to the value reported in the present study for Cape gannets. These two species endemic to the Benguela Upwelling System are in the lower spectrum of seabirds' WEI (Tieleman and Williams 2000). From Table 1 of Tieleman and Williams (2000), WEI can be calculated for three seabird groups. WEI for Laridae was 0.22 ± 0.040 ($n = 4$), for Spheniscidae 0.18 ± 0.068 ($n = 5$) and for Procellariidae 0.27 ± 0.108 ($n = 7$). Variation in life history strategies and environmental conditions likely accounts for these differences between seabird groups.

According to Tieleman and Williams (2000), desert environments have three characteristics that might favour selection for lower FMR and BMR, which they consider to be the main reason for maintaining low WEI: (1) individuals with low FMR would fare better in deserts that characteristically have low productivity; (2) limited supply of drinking water may influence the energy balance of desert birds; and (3) the relatively high environmental temperatures in deserts reduce thermoregulatory requirements and might result in a combined reduction of FMR and BMR. Most likely, these factors act in concert to select for a combination of reduced FMR and BMR coupled with low rates of water flux in desert birds (Tieleman and Williams 2000). In the case of Cape gannets, the low primary production of deserts could be equated to the effort needed to locate patches of food in the marine environment; on average Cape gannets made foraging trips of 'on average 24.6 h (Mullers and Navarro 2010) during our study. However, they do not conform to the prediction of reduced metabolic rates as it is well established that seabirds have higher FMR than terrestrial birds (Birt-Friesen et al. 1989; Tieleman and Williams 2000). Some seabirds have relatively low FMR using soaring flights as a means to conserve energy (Birt-Friesen et al. 1989), but not Cape gannets (Mullers, Navarro, Daan, et al. 2009). Comparable to desert birds, Cape gannets have limited access to water during the breeding season. Higher temperatures increase the need for evaporative cooling, resulting in an increased rate of water flow (Schleucher et al. 1991), which in turn could be reduced by lowering endogenous heat production and/or increasing tolerance to hyperthermia. The benefits of point 3, i.e. reduced metabolic rates by saving energy in thermoregulation do not seem to apply to Cape gannets, which are subjected to heat stress during the breeding season and have the need to invest energy

in gular fluttering and increase water flow through evaporative cooling (Hochscheid et al. 2002). Cape gannets must therefore have developed different strategies to maintain low WEI. One confounding factor that must be taken into consideration is the fact that adult Cape gannets, like most seabirds, can drink seawater as excess salt is eliminated by salt glands.

WEI can be difficult to interpret and should only be discussed in light of the environmental conditions of the species (Tieleman and Williams 2000). Cape gannet chicks completely depend for their water on the food provided by their parents and they spend their first few months on the breeding island where heat and solar radiation can be severe (Hochscheid et al. 2002). WEI calculated from Table 1 of Tieleman and Williams (2000) for seabirds breeding in polar regions was 0.25 ± 0.110 ($n = 10$). Chicks from these species also have limited access to drinking water, but have no evaporative stress and thus less need to have evolved water saving strategies. The low WEI found in gannets is likely sustained through an energy (Batchelor and Ross 1984) and lipid (FAO 1989)-rich diet. Fish prey species differ considerably in macronutrient (lipid and protein) and water composition, and to sustain growth and water balance, adult seabirds need to supply the growing chicks with a nutritionally balanced diet (Machovsky-Capuska et al. 2016). For example, water content of prey species varies inversely with lipid content (Montevocchi and Piatt 1984; Machovsky-Capuska et al. 2016) and prey selection should thus complement all nutritional requirements of the chicks. Nutritional composition of prey also varies between locations, between years and even within years (Machovsky-Capuska et al. 2016). Variation in foraging behaviour of Cape gannets between and within seasons and also between sexes (Mullers and Navarro 2010) might be a consequence of the different foraging strategies to acquire these nutrients (Machovsky-Capuska et al. 2016). Machovsky-Capuska et al. (2016) suggest that predators benefit from the opportunity to catch a variety of prey species that are nutritionally complementary, even when each species by itself would be insufficient to maintain nutritional requirements. If, however, prey availability is limited, as for the Cape gannets during this study (Mullers, Navarro, Crawford, et al. 2009), parents might not be able to complement each other to deliver all nutrients necessary to sustain their chick's growth (Mullers, Navarro, Crawford, et al. 2009) and water balance (this study).

The water intake through the diet is presumably enough to balance the water loss through evaporative cooling and excretory faecal water loss. It is recognised that fat reserves are not only an energy source, but also a water source as complete combustion of 1 g of fat produces about 1.1 g of metabolic water (Mellanby 1942). Therefore, a lipid-rich diet is not only important for chicks to sustain growth (Mullers, Navarro, Daan, et al. 2009), but also to maintain water balance in the breeding colony. Chicks that die during development likely die of starvation, but the possibility of a disturbed water balance as a reason should not be dismissed. Cape gannets seem to out-perform desert birds in their water economy, as desert birds maintain a low WEI by also having a low FMR (Nagy 2004), whereas Cape gannet chicks do not maintain low FMR, but are able to keep a mean WEI comparable to that of desert birds.

Adaptive purpose

During the several stages of their lives, Cape gannets would benefit from maintaining a low WEI. Gannet chicks develop dark plumage after about six weeks, which has higher energetic costs associated to compensate for the increased thermal load (Hochscheid et al. 2002). To deal with heat in the colonies, juveniles use gular fluttering more frequently than parents, during which substantial amounts of water can be lost (Schleucher et al. 1991; Ellis et al. 1995).

Water saving efficiency increases when chicks grow older and is optimal when required for a prolonged period without food and water. Mortality rates of Cape gannets at different life stages is highest just after fledging (Oatley et al. 1992), which is related to fledging mass (Jarvis 1974). When Cape gannet fledglings leave their nest, they spend several days to a week on the breeding island without being fed by their parents (Jarvis 1974). Once the conditions are right they will go to sea, after which they have to learn how to catch their own food. Cape gannets have adapted to overcome this prolonged period of not receiving any food by storing extra fat that is utilised during this stage (Navarro 1992). Fat reserves in seabird fledglings are thus considered to be crucially important for the initial survival after fledging (e.g. Horswill et al. 2014). However, during this period, gannet chicks also receive no water for several days to more than a week and we therefore propose that the mechanism to conserve water may be as important for survival as energy storage. The small WEI in adults might be a physiological adaptation to the necessity in early development and an adaptation to the breeding season where adults have to stay for more than 24 h on the nest (Mullers and Tinbergen 2009).

The actual mechanisms as to how the Cape gannets manage to maintain low WEI remain speculative, but the fitness consequences of maintaining water balance in a hot and dry environment can be a crucial selective force. Potentially the metabolic water production from lipid-rich food equals the loss through evaporative cooling (Bozinovic and Gallardo 2006). The high-quality food sustains high FMR (Ellis and Gabrielsen 2002), growth of the chicks (Mullers, Navarro, Crawford, et al. 2009) and possibly allows gannets to maintain a low WEI (this study). Therefore, the costs of the switch in diet from high-quality prey to low-quality fish offal (Mullers, Navarro, Crawford, et al. 2009) due to the shift in natural prey species (Coetzee et al. 2008), might not only have fitness consequences through adult body condition and reproductive performance (Grémillet et al. 2016), but might also have hidden costs in not maintaining water balance. Temporary decreases in the quality of food could thus affect survival through different pathways and have large detrimental effects on the species numbers (Crawford et al. 2008). The effects of climate change on the marine environment are complex, generating abiotic changes that require biological responses (Harley et al. 2006). The rise in temperature will further increase the need for seabird species breeding in the Benguela and comparable systems to maintain high water efficiency. Future physiological studies should focus on the mechanisms behind the water efficiency in seabirds to predict the ability for these species to adapt to increasing temperatures.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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