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ORIGINAL PAPER

Ibis and spoonbill chick growth and energy requirements: implications for wetland and water management

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Abstract Colonial-nesting waterbirds such as ibis and spoonbills (Threskiornithidae) can account for a significant proportion of energy flow through wetlands, particularly during large breeding events. However when food availability is reduced, chicks may starve and adults may abandon nests. If the energy required to rear chicks could be calculated, data quantifying prey energy value and availability could be used to develop landscape scale management targets to ensure that food requirements are met to support chicks until they attain independence, thereby maximising recruitment. We calculated ibis and spoonbill chick biometrics and energy requirements through (a) an international literature review, extracting and synthesising the best available growth and energy data; (b) new measurements of ibis and spoonbill chick biometrics for selected species; and (c) analysis of the resulting databases to construct growth curves and predict energy requirements for selected species. Here we present the first models of Royal Spoonbill growth and of Royal Spoonbill and Australian White Ibis chick energy requirements. The total energy estimated to raise a single Royal Spoonbill chick from hatching to independence was 71,290 kJ and for an Australian White Ibis chick was 67,160 kJ. Using prey energy values from the literature, extrapolations indicate that for either species, a nesting event of 1000 nests producing three chicks per nest would require an estimated ten tonnes of freshwater crayfish (*Cherax destructor*) or eight tonnes of invasive juvenile carp (*Cyprinus carpio*) to support chicks from hatching to independence. Effective water and wetland management is critical to optimise both energy availability in foraging sites and breeding success.

Keywords Threskiornithidae · *Platalea regia* · *Threskiornis molucca* · Food · Energy · Biometrics

Introduction

Colonial-nesting waterbirds such as ibis and spoonbills (Threskiornithidae) can account for a large proportion of energy flow through wetlands and are often used as bio-indicators, usually with a focus on the size, frequency, and success of their breeding events (Kingsford et al. 2013). Colonial-nesting species may congregate in tens to hundreds of thousands (10,000's to 100,000's) to breed, often

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concentrating foraging efforts within specific limited areas (Jenkins et al. 2009). It is estimated that raising young may double the daily energy requirement of parent birds (Hancock et al. 1992; Kushlan 1977a).

When food availability is reduced during breeding events, colonial-nesting waterbirds may change their behaviour to reduce energy expenditure (Elliott et al. 2014). In cases where the availability of food drops below a certain level, chicks may starve or be abandoned (Brandis 2010; Herring et al. 2011; Kingsford and Auld 2005). For many species, food availability is positively related to the extent, depth and duration of flood inundation of suitable habitat. This is because inundation is required to promote the growth and reproduction of their preferred food sources, for which many colonial-nesting waterbirds have developed specialised foraging techniques and associated morphological adaptations. Prematurely or rapidly falling water levels are therefore an indicator of potential loss of food resources and foraging opportunities (Brandis 2010; Herring et al. 2011; Kingsford and Auld 2005).

Allocation of valuable management resources such as ‘environmental water’ is frequently targeted at supporting completion of breeding events, usually by supplying water to prevent nest abandonment due to falling water levels (Brandis 2010; Brandis et al. 2011; Kingsford and Auld 2005). In Australia, breeding sites of Straw-necked Ibis (*Threskiornis spinicollis*), Glossy Ibis (*Plegadis falcinellus*), and Royal Spoonbills (*Platalea regia*) are intensively managed in this way (Brandis et al. 2011; Kingsford and Norman 2002). However, while knowledge exists regarding water management of nesting sites to prevent nest abandonment, there is limited knowledge about food, energy, or foraging habitat requirements to prevent chick starvation and ensure sufficient recruitment to maintain a sustainable population size. Demographic data for Threskiornithidae populations are rare, particularly in Australia, making it difficult to estimate previous or existing recruitment rates or how many chicks must be recruited to ensure breeding adults are replaced in the population. However while ibis and spoonbill species in Australia are not yet listed as species of conservation concern, their populations are thought to be in steep decline due to changes in flood inundation regimes and associated resource loss, and similar species internationally are listed as endangered for similar reasons. While effective recruitment requires survival of eggs, chicks in the nest, juveniles out of the nest, and sub-adults up to adult breeding age (thought to be approximately 3 years for some species), supporting chick survival at the nesting site is a first step via which managers of wetlands and water can support populations.

Better understanding of chick energy requirements is needed to inform management of food sources and improve chick survival. However direct metabolic measurements are rare worldwide and do not exist for Australian species. In order to estimate chick energy requirements without direct metabolic measurement, data are required describing waterbird biometrics at a range of age stages, in order to apply allometric relationships between metabolism and body size (White 2011). Body mass in particular has a strong allometric relationship with metabolism and accounts for over 90% of interspecific variation in energy expenditure (White 2011). Using allometric models, the daily energy expenditure of a species can be calculated from body mass, then combined with an estimate of digestion efficiency to give a daily energetic requirement (Kendeigh 1970; Nagy 1987). However, biometric data are rare worldwide and especially in Australia, even for species of management interest (Kingsford and Norman 2002). In Australia, some limited data exist describing the growth of Australian White Ibis *Threskiornis molucca* (Marchant and Higgins 1990; Smith et al. 2013) and Glossy Ibis (Miller and Burger 1978; Williams 1975), but no growth data are available for the other three species of Australian Threskiornithidae, the Straw-necked Ibis, Royal Spoonbill, and Yellow-billed Spoonbill (*Platalea flavipes*). These species are of particular management interest in Australia when considering environmental water allocations.

If the energy required by Threskiornithid chicks to survive to independence can be calculated, meaningful management targets can be set to ensure that sufficient food can be provided to support a specified number of chicks. The aim of this study was develop chick growth and energy models to inform management, through (a) an international literature review, including extraction and synthesis of all available Threskiornithid biometric and energy data; (b) field measurement waterbird chick biometrics for two Australian species, Royal Spoonbills and Australian White Ibis; and (c) analysis of the resulting databases to construct growth curves and predict chick energy requirements.

Methods

Chick growth and energy models were developed using two sources of data: (1) an international literature review, including extraction and synthesis of all available Threskiornithid biometric and energy data; (2) field measurement of waterbird chick biometrics. Biometric data were used to construct predictive growth models, which were then used to develop models of chick energy requirements for three species: Royal Spoonbill, Australian White Ibis and Glossy Ibis.

Synthesis of growth and energy data

An extensive global literature review was conducted with the aim of extracting all existing data describing biometrics including body mass, growth, energy requirements and energy expenditure of species in the family Threskiornithidae. The approach used transparent and consistent search and filtering methods with specific inclusion and exclusion criteria (CEE 2018). Final searches were conducted in: Web of Science Core Collection; Web of Science All Databases; NRM Knowledge Online; Trove; and Google Scholar (Supplementary Material Table S1).

In order to use all available data, mean values were estimated where none were given, assuming a normal distribution, and maximum and minimum values were used to represent variability. Where sample sizes were not reported, the minimum possible sample size for the reported values was allocated. Hence, the synthesised values presented here represent the mean of published means, the maximum and minimum published values, and the minimum possible sample sizes for each species. Where more accurate estimates of variability and sample size were available, standard deviations are presented instead.

To compare chick body mass growth between Threskiornid species for which data were available, values were divided by the mean adult body mass of the species and graphed as the proportion of adult body mass. Where adult body mass was provided, this value was used to calculate the proportion of adult body mass. Where no adult body mass was provided the mean adult body mass derived from the literature review was used. The same approach to the selection of adult body mass values was used to derive mass specific energy expenditures where none were calculated in the relevant studies.

Field data collection

Due to the scarcity of chick biometric data in the literature, additional field data collection was conducted to provide empirical data for modelling of growth and energy requirements. Royal Spoonbill and Australian White Ibis chicks were measured during December 2017 and January 2018 at the Reed Beds Wetland, Mathoura, NSW (35.8393° S, 144.9475° E) and Middle Lake, Kerang, Victoria, (35.6639° S, 143.8754° E), Australia. These are sites at which ibis or spoonbill breeding is estimated to occur in approximately seven of every 10 years. Reed Beds Wetland dries out each year, while Middle Lake is permanently inundated. Environmental conditions were within the range of variability usual for these sites. Chick biometrics were collected for 35 Australian White Ibis chicks ranging from 2 to 33 days old, and 27 Royal Spoonbill chicks ranging from 9 to 30 days old (up to the age of flight when capture becomes difficult). Body mass, bill length, head-bill length, wing length, and tarsus length were recorded for each chick using Reichenow's (1913) standard techniques. Chicks were allocated an age in days using species specific diagnostic features derived from monitoring camera data (Wenger and McGinness 2018). Rather than perform repeated measurements on the same chicks, measurements were taken of chicks of varying age classes. While single measurements on multiple chicks mean that there is potential lack of independence of observations at site level, this approach was taken to reduce disturbance to individual chicks, maintain independence of data points, and obtain results representing colony level growth. All animal handling was conducted under UNSW ACEC (Animal Care and Ethics Committee) Authority Approval No. 17/122B.

Predictive growth models

Predictive growth models were developed for three species: Royal Spoonbill, Australian White Ibis and Glossy Ibis. If well fitted, species specific growth models may be used to predict growth parameters at ages for which no measured data exist (Ricklefs 1968). Avian growth curves often cease at 25–40 days of age, when values approach 90% of their adult values and recapture of chicks becomes difficult due to their mobility (Kushlan 1977b; Smith et al. 2013). However, the success of a managed breeding event at a particular site may be judged by the number of chicks that survive to the age at which foraging independence from the parent birds is reached. This is approximately 50 days for Threskiornithids, since first flight occurs around 30 days of age (Wenger and McGinness 2018) and foraging independence is estimated to occur ~ 21 days after the chick's first flight (Baynard 1913; Dementiev and Gladkov 1951; Marchant and Higgins 1990). This is beyond the scope of most existing growth curves. However if the average mass of an adult of the species is known, a predictive growth curve allows the estimation of chick mass up until foraging independence (Ricklefs 1968). This predictive model can then be used in conjunction with allometric equations to estimate daily chick energy requirements from hatching to independence (Kushlan 1977c). Following this logic, we used existing data from the literature together with the field-collected data to create growth curves that were then extrapolated to 50 days (foraging independence) based on adult mass data from the literature and subsequently used to estimate daily chick energy requirements. This process is described in more detail below.

When fitting growth curves to biological data a model must be chosen that accurately describes the growth pattern of the organism, but also allows for meaningful interspecific and intraspecific comparisons (Ricklefs 1967; Tjørve and Tjørve 2010). Avian growth follows a sigmoidal curve, with the most commonly fitted curves being the Gompertz, logistic, and von Bertalanffy models (Lok et al. 2014; Ricklefs 1968; Tjørve and Tjørve 2010).

$$\text{Gompertz model}: y_t = A\exp(-\exp(-k(t - T_i))) \tag{1}$$

$$\text{Logistic model}: y_t = {}^{A}\!/\!(1 + \exp(-k(t - T_i))) \tag{2}$$

$$\text{von Bertalanffy model}: y_t = A(1 - \exp(-k(t + A_0)))^3 \tag{3}$$

where t represents a given age, and y_t represents the value of the growth parameter at that age. These curves mainly differ in the placement of their inflection point (T_i), which describes the age at which the maximum growth rate occurs. The inflection point T_i occurs earliest in the logistic model and, because it reaches an earlier asymptote, is more suited to fast growing parameters compared with the other two models, with T_i occurring latest in the von Bertalanffy curve. Examples of fast growing biometric parameters suited to a logistic growth model include wing length in Red-throated Loon (*Gavia stellata*) chicks (Rizzolo et al. 2015) and tarsus length in American White Ibis (*Eudocimus albus*) chicks (Kushlan 1977b). In addition to T_i, descriptive parameters predicted by these growth models include:

- the growth rate constant (k), which describes the rate that the slope changes with age
- the upper asymptote (A)
- the lower asymptote (A_0), for the von Bertalanffy model only

To improve the reliability of avian growth models, a fixed asymptote may be used (Tjørve and Tjørve 2010). Because the upper asymptote of a growth model (A) effectively represents the eventual adult mass or length of a physical parameter, where numerous and reliable adult measurements are available, the model can be better informed by affixing the asymptote to known adult values (Tjørve and Tjørve 2010). Alternatively, a free asymptote (estimated or fitted) may be used (Tjørve and Tjørve 2010).

Gompertz, logistic, and von Bertalanffy models were all fit to the data for each of the three species (Royal Spoonbill, Australian White Ibis and Glossy Ibis) using the nls function from the stats package in R (R Core Team 2016; Wickham 2017). In the interest of maximising the dataset and increasing sample size, mean body mass values for Australian White Ibis chicks (n = 7) from the literature review were included in the analyses (Marchant and Higgins 1990; Smith et al. 2013). Both free and fixed asymptote models were tested for all three species and goodness of fit was assessed using Akaike's Information Criterion (AIC) (Motulsky and Christopoulos 2004). The most representative models for the Royal Spoonbill and Australian White Ibis had the asymptote (A) fixed to the mean adult value for the relevant biometric parameter, obtained by calculating the mean of means for each species from the literature review, while a free asymptote provided a better fit for Glossy Ibis. Model sensitivity to the fixed asymptote value for the Australian White Ibis was analysed by re-running the best fitting body mass growth model with the maximum and minimum study means for adult Australian White Ibis from the literature review (max = 1901 g, Marchant and Higgins 1990; min = 1685 g, Smith et al. 2013) and comparing total predicted energy requirements from hatching to foraging independence with the base model. Initial parameters for the models were estimated from growth data for the same species, obtained from the literature search for Glossy Ibis (Miller and Burger 1978; Williams 1975) and from both the literature and from field data from this study for Royal Spoonbill and Australian White Ibis (Table 1). The only exception was that for Royal Spoonbill head-bill length, a mean value for Eurasian Spoonbill (*Platalea leucorodia*) was used, as no adult head-bill values were available for Royal Spoonbill.

Chick energy requirement models

The energy needs of growing chicks are most commonly reported in terms of field metabolism, or daily energy requirements, rather than the intake of energy required for survival (Fort et al. 2011; Rizzolo et al. 2015; Santoro et al. 2015). To convert energy expended into energy required, an estimate of the digestive efficiency, meaning the proportion of energy consumed that is assimilated, is required (Ricklefs 1974; Sutherland et al. 2004). Experimentally determined estimates of Threskionithid digestion efficiency are limited to Kushlan's (1977a, c) American White Ibis (*Eudocimus albus*) studies, which both resulted in estimates of 79%. Consequently, Santoro et al.'s (2015) data describing wild Glossy Ibis chick daily energy expenditure derived from doubly-labelled water measurements were extracted and divided by Kushlan's (1977c) mean estimated digestive efficiency for American White Ibis chicks. While gut length and digestive efficiency may differ between these species, we expect the effect of any differences to be relatively minor and the models can be updated when species-specific data become available. A linear model was fit to the $\log_{10}$ of the resultant data using the lm function in R, with goodness of fit assessed using the coefficient of determination (R Core Team 2016).

Table 1 Initial parameter values used to fit growth curves to ibis and spoonbill biometric data, derived from the literature review and field measurements

Species	Parameter	Body mass	Wing	Bill	Head-bill	Tarsus	References
Royal Spoonbill	A	1685	366.9	186.9	248.5[a]	127.1	Lok et al. (2014) and field measurements
	A_0	− 1.3	− 3.1	− 8	− 12	− 7	
	T_i	9.7	14.7	11.3	7.9	10.6	
	k	0.147	0.095	0.056	0.052	0.157	
Australian White Ibis	A	1847	356.5	167.1	223	93	Smith et al. (2013) and field measurements
	A_0	− 1.8	− 4.2	− 6.7	− 11.2	− 12.3	
	T_i	8	15.5	11.6	7.4	9.2	
	k	0.124	0.077	0.041	0.055	0.116	
Glossy Ibis	A	617	–	–	–	–	Miller and Burger (1978), Williams (1975)
	A_0	− 1.8	–	–	–	–	
	T_i	7	–	–	–	–	
	k	0.178	–	–	–	–	

Values for the asymptote (A) equal the mean of the relevant biometric from the literature review

The growth rate constant was derived using the equation $k = (e * g_{\max})/A$, where $g_{\max}$ is the maximum growth rate (Lok et al. 2014)

[a] Mean value for Eurasian Spoonbill (*Platalea leucorodia*) used as no adult head-bill values available for Royal Spoonbill

The assumptions of linear regression were tested with the gvlma package in R (Pena and Slate 2014). A log-linear model was used for consistency with accepted allometry techniques (White 2011) and so that a scaling coefficient, the slope of the logarithm of metabolism and body mass, could be produced for comparison with the existing literature (White 2011). Energetic models were based on body mass because it is the best biometric predictor of daily energy requirements (Santoro et al. 2015).

Prior to estimating the daily energy requirements of Royal Spoonbills and Australian White Ibis, a model was created based on the allometric energy requirements of Glossy Ibis chicks and cross-validated with all available measured Threskiornithid chick energetic requirements from the literature. The body mass growth model calculated for Glossy Ibis was used to predict Glossy Ibis body mass for 0–50 days of age. The predicted body masses were then used with the derived allometric equation to model the daily energy requirement of a Glossy Ibis chick from hatching to independence. These results were then cross-validated with all mass specific energy requirements (energy required per gram of body mass) for ibis species with published chick and/or adult values from the literature review (Table 2, Supplementary Material Table S2). The mass specific energy requirement was calculated by dividing the total daily energy requirement by the body mass of the measured bird (Table 2). Further cross-validation was performed by comparing energetic requirements of ibis species extracted from the literature review with modelled energetic requirements for a Glossy Ibis of the same body mass or age, where known. Energetic models were then created for the Australian White Ibis and the Royal Spoonbill and estimations of mean individual energy requirements calculated 0–50 days of age.

Results

Synthesis of growth and energy data

Literature searches located 105 studies describing biometrics including body mass, growth, energy requirements and energy expenditure of species in the family Threskiornithidae, including 53 references extracted from Hancock et al. (1992). Additional studies on non-Threskiornithid species were used to assess and inform methods and models. Adult biometric data were collected from the literature for 30 species and juvenile biometric data were collected for seven species across 66 studies from 18 countries (Supplementary Material Table S2). This represents the most extensive collation of biometric data on Threskiornithid species to-date.

Predictive growth models

Growth patterns in body mass have been described for eight species of ibis and two species of spoonbill globally. Of these, descriptive growth models have only been applied to four species: American White Ibis, Red-naped Ibis (*Pseudibis papillosa*), Eurasian Spoonbill, and Australian White Ibis (Kushlan 1977c; Lok et al. 2014; Smith et al. 2013; Soni et al. 2009). Body mass growth records generally ceased at around 30–40 days of age, when an asymptote was approached (Kushlan 1977b, c; Lok et al. 2014). While chicks can reach up to 90% of adult body mass by 23 days old, it may take more than a year for full adult body mass to be reached (Kushlan 1977c). Maximum growth rates in body mass occurred just prior to 10 days of age (T_i = 7–10 days old, Table 3). Variability in body mass increased with bird age, between and within species. Between species, mean hatching body mass ranged from 3 to 5% of mean adult body mass in wild chicks, but by 30 days of age species differed by 34% of mean adult body mass (Fig. 1). Within species, the growth rate of captive chicks followed a similar curve shape but was slower and reached a lower asymptote than wild chicks (Archibald et al. 1980; Kushlan 1977c).

Predictive growth curves were fit to biometric data for Glossy Ibis, Australian White Ibis, and Royal Spoonbill chicks (Figs. 2, 3, 4). The Gompertz and von Bertalanffy models provided better goodness of fit for all biometric parameters compared to the logistic model, except for Royal Spoonbill wing growth (Table 4). There was little difference in the goodness of fit of the von Bertalanffy and Gompertz models for most parameters, so the model with the lowest AIC was selected in most cases (Supplementary Material Tables S3, S4). An exception was made for the Royal Spoonbill body mass model, because the von Bertalanffy model (AIC evidence ratio 1.3) provided an unrealistic y-intercept, predicting chick mass to be only 3 g at hatching. The Gompertz model provided a

Table 2 Summary of the available data on the daily energy expenditure of spoonbills and ibis (± SD)

Species	Age class or mass	N	Breeding? (Y/N)	Energy expenditure (kJ bird^{-1} day^{-2})	Energy requirement (kJ bird^{-1} day^{-2})	Weight specific energy requirement (kJ g^{-1} day^{-2})	Method	References
American White Ibis	Adult	NA[a]	Y	680[b]	972	1.09	Allometry (Wiens and Dyer 1977)	Bildstein (1987)
Eudocimus albus	Adult	NA^	Y	689	864	0.911	Allometry (Kendeigh 1970)	(Kushlan (1977a)
	Chick 0–40 days[c]	5	N	719 ± 159	909 ± 187	1.99 ± 0.86	Free feeding Kendeigh 1970)	Kushlan (1977c)
Glossy Ibis *Plegadis falcinellus*	Chick 300–550 g	44	N	481 ± 80	609 ± 101	1.46 ± 0.17	Doubly labelled water (Butler et al. 2004)	Santoro et al. (2015)
Northern Bald Ibis *Geronticus eremita*	Adult	9	N	1440 ± 720	1823 ± 911	1.31 ± 0.65[d]	Doubly labelled water (Visser and Schekkerman 1999)	Bairlein et al. (2015)

Energy requirement was calculated by multiplying the daily energy expenditure by Kushlan's (1977a, c) digestion efficiency of 79% for American White Ibis, and the weight specific energy requirement was calculated by dividing the total daily energy requirement by the body mass of the measured bird

[a] Sample sizes not given because data were calculated theoretically by the authors and not directly measured

[b] Represents the mean of the author's calculated values for the male (745.6 kJ day^{-1}) and female (614.6 kJ day^{-1}) of the species

[c] Chicks reared in captivity

[d] Body mass not given; mean adult body mass of 1393 g used to calculate weight specific energy requirement

Table 3 Growth model parameters for selected species derived from the literature

Species	Model	Biometric parameter (g or mm)	k (growth rate constant)	A (upper asymptote)	Ti (time of inflection; days)	References
American White Ibis	Logistic	Body mass	0.185	7000	–	Kushlan (1977b)
Eudocimus albus	Gompertz	Bill	0.043	125.5	–	
	Logistic	Tarsus	0.180	94.5	–	
	von Bertalanffy	Tail	0.020	95	–	
Red-naped Ibis	Gompertz	Bill	0.0013	362	–	Soni et al. (2009)
Pseudibis papillosa		Tarsus	0.1359	84	–	
		Tail	0.1189	165	–	
Eurasian Spoonbill[a]	Gompertz	Body mass	0.147 ± 0.005	1555 ± 29	9.7 ± 0.2	Lok et al. (2014)
Platalea leucorodia		Wing	0.095 ± 0.004	355 ± 7	14.7 ± 0.3	
		Bill	0.056 ± 0.002	129 ± 3	11.3 ± 0.5	
		Head-bill	0.052 ± 0.002	184 ± 5	7.9 ± 0.6	
	Logistic	Tarsus	0.157 ± 0.005	152 ± 2	10.6 ± 0.3	

Species	Model	Biometric parameter	Model parameters[b]				References
			a	b	c	d	
Australian White Ibis	Quasi-Newton sigmoid[b]	Body mass	761.73 ± 48.75	0.18 ± 0.02	−11.28 ± 0.60	614.81 ± 31.58	Smith et al. (2013)
Threskiornis molucca		Wing	163.40 ± 7.14	0.13 ± 0.01	−17.07 ± 0.38	151.33 ± 3.17	
		Bill	53.04 ± 5.37	0.10 ± 0.01	−11.57 ± 1.18	46.49 ± 2.82	
		Head-bill	69.73 ± 6.90	0.10 ± 0.01	−9.04 ± 1.33	71.49 ± 4.43	
		Tarsus	44.61 ± 3.06	0.17 ± 0.01	−9.41 ± 0.71	47.82 ± 2.22	
		Tail	59.76 ± 4.25	0.18 ± 0.02	−23.56 ± 0.60	65.41 ± 2.44	

Asymptote values are given in grams or millimetres

[a] Parameters for Lok et al. (2014) represent the average value for male and female growth curves combined

[b] Equation fit by Smith et al. (2013) $y_t = a\frac{\exp(b(t+c))-1}{\exp(b(t+c))+1} + d$ where t is age in days and y_t is the biometric parameter. Model parameters: a = the lateral position of the curve (values where inflection points lie); b and c determine the asymptote; d = the specific growth rate

chick mass of 64 g at hatching, which is more in line with published values for Threskiornithid hatchlings at 0 days (Australian White Ibis 34–70 g, Marchant and Higgins 1990; African Spoonbill (*Platalea alba*) 33–39 g, Sweeney 1993). A free asymptote was selected for the Glossy Ibis body mass growth model because it provided a better fit for chick growth from 0 to 30 days than the fixed asymptote model (AIC evidence ratio 951, Fig. 2). Consequently, the predicted asymptotic value of this model fell toward the lower end of adult body mass values from the literature review (predicted = 484.7 ± 21.4 g, literature review min–max: 485–768 g).

Variability in all biometric measurements increased with age in Australian White Ibis chicks, particularly for body mass and tarsus length. Bill and head-bill length were the least variable parameters for both Australian White Ibis and Royal Spoonbill chicks (Supplementary Material Figs. S1 and S2). Biometric parameters differed within species in the rate at which they approached asymptotic mass. Tarsus length reached an asymptote before 30 days of age in both Royal Spoonbills and Australian White Ibis, and 90% of adult body mass was attained by both species before the independence age of 50 days. Bill and head-bill length were the slowest growing parameters for both species, with only 78% and 83% for Australian White Ibis and 73% and 78% for Royal Spoonbill of mean adult size reached by independence, respectively (Supplementary Material Figs. S1 and S2). There were also interspecies differences in body mass growth. Royal Spoonbill chicks approached asymptotic body mass earlier than Australian White Ibis chicks, reaching 90% of mean adult body mass at just 25 days old, compared to 38 days old for white ibis chicks.

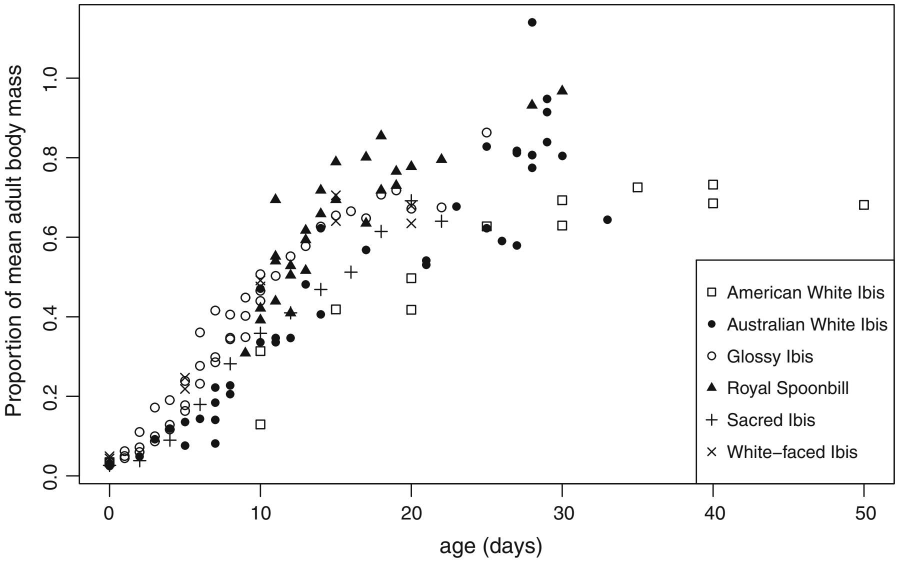

Fig. 1 Plot of mean wild chick body mass as a proportion of mean adult mass of species in the Threskiornithidae family. Data were sourced from the literature (n = 94, hollow points), with individual values for the Royal Spoonbill (n = 27) and Australian White Ibis (n = 35) (filled points) sourced from the current study (Garrett 1996; Kopij 1999; Kushlan 1977b, c; Marchant and Higgins 1990; Miller and Burger 1978; Smith et al. 2013; Williams 1975)

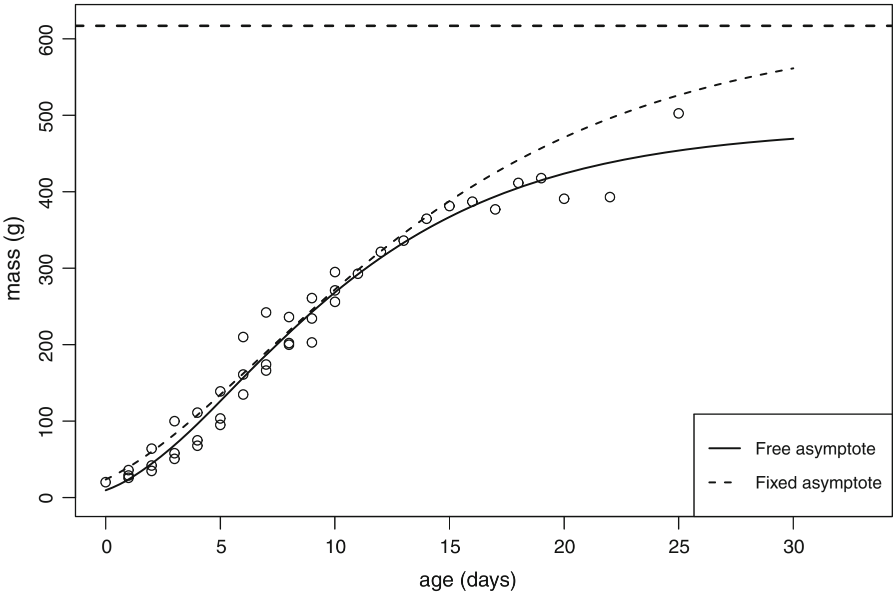

Fig. 2 Body mass growth models for Glossy Ibis chicks based on data extracted from the literature review (n = 43). The unbroken line represents the best fitting curve, the broken curve represents a curve modelled with fixed asymptote, and the horizontal broken line represents the average adult body mass derived from the literature review

Chick energy requirements

Only five studies have examined energy expenditure for the growth and survival of wild or captive Threskiornithids (Table 2). All five focused on ibis species, with two of these exploring chick energy requirements. No estimations of energetic allometry specific to the Threskiornithidae were found. No energetic studies have been performed on Australian spoonbills or ibis of any age group. Experimentally

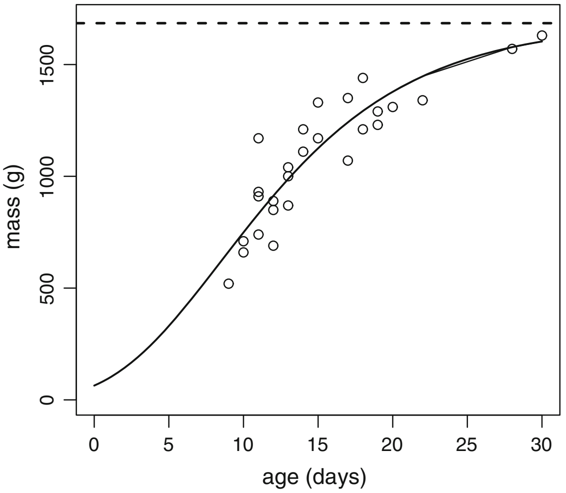

Fig. 3 Growth models for body mass of Royal Spoonbill chicks (n = 27) in the Murray Riverina region during the 2017–2018 breeding season. Unbroken lines represent the best fitting curve and broken lines represent the average adult value for the parameter derived from the literature review

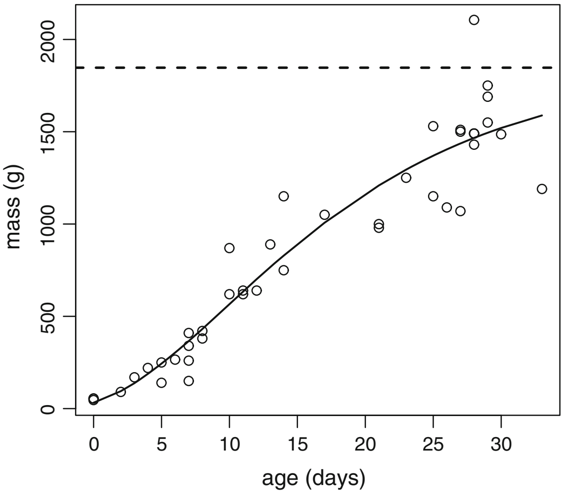

Fig. 4 Growth models for body mass of Australian White Ibis chicks in the Murray Riverina region during the 2017-2018 breeding season (n = 35) and from the literature review (n = 7). Unbroken lines represent the best fitting curve and broken lines represent the average adult value for the parameter derived from the literature review

determined estimates of Threskionithid digestion efficiency are limited to Kushlan's (1977a, c) American White Ibis studies, which both resulted in estimates of 79% (Table 5).

Glossy Ibis energy requirements

The Glossy Ibis energetic allometry model produced a scaling coefficient (log-linear slope) of 0.78 ± 0.11 with an intercept of 0.73 ± 0.29 (P = 0.000, R^2 = 0.55, Fig. 5) to fit the equation:

$$log_{10}DER = 0.7315 + 0.7825 * log_{10}mass \quad (4)$$

All assumptions of linear regression were met. This equation was then used in conjunction with predicted daily body mass values from the Glossy Ibis von Bertalanffy growth model to predict daily energy requirements for the first 50 days of age, then compared with the mass specific daily energy requirements (kJ g^{-1} day^{-2}, mDER) from the literature. The energy model took the following mathematical form, where *DER* is the daily energy requirement of the chick in kilojoules and *t* is the age in days:

$$DER = 10^\wedge\left(0.7315 + 0.7825 * log_{10}\left(484.7421 * \left(1 - exp\left(-0.1406 * (t + 2.2375)\right)\right)^\wedge 3\right)\right) \quad (5)$$

The predictive model produced similar mDERs to those observed by Santoro et al. (2015) for Glossy Ibis chicks (Fig. 5; Supplementary Material Table S5). However, while Kushlan's (1977c) mDER for the American White Ibis (1.99 ± 0.80) and the predicted values (1.51 ± 0.15) from 5 to 40 days of age were not significantly different (P = 0.14, F = 2.45), the predicted values did not decline as sharply as Kushlan's (1977c) values over the 35 days of growth compared. For further validation, the allometric prediction was compared to Bairlein et al.'s (2015) doubly-labelled water measurement of adult energy requirements for the Northern Bald Ibis (*Geronticus eremita*) using mean adult body mass from the literature (1393 g) and found to be within the published range of error (predicted = 1555 kJ day^{-1}, published = 1823 ± 911 kJ day^{-1}).

Royal Spoonbill and Australian White Ibis energy requirements

The cross-validated Glossy Ibis energetic allometry model was applied to the estimated daily body mass of Royal Spoonbill and Australian White Ibis chicks (Fig. 6). The energy models took the following mathematical forms, where *DER* is the daily energy

Table 4 Estimated parameters for the best fitting growth models for Royal Spoonbill (n = 27) and Australian White Ibis (n = 35) chicks based on data collected during the breeding season of 2017–2018

Biometric parameter	Best fitting model	Upper asymptote (A)	Growth rate constant (k)	Age at inflection (T_i)	Lower asymptote (A_0)
Royal Spoonbill					
Body mass	Gompertz	1685	0.140 ± 0.018	8.5 ± 0.1	–
Wing length	Logistic	366.9	0.135 ± 0.014	14.1 ± 0.4	–
Bill length	Bertalanffy	186.9	0.0307 ± 0.0023	–	24.9 ± 3.0
Head-bill length	Bertalanffy	248.5	0.0332 ± 0.0028	–	26.7 ± 3.5
Tarsus length	Gompertz	127.1	0.202 ± 0.023	7.8 ± 0.5	–
Australian White Ibis					
Body mass	Bertalanffy	1847	0.0823 ± 0.0065	–	3.6 ± 1.4
Wing length	Gompertz	356.5	0.104 ± 0.0059	12.8 ± 0.4	–
Bill length	Bertalanffy	167.1	0.0377 ± 0.0015	–	17.3 ± 1.4
Head-bill length	Bertalanffy	223	0.0394 ± 0.0016	–	21.0 ± 1.5
Tarsus length	Gompertz	93	0.173 ± 0.021	5.8 ± 0.5	–
Glossy ibis					
Body mass	Bertalanffy	484.7 ± 21.4	0.140 ± 0.013	–	2.2 ± 0.6

Also includes values derived from the literature for Australian White Ibis chicks (body mass n = 7, all other parameters n = 1) (Marchant and Higgins 1990; Smith et al. 2013) and Glossy Ibis chicks (body mass n = 98) (Miller and Burger 1978; Williams 1975) ± standard error. No standard error is given for the upper asymptote (A) because values were fixed to those of the relevant mean adult value from the literature review, except for Glossy Ibis body mass where a free asymptote was used

Table 5 Summary of the available data on digestion efficiency in spoonbills and ibis (± SD)

Species	Age class	N	Digestion efficiency (%)	Source	References
American White Ibis	Adult	NA[a]	70	Literature source (Kale 1965)	Bildstein (1987)
Eudocimus albus	Adult	3	79.7	Experimentally determined (Kendeigh 1970)	Kushlan (1977a)
	Chick 0–40 days	5	79 ± 5	Experimentally determined (Kendeigh 1970)	Kushlan (1977c)

[a] Sample size not given because data were calculated theoretically by the author and not directly measured

requirement of the chick in kilojoules and t is the age in days:

Royal Spoonbill

$$DER = 10^\wedge\left(0.7315 + 0.7825 * \log_{10}\left(1685 * \exp\left(-\exp\left(-0.1395\right)\right) * \left(t - 8.4962\right)\right)\right) \quad (6)$$

Australian White Ibis

$$DER = 10^\wedge\left(0.7315 + 0.7825 * \log_{10}\left(1847 * \left(1 - \exp(-0.08229 * (t + 3.63412))\right)^\wedge 3\right)\right) \quad (7)$$

Royal Spoonbill chick daily energy requirements (DER) began at 139 kJ day^{-1} at hatching and reached a maximum daily increase in energy demand with growth at ~ 8.5 days old (Fig. 6) before peaking at 1800 kJ day^{-1} at 50 days old. Australian White Ibis

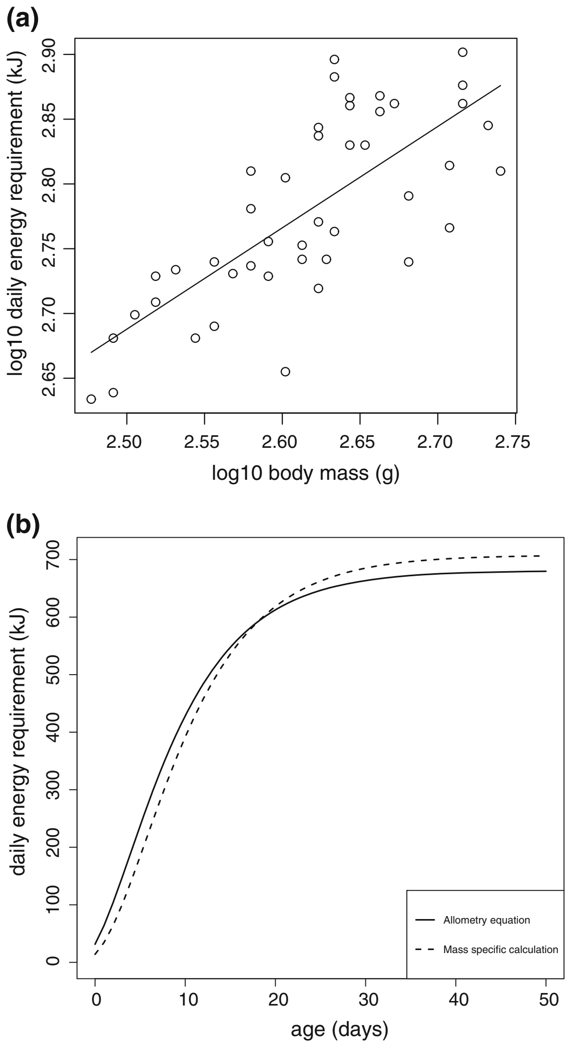

Fig. 5 Graphs of Glossy Ibis chick energetic allometry (left) created using data collected by Santoro et al. (2015) (n = 44) and Glossy Ibis predictive energy model up until independence age (right) based on the resultant allometric equation and growth model predictions. Daily energy requirements were also predicted using the mean mass specific daily energy requirement from Santoro et al. (2015) for comparison (broken line)

DER ranged from 81 kJ day^{-1} at hatching to 1884 kJ day^{-1} at 50 days old, reaching a maximum daily increase in energy demand slightly later than Royal Spoonbill chicks at ~ 10 days old (Fig. 6).

Based on the predictive models, the total energy required for a single Royal Spoonbill chick from hatching to foraging independence is 71,290 kJ and for that for an Australian White Ibis chick is 67,160 kJ. The total energy requirement from hatching to foraging independence in Australian White Ibis chicks was robust to variations in the model asymptote, based on asymptotes derived from minimum and maximum study means for adult Australian White Ibis body mass from the literature review, providing a range of 65,588–67,563 kJ (− 2.3% to + 0.6% variation from base model).

Discussion

There is a paucity of data available describing the growth and energy requirements of the Threskiornithidae. The most important knowledge gaps identified via this review were: (1) no direct measurement of spoonbill energetics worldwide, and very limited direct measurement of ibis energetics; (2) no estimates of the biomass of food required for wild Threskiornithid chick rearing; (3) no direct measurements or estimates of the energetics of any Australian spoonbill or ibis species; (4) no growth curves for the Australian spoonbills or Straw-necked Ibis. This study has begun to fill some of these knowledge gaps, through the extraction and synthesis of the best available data globally on Threskiornithid energetics, growth, and biometrics, and by creating the first growth model for Royal Spoonbill chicks and developing the first predictive energetic models of Australian waterbird chick energy requirements. The general agreement between modelled predictions and measured values for other species (Bairlein et al. 2015) suggests that these models and predictions could be extrapolated to other similar species.

Growth

Body mass was the most commonly recorded growth parameter in Threskiornithids, being the most important biometric predictor of many aspects of physiology and life history (Calder 1984; Cornioley et al. 2017). However measurement of body mass often ceases well before independence. The Royal Spoonbill and Australian White Ibis growth models developed here were able to estimate biometric parameters up until independence, at 50 days of age, by using fixed asymptotes based on empirical data. The Australian White Ibis body mass growth model produced similar predictions to Smith et al.'s (2013) model from the 2005–2006 breeding season in Greater Sydney for young chicks, and provided improved predictions after 20 days of

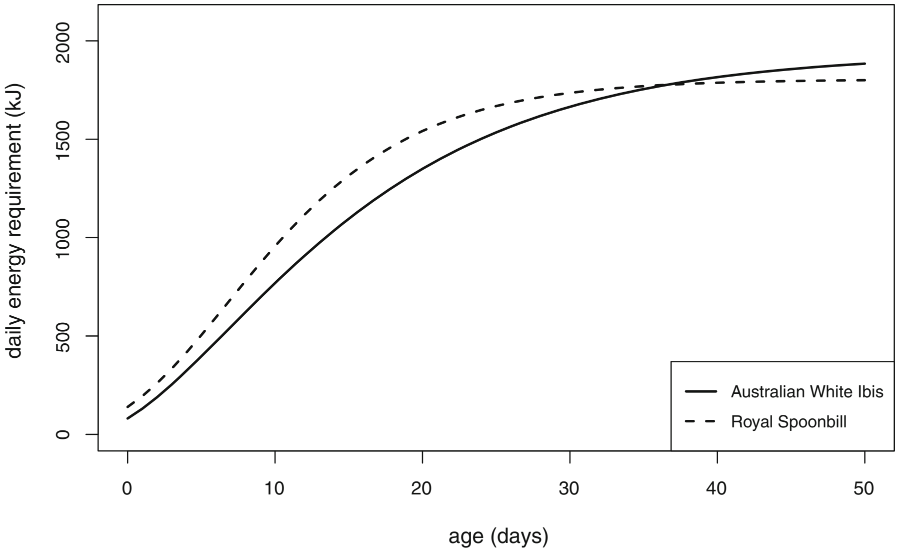

Fig. 6 Predictive energy models for Royal Spoonbill and Australian White Ibis chicks up until independence age, based on species specific growth model predictions

age (Supplementary Material Fig. S1e). Reasonable model accuracy during the later stages of chick growth is important because older birds become progressively more difficult to catch and age with confidence as they gain mobility (Lok et al. 2014; Smith et al. 2013).

Some common patterns in growth were apparent in the Australian White Ibis and Royal Spoonbill growth models that were supported by patterns identified in the literature. The tarsus grew fastest in all Threskiornithid species with full adult length reached before fledging. The tarsus is important for both terrestrial locomotion and foraging in Threskiornithids (Nti-amoa-Baidu et al. 1998), so a larger tarsus may allow birds to commence foraging and escape predators at an earlier age, hence reducing reliance on the parent bird for food and increasing the chance of survival (Soni et al. 2009). The bill and head-bill length were the slowest growing and least variable parameters for all Threskiornithids, only reaching 70–80% of adult size by fledging (Supplementary Material Figs. S1 and S2) (Kushlan 1977b; Lok et al. 2014; Smith et al. 2013; Soni et al. 2009). This slower bill growth rate could enable chicks to receive food directly from the parent bird for as long as possible via the insertion of the chick's bill into the parent's gullet—a smaller bill may facilitate this process.

Body mass in Royal Spoonbill chicks approached mean adult mass 13 days faster than the Australian White Ibis, before reaching a 9% lower mean adult mass (Figs. 3, 4). The smaller comparative size of Australian White Ibis fledglings may confer metabolic savings during the first 30 days of life, until the chick becomes more mobile and can forage to supplement parental food deliveries (Kushlan 1977b).

Due to the relatively early asymptote and variability in body mass, bill or head-bill measurements may be a better predictor of chick age if hatching date is not known (Lok et al. 2014; Smith et al. 2013). Bill and head-bill measurements grow slower than all other commonly measured biometric parameters; for example, these parameters only reached ~ 60% of adult size at 40 days of age in wild Red-naped Ibis (*Pseudibis papillosa*), Eurasian Spoonbills, and Australian White Ibis (Lok et al. 2014; Smith et al. 2013; Soni et al. 2009). In black-faced spoonbills (*Platalea minor*) and American White Ibis the bill continued to grow in length until ~ 70 days old (Jong-Ryol et al. 1999; Kushlan 1977b). In addition, the variability in bill and head-bill size at a given age remains relatively consistent in comparison to body mass, despite sexual dimorphism in bill size (Babbitt and Frederick 2007; Lok et al. 2014; Smith et al. 2013; Soni et al. 2009). Such differences are useful in determining chick age in the field for management purposes, including predicting how much longer water may need to be supplied in the nesting wetland.

Within species, the growth rate of captive chicks followed a similar curve shape to that of wild chicks, but was slower and reached a lower asymptote than wild chicks (Archibald et al. 1980; Kushlan 1977c). This is particularly interesting since captive chicks were offered food regularly until satiated, and hence probably received a greater quantity of food than their wild counterparts (Kushlan 1977c; Sweeney 1993; Xi et al. 2001). This suggests that the quality or diversity of the food offered and/or the biomechanics of wild existence may play an important role in the accumulation of body mass during growth, highlighting the importance of field studies for ecological relevance. Kushlan's (1977c) captive American White Ibis chicks also fledged 10 days later than their wild counterparts, reinforcing the potential importance of body mass energy reserves in fledging. Variability in body mass growth may further be explained by sexual size dimorphism, which is exhibited by all spoonbills and ibis (Figuerola et al. 2006; Fuchs et al. 2017; Kushlan 1977d), hatching order (Jong-Ryol et al. 1999; Kopij et al. 2000), and food availability (Lorenz 2014; Miller and Burger 1978).

Energy

The energy models presented here used the best available empirical energetic measurements of wild Threskiornithid chicks (Table 4) together with empirically collected growth data to predict spoonbill and ibis energetics (this study). The models used doubly-labelled water measurements from the Glossy Ibis (Santoro et al. 2015), a species that breeds in the same Australian wetlands as the Royal Spoonbill and Australian White Ibis (Brandis et al. 2011), as the basis of the allometry model rather than generalised non-passerine equations as previous studies have done (Bildstein 1987; Kushlan 1977a, c; Santoro et al. 2015). The use of wild chicks meant that no adjustments were needed to account for differences in captivity, further increasing the reliability of the models (Kendeigh 1970; Kushlan 1977c). Ideally, the energy models would have been created with species or genus specific energetic measurements, but the similarity in mDER between the Glossy Ibis metabolism used in the models and measured adult Northern Bald Ibis metabolism increases confidence in the transferability of the allometry model to other Threskiornithid species (Bairlein et al. 2015; Santoro et al. 2015). No other estimates of spoonbill energetics exist in the literature for any spoonbill species globally.

The allometric model developed suggests that chicks require more energy per gram of body mass than adult birds to survive, highlighting the need to quantify chick energy requirements to inform management. The scaling coefficient of 0.78 derived from the Glossy Ibis chick allometric model is slightly steeper than the range of values published in White's (2011) literature review of adult bird metabolism (0.635–0.744). However, steeper metabolic scaling in growing birds is not surprising. Chicks must amass energy during growth to support them as they recruit into the adult population (Kushlan 1977c). They require energy to maintain their current physiology as well as additional energy for biosynthesis and growth not required by adult birds (Ricklefs 1974).

Starvation is most threatening to Threskiornithid chicks during the first 10 days after hatching, with the highest mortality from starvation in Eurasian Spoonbills and greatest variability in White-faced Ibis (*Plegadis chihi*) growth rates recorded during this time (Garrett 1996; Lok et al. 2014). The energy models predicted the maximum rate of increase in chick energy requirements at the same time as maximum growth, around 8.5 days for the Royal Spoonbill and 10 days for the Australian White Ibis. This matches the published range in time of maximum growth rates for Threskiornithid chicks (T_{i} = 7–10 days old), and may explain why chicks are more susceptible to starvation at this age, with a sharp increase in energy requirements increasing the difficulty of parental provision of sufficient food (Kushlan 1977c; Nagy 1987). This difficulty is likely to be exacerbated where insufficient foraging habitat within range or insufficient food sources are available due to insufficient flood area or duration, habitat modification or other factors.

The predicted daily energy requirements of the Australian White Ibis and Royal Spoonbill were nearly identical at 50 days (foraging independence), being 1884 kJ day^{-1} and 1800 kJ day^{-1} respectively. These predictions are in close agreement with the mean daily energy requirement of Northern Bald Ibis at 1823 ± 911 kJ day^{-1} (Bairlein et al. 2015), which at adult size has a similar mean body mass (1393) to juvenile Australian White Ibis and Royal Spoonbills (1576 and 1543 g respectively), affirming the utility of the models.

Although generalised non-passerine energetic allometry models exist, there is substantial variability between and within bird families due to differing life strategies (Fort et al. 2011; Kendeigh 1970; White 2011). Application of a generalised energetic model to a species whose metabolism has not been measured in the development of the model may lead to inaccurate predictions and create a model that is not biologically relevant (Fort et al. 2011). In addition, these generalised models often predict basal metabolic rate or existence metabolism, which must first be converted to free-living daily energy expenditure, and then to daily energy requirement (White 2011). These extra steps often rely on non-species specific relationships and would likely result in compounding errors, giving an unreliable result. Pennycuick (1989) estimated that calculations of flight metabolism based on basal metabolic rates can be in error up to a factor of 10. Hence, the models put forward in this study represent some of the most accurate energetic estimations for the Threskiornithidae to date.

Management implications

The predictions from the energy models developed in this study can be used to assess the needs of spoonbill and ibis breeding events in terms of wetland ecosystem energy flow and be incorporated into ecological models to meet management targets such as fish reproduction and recruitment. This type of modelling will support efforts to meet targets in wetland ecosystem and waterbird population management. For example, the Australian Murray Darling Basin Authority (2014) has identified key environmental water management targets that include increased waterbird breeding and abundance by 2024. Using the Royal Spoonbill and Australian White Ibis energy models, the amount of energy required for the successful fledging of a selected number of birds can be estimated and flows and wetland habitats managed to promote the availability of sufficient food to meet those energy needs.

The main components of Royal Spoonbill and Australian White Ibis diets are small fish, crustaceans, amphibians and invertebrates (Barker and Vestjens 1989). The proportions of different prey types in the diet vary spatially and temporally (Barker and Vestjens 1989). Two of the most abundant and widespread prey items consumed by these species are the freshwater crayfish commonly known as the yabbie (*Cherax destructor*) and the invasive common carp (*Cyprinus carpio*). Mean energy content values reported for yabbies range from 14.60 ± 0.15 kJ/g (Jones et al. 1996) to 20.6 ± 0.1 kJ/g (Musgrove and Geddes 1995); values reported for carp range from 22.36 to 27 kJ/g (Heinitz et al. 2018). Using these values, it is possible to calculate an approximate biomass of yabbies or carp needed in nearby foraging habitats to support a specific breeding event—acknowledging that ibis and spoonbills feed their chicks a variety of prey species. For example, a small-scale breeding event of approximately 1000 nests with average clutch sizes of 2–4 eggs producing an average of three chicks per nest will require enough food to support 3000 chicks. Using the energetic model produced in this study, for an Australian white ibis or royal spoonbill breeding event of this size an estimated 10 tonnes of yabbies or 8 tonnes of juvenile carp would be required to support chick energy requirements from hatching to independence. If the mean energy content of the diet of a bird species is known, another approach can be used to calculate the biomass of food required. For example, Kushlan's (1977a) mean value for American White Ibis in the Florida Everglades USA of 3.4 kJ/g wet food results in an estimate of 3.7 tonnes of mixed prey required to support fewer than 200 chicks from hatching to independence.

In terms of whole-of-system wetland management, these calculations are conservative, because they do not include the food required by the nesting adults or by juveniles older than 50 days. Additionally, it is likely that adult energy needs are increased during breeding periods relative to non-breeding periods. Further research is required to quantify adult and juvenile energy needs, to refine models and predictions taking into account diet composition and variability, and to quantify food and energy availability in a range of habitats and compare it to waterbird needs.

These models emphasise the large quantity of food needed to support successful waterbird breeding and the consequent importance of effective wetland management to support foraging habitats and waterbird food sources. Management options to promote food availability include water management interventions or actions targeted toward the reproduction, recruitment and survival of preferred prey, such as 'environmental flows' and aquatic refuge conservation. For example, temporally staggered watering of a series of wetlands within foraging range of the nesting site will promote successional changes in vegetation and prey populations and provide a range of foraging and prey options. Other options include vegetation management actions such as provision of appropriate wetting regimes and removal or control of invasive weeds; pest animal management actions such as feral pig and fox control; and minimisation of the impacts of toxins, diseases and poisons such as herbicides and insecticides on both prey and waterbirds. Timing will be important, with a balance to be found between maximising positive impacts on prey populations and minimising adverse impacts on waterbirds and other fauna.

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Author contributions HM conceived the idea, obtained funding, formulated the questions and methods, supervised the research and edited the paper; LO collected the data, analysed the data and wrote the paper.

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Compliance with ethical standards

Conflict of interest The authors declare no potential conflicts of interest.

Ethics approval This research was conducted in compliance with the CSIRO Animal Ethics Committee Authority Number 2015-17 and the University of NSW Animal Care and Ethics Committee Authority Number 17/122B.

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