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A review of estimates of daily energy expenditure and food intake in cormorants (*Phalacrocorax* spp.)

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ABSTRACT

Daily energy expenditure (DEE) and daily food intake (DFI) are key parameters in estimating population level consumption by cormorants. A number of different methods are still employed in estimating these parameters along with different estimates for assimilation efficiency (if used) and prey energy density. The pellet/fish size reconstruction and percent adult body weight methods underestimate DFI for a number of reasons including an implied underestimation of DEE. In the absence of study-specific data, an assimilation efficiency of 0.80 and prey energy density of 5.42 kJ·g^{-1} are recommended. The bioenergetic model for field metabolic rate from Ellis and Gabrielsen (2002) is recommended for adults during the nesting season and their model for basal metabolic rate (BMR × 2.5) is recommended for adults or sub-adults outside the nesting season. Comparisons between empirical and bioenergetic models for chick DFI are also made with recommendations on estimating DFI.

Introduction

Daily energy expenditure (DEE; kJ·day^{-1}·bird^{-1}) and daily food intake (DFI; g·day^{-1}·bird^{-1}) by cormorants and shags (Phalacrocoracidae) are key parameters when estimating prey biomass consumption. Numerous studies have estimated DEE and DFI using a variety of methods and incorporated these values into population levels of consumption (Grémillet et al. 2000, Dalton et al. 2009). Conceptually, the approach is straightforward. An estimate of per capita consumption is scaled to the population level based on the number of cormorants occupying an area expressed as nest counts or density estimates. This extrapolation is a significant step where small inaccuracies or inconsistent methods for estimating per capita consumption propagate to large discrepancies at the population level. Considering the importance and controversy regarding the effects of cormorants in coastal food webs of the Laurentian Great Lakes, and elsewhere (Harris et al. 2008), then some level of agreement on methods and estimates of per capita consumption are needed.

Estimates of DFI have been based on: (1) pellet analysis and reconstructing fish sizes consumed by birds (Privileggi 2003, Gagliardi et al. 2007); (2) percent of adult body weight (Johnson et al. 2002, Rudstam et al. 2004); (3) energy expenditure through activity time budgets and activity-specific DEE (Grémillet et al. 2000, 2003); (4) allometric bioenergetic models as a function of mass and converting this to DFI through division by prey energy density and assimilation efficiency (Madenjian and Gabrey 1995, Barquete et al. 2008); (5) respirometry and doubly labelled water techniques (Keller and Visser 1999, Enstipp et al. 2005), and (6) other methods such as automatic balances and stomach temperature tags (Grémillet et al. 1999, 2000). Different studies may or may not have employed prey assimilation efficiency with values varying among studies if used (0.79 in Glahn and Brugger 1995, 0.77 in Keller and Visser 1999, 0.85 in Diana et al. 2006, 0.80 in Seefelt and Gillingham 2008). Finally, prey energy density (kJ·g^{-1}) varies with fish species and this can alter prey consumption estimates depending on diet composition. Together, there is uncertainty when comparing population-scale prey consumption from one study to the next and this has led to efforts at standardizing DEE and DFI approaches (Carss et al. 1997). "Getting the sums right" for cormorant consumption has been a consensus for many years (Feltham and Davies 1996, Harris et al. 2008).

Until some agreement is reached on the methods employed in assessing population level prey consumption then addressing this issue in areas such as the Laurentian Great Lakes basin will continue to be, in large part, debates over small details that scale-up to substantial differences among estimates of effects. This situation is illustrated by the use of different assimilation efficiencies. Different cormorant studies have employed assimilation efficiencies ranging from 0.77 (Keller and Visser 1999) to 0.85 (Diana et al. 2006). If, as an example, an estimate of DEE converts to 400–420 g·day^{-1} of food then dividing this estimate by assimilation efficiency results in DFI. The difference between an estimate of 0.77 and 0.85 in this case is a per capita difference of 50 g in DFI. Using nest counts from the North Channel, Lake Huron, as an example (Ridgway et al. 2006), a difference of 50 g for a population of 20,000 adult nesting cormorants results in approximately a 1 metric tonne per day (t·day^{-1}) difference in total prey consumption as a function of the assumed per capita assimilation efficiency.

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Recognition of this uncertainty has led to attempts at overcoming differences among studies by recommending common methods as well as parameter values for assimilation efficiency, prey energy density, and DEE and DFI for methods such as time energy budgets (Carss et al. 1997). Others recommend dropping bioenergetic models in favour of focal animal sampling to capture colony-specific patterns of energy expenditure (Grémillet et al. 2000). Others follow recent updates on allometric equations to set energy expenditures (Barrett et al. 2006, Dalton et al. 2009).

The objective of this paper is to summarize recent literature on DEE and DFI in cormorants and shags to determine if there is a convergence on methods, assess the magnitude of differences among methods and point to common approaches for assessing DEE and DFI. It will provide biologists and managers with an overview of the range of methods and parameter values that lie behind estimates of population consumption for this group of waterbirds. References to double-crested cormorants (*Phalacrocorax auritus*) are made in different examples but considerations of standard methods apply to all species.

Table 1
Daily food intake (DFI) and daily energy expenditure (DEE) estimates for cormorants and shags (Phalacrocoracidae) based on bioenergetics, respirometry and doubly labelled water methods.

Species	Daily food intake (g·day^{-1})	Daily energy expenditure (kJ·day^{-1})	Body mass (g)	Location	Method	Source
P. carbo	661* (0.85 and 5.5 kJ·g^{-1})	**3089**	3250	Atlantic coast, Norway	Bioenergetic model^{G} (3×BMR)	Barrett et al. 1990.
P. carbo	957* (0.80 and 5.35 kJ·g^{-1})	**4094**	3250	Barents Sea, Norway	Bioenergetic model—nesting season^{BF}	Barrett et al. 2002
P. carbo	640* (0.80 and 5.35 kJ·g^{-1})	**2741**	3250	Barents Sea, Norway	Bioenergetic model—non-nesting season^{G}	Barrett et al. 2002
P. carbo	1248* (0.80 and 4.1 kJ·g^{-1})	**4094**	3250	Norwegian Sea, Norway	Bioenergetic model—nesting season^{BF}	Barrett et al. 2002
P. carbo	836* (0.80 and 4.1 kJ·g^{-1})	**2741**	3250	Norwegian Sea, Norway	Bioenergetic model—non-nesting season^{G}	Barrett et al. 2002
P. carbo	**400–800**	1734–3469*	–	River Ribble, England	Bioenergetic model$^{F\&D}$	Wilson et al. 2003
P. aristotelis	428* (0.85 and 5.5 kJ·g^{-1})	**2002**	1800	Atlantic coast, Norway	Bioenergetic model^{G}	Barrett et al. 1990
P. aristotelis	614* (0.80 and 5.5 kJ·g^{-1})	**2702**	1836	Barents Sea, Norway	Bioenergetic model—nesting season^{BF}	Barrett et al. 2002
P. aristotelis	407* (0.80 and 5.5 kJ·g^{-1})	**1790**	1836	Barents Sea, Norway	Bioenergetic model—non-nesting season^{G}	Barrett et al. 2002
P. aristotelis	814* (0.80 and 4.15 kJ·g^{-1})	**2702**	1836	Norwegian Sea, Norway	Bioenergetic model—nesting season^{BF}	Barrett et al. 2002
P. aristotelis	539* (0.80 and 4.15 kJ·g^{-1})	**1790**	1836	Norwegian Sea, Norway	Bioenergetic model—non-nesting season^{G}	Barrett et al. 2002
P. brasilianus	425* (0.80 and 5.9 kJ·g^{-1})	**2007**	1568	Lagoa dos Patos, Brazil	Bioenergetic model$^{E\&G}$	Barquete et al. 2008
P. auritus	627* (0.80 and 5.5 kJ·g^{-1})	**2760**	1890	Lake Erie	Bioenergetic model$^{BF;\ K}$	Madenjian & Gabrey 1995
P. auritus	504* (0.79 and 4.84 kJ·g^{-1})	**1927**	2270	Delta region, Mississippi	Bioenergetic model$^{A\&P;\ H}$	Glahn & Brugger 1995
P. auritus	519*	**2250** (at 15°C; BMR×2.5)	2000	North Platte River, Wyoming	Bioenergetic model^{K}	Derby & Lovvorn 1997
P. auritus	550* (0.80 and 6.54 kJ·g^{-1})	**2876**	2000	Beaver Islands, Lake Michigan	Bioenergetic model$^{BF;\ K}$	Seefelt & Gillingham 2008
P. auritus	518* (0.779 and 5.92 kJ·g^{-1})	**2391**	2051	Bride Lake, Connecticut	Bioenergetic model$^{E\&G}$	Dalton et al. 2009
Phalacrocorax sp	441*	**1913**	2000	Literature summary	Bioenergetic model	Brit-Friesen et al. 1989
Phalacrocorax sp.	473*	**2052** (3.76 W)	2000	Literature summary	Bioenergetic model—isotope turnover	Daan et al. 1991
Phalacrocorax sp.	**673** (0.7765 and 5.42 kJ·g^{-1})	2832*	2000	Literature summary	Bioenergetic allometric model	Feltham & Davies 1996
Phalacrocorax sp.	542*	**2352** (FMR)	2000	Literature summary	Bioenergetic model—nesting season	Ellis & Gabrielsen 2002
Phalacrocorax sp.	436*	**1891** (FMR = BMR×2.5)	2000	Literature summary	Bioenergetic model—non-nesting season	Ellis & Gabrielsen 2002
P. carbo sinensis	494*	**2144** (FMR = **3.1**W·kg^{-1} (BMR)×4.0)	2000	Laboratory	Respirometry	Schmid et al. 1995
P. carbo sinensis	539* (0.7765 and 5.0 kJ·g^{-1})	**2094** (SD ± 174)	2122	Lake Chiemsee, Germany	Doubly labelled water	Keller & Visser 1999
P. penicillatus	434*	**1883** (RMR = **10.9** W·kg^{-1})	2000	Laboratory	Respirometry	Ancel et al. 2000
P. aristotelis	426*	1848 (**5.28** W·kg^{-1}; BMR×2.5)	1619	Laboratory	Respirometry	Bryant & Furness 1995
P. aristotelis	471*	2043 (FMR = **4.73**W·kg^{-1} (BMR)×4)	2000	Laboratory	Respirometry	Enstipp et al. 2005
P. auritus	594*	**2523** (@ (at 15°C; BMR×2.7) (0.85 & 5.0 kJ·g^{-1})	2000	Lake Huron, Michigan	Respirometry, regression model^{H}	Diana et al. 2006
P. auritus	480*	**2082** FMR = BMR (**4.59** W·kg^{-1})×2.5	2100	Laboratory	Respirometry	Enstipp et al. 2006

Estimates of DFI or DEE provided in each study are in bold. Derived estimates of DFI or DEE are marked with an asterisk (see Methods). Bioenergetic models used in studies are identified by the first letter of literature source: $^{A\&P}$Aschoff and Pohl (1970); ^{H}Hennemann (1983); ^{K}Kendiegh et al (1977); ^{BF}Brit-Friesen et al. (1989); ^{G}Gabrielsen (1994); $^{F\&G}$Feltham and Davies (1996); $^{E\&G}$Ellis and Gabrielsen (2002). 1 W = 1 J·s^{-1}.

Methods

Reports of DEE and DFI in cormorants and shags were obtained from the literature (Tables 1 and 2). Web-based searches also uncovered key publications such as an earlier effort on this topic by the "Diet Assessment and Food Intake Working Group" (Carss et al. 1997). Estimates of either DEE (kJ·day^{-1}·bird^{-1}) or DFI (g·day^{-1}·bird^{-1}) reported by each study were recorded and listed in Tables 1 and 2 in bold. If study-specific estimates of assimilation efficiency and prey energy density were used these value were also listed and used in estimating DFI if DFI was not already estimated. Otherwise, an assimilation efficiency of 0.80 and a prey energy density of 5.42 kJ·g^{-1} were used in estimating DFI or DEE depending on which of these two parameters was provided in each study (see below; Feltham and Davies 1996, Carss et al. 1997). If only one or the other parameter were provided, such as DFI only in studies employing the pellet/fish size reconstruction and percent adult body weight methods, then study-specific estimates of assimilation efficiency and prey energy density were used or the default values listed above. For studies estimating DFI by the pellet/fish size reconstruction or percent of adult body weight methods, it was assumed that the estimate of consumption (g·day^{-1}·bird^{-1}) included assimilation efficiency (0.80) along with a prey energy density = 5.42 kJ·g^{-1}.

To compare across studies, including estimates based on general bioenergetic models, all estimates for either DEE or DFI were re-calculated assuming assimilation efficiency was 0.80, prey energy density was 5.42 kJ·g^{-1} (recommended by Carss et al. 1997), and an adult mass of 2000 g for general bioenergetic models. For studies reporting only DFI such as pellet-based or percent body weight approaches, it was assumed that assimilation efficiency was included in the estimate provided by the authors otherwise the estimate would require an assumption of perfect assimilation of prey. Estimates for males and females were treated separately where provided. Different methods were compared based on means (±95% CI).

Assimilation efficiency

A number of studies on prey consumption in cormorants have incorporated the grand mean of percent prey assimilation estimated from feeding trials with double-crested cormorants (77.65% or 0.77; Brugger 1993). This estimate is based on data from channel catfish (*Ictalurus punctatus*, 0.797 and 0.786), gizzard shad (*Dororsoma cepedianum*, 0.776) and bluegill (*Lepomis macrochirus*, 0.747) as prey. In the absence of other data, this estimate had been recommended as a parameter option for all cormorants and shags by the Diet Assessment and Food Intake Working Group (Carss et al. 1997). The percent of prey assimilation by European shags (*P. aristotelis*) was approximately 80% for two prey types (sandeel (*Ammodytes marinus*); 80.99 ± 1.14 SD; whiting (*Merlangius merlangus*); 79.52 ± 1.16 SD; Hilton et al. 2000). The mean and overall standard deviation of the double-crested cormorant study (Brugger 1993; 77.65% ± 2.02) was used to construct a normal distribution from which the probability of assimilation efficiency being between 0.78 and 0.82 was determined using the formula for the normal curve. The same approach using data from the European shag study (Hilton et al. 2000) was also used to determine the probability of assimilation

Table 2
Daily food intake (DFI) and daily energy expenditure (DEE) estimates for cormorants and shags (*Phalacrocoracidae*) based on pellet analysis/fish size and percent adult body weight (A), and other methods (B).

Species	Daily food intake (g·day^{-1})	Daily energy expenditure (kJ·day^{-1})	Body mass (g)	Location	Method	Source
(A) Pellet and fish size; percent adult body size						
P. carbo	**364**	1578*	–	Lake Wolderwijd, Netherlands	Pellets and fish size	Noordhuis et al. 1997
P. carbo	**460**	1995*	–	Wadden Sea, Netherlands	Pellet mass and fish size	Leopold et al. 1998
P. carbo	**340–520**	1474–2235*	–	Great Britain	17–26% body mass	Kirby et al. 1996
P. carbo	**295**	1279*	–	Lake Vico, Italy	Pellet mass	Martucci 1997
P. carbo	**371** (SD ± 284)	1609*	–	Insubria Region, Italy	Pellets and fish size	Gagliardi et al. 2007
P. carbo sinensis	**363** (95%CI, 275–452)	1574* (95%CI, 1192–1960)	–	Lakes Wolderwijd and Veluwemeer, Netherlands	Pellets and fish size	Dirksen et al. 1995
P. carbo sinensis	**350–400** (May–Aug)	1518–1734*	–	Vistula Lagoon, Poland	Pellets and fish size	Stempniewicz et al. 2003
P. carbo sinensis	423 (breeding); 238 (non-breeding)	1834* breeding; 1032* non-breeding	–	Baltic coast, Estonia	Pellet mass; literature value	Eschbaum et al. 2003
P. carbo sinensis	**491**	2129*	–	Schwedt, Germany	Pellets and fish size	Wolter & Pawlizki 2003
P. carbo sinensis	**434**	1882*	–	Northern Adriatic Sea	Pellets and fish size	Privileggi 2003
P. carbo sinensis	**512**	2220*	–	Lake Ymsen, Sweden	Pellets and fish size	Engström & Jonsson 2003
P. carbo sinensis	**350–400**	1518–1734*		Saxony, Germany	Pellet mass	Seiche 2003
P. carbo carboides	**419**	1817*	–	Gippsland lakes, Australia	Pellets and fish size	Coutin & Reside 2003
P. auritus	**253** (95% CI 235–270)	1097*	–	Lake Erie, Ohio	Pellet mass	Burr et al. 1999
P. auritus	**400–500**	1734–2168*	2000	Literature summary	20–25% body mass	Hatch & Weseloh 1999
P. auritus	**456**	1977*	2280	Oneida Lake, New York	20% body mass and pellet content	VanDeValk et al. 2002; Rudstam et al. 2004
P. auritus	**470**	2038*	1880	Little Galloo Island, Lake Ontario	25% body weight	Johnson et al. 2002
P. auritus	**320** (0.80 and 4.6 kJ·g^{-1})	1472*	1885	Lake Erie	20% body mass; Hatch & Weseloh 1999	Hebert & Morrision 2003
B. Time budgets; temperature tags; balances						
P. carbo	672* (540–803) (0.776 and 5.33 kJ·g^{-1})	**2779**	3200	Loch Leven, Scotland	Time energy budget; pellets & and fish size	Grémillet et al. 2003; Stewart et al. 2005
P. carbo carbo	809* ♂ 582* ♀ (0.77 and 4 kJ·g^{-1})	**3236** ♂ **2327** ♀	3200 ♂ 2300 ♀	Chausey Islands, France	Time energy budget, nesting season	Grémillet et al. 2000
P. carbo carbo	**638** ♂ (±445) **450** ♀ (±373)	2552* ♂ 1,800* ♀ (4 kJ·g^{-1})	3200 ♂ 2300 ♀	Chausey Islands, France	Stomach temperature	Grémillet et al. 2000
P. carbo carbo	**540** ♂ **390** ♀ (0.77 and 4 kJ·g^{-1})	1663* ♂ 1201* ♀		Chausey Islands, France	Automatic balance	Grémillet et al. 2000, 1999; Grémillet 1997
P. carbo sinensis	237* ♂ 24 * ♀ (0.77 and 4 kJ·g^{-1})	**935** ♂ **970** ♀	2230	Lake Selent, Germany	Time energy budget during nesting; respirometry	Grémillet et al. 1995

Estimates of DFI or DEE provided in each study are in bold. Derived estimates of DFI or DEE are marked with an asterisk (see Materials and methods).

efficiency being between 0.78 and 0.82. The probability that assimilation efficiency is 0.85, as suggested in some studies (Barrett et al. 1990, Diana et al. 2006), was also assessed based on the above data distributions.

Chick DEE and DFI

Consumption by chicks has been based on bioenergetic models (Madenjian and Gabrey 1995) or empirical DFI estimates (Fowle 1997, Rudstam et al 2004). Models of chick growth and DEE were drawn from the literature and compared to empirical estimates. The equation from Derby and Lovvorn (1997), based on Dunn (1975), was used to model chick growth:

$$M = M_{\mathrm{ASM}} \cdot exp\left(-4e^{-0.09N}\right) \tag{1}$$

where N is chick age in days, M is mass (g) and M_{ASM} is asymptotic mass (g) of fledglings. For the North Channel, Lake Huron, mass at fledging averaged 1651 g·bird^{-1} over 2 years (1612 g SD ±242 in 2006; 1691 g SD ±255 in 2007; Chastant 2008) so M_{ASM} was set at 1900 g (approximately 1 SD above mean fledging mass (1651 g) and 5% below adult mass). Chick mass was used in three allometric models of chick DEE employed in three studies (Derby and Lovvorn 1997, Grémillet et al. 2000, Ellis and Gabrielsen 2002). Growth estimates and consumption were extended to 40 days because model-based chick mass was approximately 1700 g by that time. The models are:

$$\mathrm{DEE} = 5.665M^{0.814} \tag{2}$$

with mass, M (g), and DEE in kJ·day^{-1} (Kendeigh et al 1977, after Derby and Lovvorn 1997).

$$\mathrm{BMR} = 3.201M^{0.719} \tag{3}$$

with mass, M (g), and BMR in kJ·day^{-1} based on model 11.5, in Ellis and Gabrielsen (2002, p. 370). DEE was based on 3.5·BMR to better reflect higher FMR:BMR ratios (Field Metabolic Rate:Basal Metabolic Rate; Ellis and Gabrielsen (2002, Table 11.5).

$$\mathrm{RMR} = 0.0563M^{0.7427} \tag{4}$$

with mass, M (g), and RMR (Resting Metabolic Rate) in Watts (J·s^{-1}) for the great cormorant (Grémillet et al. 2000). DEE was converted from W to kJ·day^{-1} and based on 2.0·RMR. A common assimilation efficiency (0.80, see below) and prey energy density (5.42 kJ·g^{-1}) were used in estimating DFI for all three models.

To further assess the match between the bioenergetic model (Ellis and Gabrielsen 2002) and laboratory-based respirometry of BMR for double-crested cormorants, the DEE of cormorant chicks from the bioenergetic model were converted to W·kg^{-1} and plotted against adult double-crested cormorant BMR from respirometry experiments (4.59 W·kg^{-1} 1SD = ±0.59; Enstipp et al. 2006).

Results and discussion

Assimilation efficiency

Based on variation in the grand mean from Brugger (1993), the probability of assimilation efficiency falling between 0.78 and 0.82 is 0.42. The probability that assimilation efficiency for the European shag falls within the same range is 0.81 for consumption of sandeel and 0.89 for whiting (based on Hilton et al. 2000). An assimilation efficiency of 0.80 is a reasonable possibility from the Brugger (1993) study and represents a parameter value in line with other studies focusing on population scale consumption in cormorants and other seabirds (Barrett et al. 2006). Assimilation efficiency close to 0.8 for two prey species was observed in the Brugger (1993) study with bluegill providing the only low estimate (0.75). The probability that assimilation efficiency is 0.85 is well below 1% based on data from both Brugger (1993) and Hilton et al. (2000).

Chick DEE and DFI

The mass of chicks on day 1 from the growth model was 49.1 g. This is close to the observed mass for new double-crested cormorant chicks (eyes closed) in the North Channel, Lake Huron (43.4 g SD ± 7.4; Chastant 2008) and eastern Lake Ontario (46.8 SD ± 11.5; Chastant 2008).

All estimates of DFI for chick growth are in close agreement. The mean DFI based on empirical studies of chick growth are: (1) 357 g·day^{-1} (range: 300–415 g·day^{-1} over 30 days; *P. carbo sinensis*; Platteeuw et al. 1995); (2) 327 g·day^{-1} (*P. auritus*; Fowle 1997), and (3) 333 g·day^{-1} (*P. auritus*; Coleman and Richmond *unpubl.*; cited in Rudstam et al. 2004). The following estimates of mean DFI after 40 days for the different bioenergetic models were: (1) 338 g·day^{-1} (Ellis and Gabrielsen 2002); (2) 332 g·day^{-1} (Kendeigh et al. 1977), and (3) 346 g·day^{-1} (Grémillet et al. 2000). For the Laurentian Great Lakes, similar DFI estimates are provided by both the empirical estimate of DFI for double-crested cormorant (327 g·day^{-1}) and the bioenergetic model estimate (338 g·day^{-1}; Ellis and Gabrielsen 2002, p. 370).

There is confirmation of the utility of the general bioenergetic model of Ellis and Gabrielsen (2002) through comparison with BMR estimates stemming from respirometry experiments on double-crested cormorants (Enstipp et al. 2006). From a relatively high value early in nesting, chick DEE converges to well within the adult BMR estimate after 30 days once chicks reach approximately 1400 g (Fig. 1). Given this match, the chick growth model (Derby and Lovvorn 1997) and the bioenergetic model (Ellis and Gabrielsen 2002) can provide estimates of DFI on a per week basis for chicks that do not reach the fledging stage. Assuming assimilation efficiency of 0.8 and prey energy density of 5.42 kJ·g^{-1} then chick DFI in weeks 1 through 4 are 82, 202, 332 and 433 g·day^{-1}, respectively.

Adult DEE and DFI

At a minimum, there are 41 studies providing at least 48 estimates of either DEE or DFI (or both) in cormorants and shags. The studies represent a continuing diversity of methods that confronted biologists more than a decade ago (Carss et al. 1997; Tables 1 and 2). A further 5 estimates can be added using general functions relating either BMR or FMR to body mass in birds (Table 1; e.g., Feltham and Davies 1996, Ellis and Gabrielsen 2002). The pellet/fish size reconstruction method

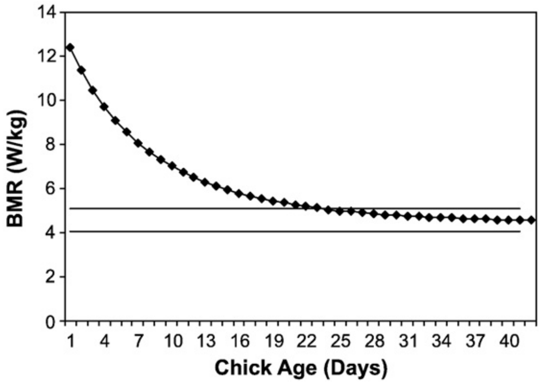

Fig. 1. Metabolic rate (3.5·BMR) of chicks (W·kg^{-1}) based on the bioenergetic model of Ellis and Gabrielsen (2002; eq. 11.5, p. 370). The horizontal lines represent ± 1 SD (± 0.51) of the mean BMR of adult double-crested cormorants (4.59 W·kg^{-1}; Enstipp et al. 2006). 1 Watt = 1 J·s^{-1}.

and percent body weight method were used for 18 estimates (Table 2), bioenergetic models were used in 17 estimates (Table 1), physiological experiments (respirometry or doubly labelled water) produced 7 estimates (Table 1), activity time budget produced 3 estimates (respirometry experiments to derive time energy budgets were not included in the bioenergetic category), and other methods such as automatic balances or stomach temperature recordings resulted in 2 estimates (Table 2). All methods continue to be represented in the literature well after the report by the “Diet Assessment and Food Intake Working Group” in Europe (Carss et al. 1997).

For all estimates based on bioenergetic models and respirometry the mean DFI was 567 g·day^{-1} (Table 1; $N = 25$; 95% CI, 508–626 g·day^{-1}) and DEE was 2472 kJ·day^{-1} (95% CI, 2218–2726 kJ·day^{-1}). Excluding studies with birds greater than 3 kg, the mean DFI was 517 g·day^{-1} ($N = 21$; 95% CI, 480–554 g·day^{-1}; SD = ±81.1) and DEE was 2253 kJ·day^{-1} (95% CI, 2097–2409 kJ·day^{-1}; SD = ± 343.2).

All pellet-based estimates and percent body weight estimates appeared to be on adult cormorants and shags less than 3 kg. The mean DFI based on these methods was 395 g·day^{-1} (Table 2; $N = 19$; 95% CI, 358–432 g·day^{-1}) and mean DEE was 1732 kJ·day^{-1} (95% CI, 1576–1888 kJ·day^{-1}). Time energy budget methods with males and females considered separately produced a mean DFI of 537 g·day^{-1} (Table 2; $N = 7$; 95% CI, 435–639 g·day^{-1}) and mean DEE of 2495 kJ·day^{-1} (95% CI, 1962–3028 kJ·day^{-1}). Of the two major approaches to estimating DEE and DFI in cormorants and shags, bioenergetic models and respirometry produced higher estimates than the pellet method and percent body weight method.

While some estimates of DFI fell within the 20–25% of adult body weight rule outlined in the most recent species summary for the double-crested cormorant (Hatch and Weseloh 1999), the confidence intervals for the pellet and percent adult weight methods were 17.9–21.6% of adult body weight (i.e., 2000 g). Confidence intervals for the bioenergetic and respirometry methods were 24.0–27.7% of adult weight. Guidelines regarding percent body weight as a measure of DFI are currently too broad and do not reflect the actual range of values found in the literature. Since small changes in per capita consumption parameters, such as assimilation efficiency, can have large consequences when extrapolated to population levels of consumption then choosing a DFI from a possible range of values is not recommended.

Use of percent body weight is an implied bioenergetic rule for endotherms so perhaps these data belong in the bioenergetic model category. There is an implied incorporation of assimilation efficiency within any DFI based on percent body weight. The overall DEE stemming from this assumption, once assimilation efficiency (= 0.80) is accounted for, will be lower than estimates of DEE from bioenergetic models. This is a limitation of the pellet method that, along with known biases regarding differential digestion of fish calcified tissue (e.g., otoliths) and assumed daily pellet production rates, compound the problems of using this method to estimate DFI (Feltham and Davies 1996, Carss et al. 1997).

Assumptions about assimilation efficiency were shown to have consequences registered in t·day^{-1} when DFI was extrapolated to the population level. Relative differences between the two most common methods can result in similar differences in DFI at the population level. Comparing the mean estimates of DFI for the pellet and fish size / percent body mass method (395 g·day^{-1}) versus the bioenergetic model/respirometry method (517 g·day^{-1}), results in a net difference of 122 g·day^{-1}. The carrying capacity for nesting double-crested cormorants for the North Channel, Lake Huron, was 11,445 nests (with alewife present; Ridgway et al. 2006). Assuming a juvenile population at 20% of nesting adults and that 75% of the adult and juvenile population forages on the North Channel each day, then a 122 g·day^{-1} difference between methods translates into approximately 2.5 t·day^{-1} of prey consumption accounted for simply by means of the method employed in estimating DFI.

The advantage of using bioenergetic models is their capacity to accommodate site-specific prey energy densities, a large literature for models relating energy expenditure to body size that stem from theory (Brown et al. 2004), and relative consistency in parameter estimates. As an example of consistency, Hennemann's (1983) model relating oxygen consumption in double-crested cormorants at 15°C results in a DFI of 539 g·day^{-1} (assimilation efficiency = 0.80; prey energy density = 5.42 kJ·g^{-1}; FMR = 2.5·(BMR)) which is close to 542 g·day^{-1} from Ellis and Gabrielsen (2002) under similar assumptions. With conversion, Hennemann’s (1983) model results in a BMR of 5.41 W·kg^{-1} which is higher than the more current BMR for double-crested cormorants of 4.59 W·kg^{-1} (Enstipp et al. 2006).

Efforts at standardizing methods for estimating DEE and DFI in cormorants have been attempted in the past (Feltham and Davies 1996, Carss et al. 1997). There is still a diversity of approaches used in estimating these parameters with some convergence on bioenergetic models as a method of choice. Different approaches are needed for different questions. Time energy budgets are useful for estimating differences between males and females in nesting activities or for allocating costs to different activities that may change across broad areas depending on cormorant behaviour and prey composition (Gremillet et al. 2000, Enstipp et al. 2007). Differences in foraging costs will be particularly acute when incorporating site-specific prey energy densities stemming from differences in local fish assemblages.

There is a diversity of approaches even within categories such as bioenergetic models as well as within regions such as the Laurentian Great Lakes (Johnson et al. 2002, Diana et al. 2006, Seefelt and Gillingham 2008) and European sites (Gremillet et al. 2003, Stewart et al. 2005). When scaled-up, this inconsistency in per capita consumption parameters can lead to real differences in population levels of consumption. Settling on a common approach is important for addressing ecological effects of double-crested cormorants in aquatic food webs, in the case of the Laurentian Great Lakes, or for other cormorant species in other locations (Harris et al. 2008). Based on the literature review and results presented in this paper, I offer the following recommendations for estimating DFI and DEE at the population level:

(1) An assimilation efficiency of 0.80 to be consistent with the larger literature on consumption by seabirds as well as more recent findings on *Phalacrocorax* sp. (Hilton et al. 2000);
(2) Prey energy density of 5.42 kJ·g^{-1} (consistent with Carss et al. 1997; otherwise site-specific or literature-based values);
(3) DFI for chicks of 327–338 g·day^{-1} (lower estimate empirical; upper estimate bioenergetic model) based on the match between double-crested cormorant BMR (Enstipp et al. 2005) and model 11.5, 3.5·(BMR), in Ellis and Gabrielsen (2002, p. 370);
(4) DFI for adults during the nesting period based on model 11.13 for FMR, in Ellis and Gabrielsen (2002, p. 388), $FMR = 16.69 \cdot m^{0.651}$ with mass (m) in grams and FMR in kJ·day^{-1}. There can be an adjustment for latitude using model 11.14, in Ellis and Gabrielsen (2002, p. 392), $FMR = 9.014. \cdot m^{0.655} \cdot [\exp_{10}\ (\text{latitude})^{0.0048}$, again with mass (g) and FMR in kJ·day^{-1}.
(5) DFI for adults during the non-nesting season (before nest construction and after fledging; summer and fall) based on lower DEE presented in model 11.5, FMR = 2.5·(BMR), in Ellis and Gabrielsen (2002, p. 370).

The ideal study of cormorant prey biomass consumption would include estimates of site-specific prey composition, site-specific prey energy density, doubly labelled water as a tool for field estimates of metabolic rate and therefore prey demand (preferably on males and females of different size and reproductive state), and density estimates incorporating detection biases to arrive at defensible population sizes in the area of study (preferably on a seasonal basis). This has not been achieved to date. Until such a comprehensive study is completed, biologists and managers in areas like the Laurentian Great Lakes must use a consistent approach for estimating prey biomass consumption. With only nest counts in hand, as in many locations in the Great Lakes basin, one approach would be to incorporate the recommended assimilation efficiency, prey energy density and assume an adult mass of 2000 g for estimating per capita consumption. Based on this review, a per capita consumption by adults of 542 g·day^{-1} bird^{-1} in the nesting season and 436 g·day^{-1} bird^{-1} in the non-nesting season are recommended (Table 1). Data on egg counts in nests within the region of interest or from other sites in the Great Lakes basin would provide basic data on chick production given an assumed hatching rate and chick survival. Together, this information would provide DFI for adults and chicks in the nesting season as well as outside the nesting season. The larger assumption in prey biomass consumption in areas like the Great Lakes basin is whether the presumed densities of cormorants present in the nesting season are also present after fledging during summer and fall periods. This question is distinct from the assumptions of per capita consumption but looms as an important consideration.

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References

Aschoff, J., Pohl, H., 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29, 1541–1552.

Ancel, A., Starke, L.N., Ponganis, P.J., Van Dam, R., Kooyman, G.L., 2000. Energetics of surface swimming in Brandt's cormorants (*Phalacrocorax penicillatus* Brandt). J. Exp. Biol. 203, 3727–3731.

Barquete, V., Bugoni, L., Vooren, C.M., 2008. Diet of neotropic cormorant (*Phalacrocorax brasilianus*) in an estuarine environment. Mar. Biol. 153, 431–443.

Barrett, R.T., Anker-Nilssen, T., Gabrielsen, G.W., Chapdelaine, G., 2002. Food consumption by seabirds in Norwegian waters. ICES J. Mar. Sci. 59, 43–57.

Barrett, R.T., Rov, N., Loen, J., Montevecchi, W.A., 1990. Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. Mar. Ecol. Prog. Ser. 66, 205–218.

Barrett, R.T., Chapdelaine, G., Anker-Nielssen Mosbech, A., Montevecchi, W.A., Reid, J.B., Veit, R.R., 2006. Seabird numbers and prey consumption in the North Atlantic. ICES J. Mar. Sci. 63, 1145–1158.

Brit-Friesen, V.L., Montevecchi, W.A., Cairns, D.K., Macko, S.A., 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology 70, 357–367.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Brugger, K.E., 1993. Digestibility of three fish species by double-crested cormorants. Condor 95, 25–32.

Bryant, D.M., Furness, R.W., 1995. Basal metabolic rates of North Atlantic seabirds. Ibis 137, 219–226.

Burr, M.T., Tinnirello, S.L., Lovell, C.D., Tyson, J.T., 1999. Diet of the double-crested cormorant in western Lake Erie. In: Tobin, M.E. (Ed.), Symposium on double-crested cormorants: population status and management issues in the Midwest. U.S. Dept. of Agriculture Tech. Bull No. 1879, pp. 73–84.

Carss, D.N., et al., 1997. Techniques for assessing cormorant and food intake: towards a consensus view. Suppl. Ric. Biol. Selvaggina 26, 197–230. http://web.tiscalinet.it/sv2001/WI%20-%20CRSG/diet_foodintake.htm.

Chastant, J.E. 2008. Population characteristics of interior double-crested cormorants breeding across the southern border of Ontario. M.Sc. thesis. Mississippi State University.

Coutin, P.C., Reside, J., 2003. Fish predation by great cormorants, *Phalacrocorax carbo carboides*, in the Gippsland Lakes, south-eastern Australia. In: Cowyx, I.G. (Ed.), Interactions between birds and fish: implications for management. Blackwell Science, Oxford, pp. 196–210.

Daan, S., Masman, D., Strijkstra, A.M., Kenagy, G.J., 1991. Daily energy turnover in birds and mammals: its relationship to basal metabolic rate. Acta XX Congr. Internal. Ornithol. 1976–1987.

Dalton, C.M., Ellis, D., Post, D.M., 2009. The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous alewife (*Alosa pseudoharengus*) in south-central Connecticut. Can. J. Fish. Aquat. Sci. 66, 177–186.

Derby, C.E., Lovvorn, J.R., 1997. Predation on fish by cormorants and pelicans in a cold-water river: a field and modeling study. Can. J. Fish. Aquat. Sci. 54, 1480–1493.

Diana, J.S., Maruca, S., Low, B., 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. J. Great Lakes Res. 32, 306–320.

Dirksen, S., Boudewijn, T.J., Noordhuis, R., Marteijn, E.C.L., 1995. Cormorants *Phalacrocorax carbo sinensis* in shallow eutrophic freshwater lakes: prey choice and fish consumption in the non-breeding period and effects of large-scale fish removal. Ardea 83, 167–184.

Dunn, E.H., 1975. Growth, body components and energy content of nestling double-crested cormorants. Condor 77, 431–438.

Ellis, H.I., Gabrielsen, G.W., 2002. Energetics of free-ranging seabirds. In: Schreiber, E.A., Burger, J. (Eds.), Biology of marine birds. CRC Press, Boca Raton, Florida, pp. 359–407.

Engström, H., Jonsson, H., 2003. Great cormorant *Phalacrocorax carbo sinensis* diet in relation to fish community structure in a freshwater lake. Vogelwelt (Suppl.) 124, 187–196.

Enstipp, M.R., Grémillet, D., Jones, D.R., 2006. The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). J. Exp. Biol. 209, 845–859.

Enstipp, M.R., Grémillet, D., Lorentsen, S.-H., 2005. Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*). J. Exp. Biol. 208, 3451–3461.

Enstipp, M.R., Jones, D.R., Lorentsen, S.-H., Grémillet, D., 2007. Energetic costs of diving and prey-capture capabilities in cormorants and shags (Phalacrocoracidae) underline their unique adaptation to the aquatic environment. J. Ornithology 148 (Suppl. 2), S593–S600.

Eschbaum, R., Veber, T., Vetemaa, M., Saat, T., 2003. Do cormorants and fishermen compete for fish resources in the Väinameri (eastern Baltic) area? In: Cowyx, I.G. (Ed.), Interactions between birds and fish: implications for management. Blackwell Science, Oxford, pp. 72–83.

Feltham, M.J., Davies, J.M., 1996. The daily food requirements of fish-eating birds: getting the sums right. In: Greenstreet, P.R., Tasker, M.L. (Eds.), Aquatic predators and their prey. Fishing News Books (Blackwell Science), Oxford, pp. 53–57.

Fowle, M.R. 1997. Population dynamics, food habits, and bioenergetics of double-crested cormorants in Lake Champlain. M.Sc. thesis, University of Vermont, Burlington, Vermont.

Gabrielsen, G.W. 1994. Energy expenditure in arctic seabirds. D. Phil. Thesis, University of Tromsø.

Gagliardi, A., Martinoli, A., Preatoni, D., Wauters, L.A., Tosi, G., 2007. From mass to body elements to fish biomass: a direct method to quantify food intake of fish eating birds. Hydrobiologia 583, 213–222.

Glahn, J.F., Brugger, K.E., 1995. The impact of double-crested cormorants on the Mississippi Delta catfish industry: a bioenergetics model. Col. Waterbirds (Spec. Publ. 1) 18, 168–175.

Grémillet, D., 1997. Catch per unit effort, foraging efficiency and parental investment in breeding great cormorants (*Phalacrocorax carbo*). ICES J. Mar. Sci. 54, 635–644.

Grémillet, D., Schmid, D., Culik, B., 1995. Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. Mar. Ecol. Prog. Ser. 121, 1–9.

Gremillet, D., Wilson, R.P., Wanless, S., Peters, G., 1999. A tropical bird in the Arctic (the cormorant paradox). Mar. Ecol. Prog. Ser. 188, 305–309.

Grémillet, D., Storch, S., Peters, G., 2000. Determining food requirements in marine top predators: a comparison of three independent techniques in great cormorants, *Phalacrocorax carbo carbo*. Can. J. Zool. 78, 1567–1579.

Grémillet, D., Wright, G., Lauder, A., Carss, D.N., Wanless, S., 2003. Modelling daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. J. Appl. Ecol. 266–277.

Harris, C.M., Calladine, J.R., Wernham, C.V., Park, K.J., 2008. Impacts of piscivorous birds on salmonid populations and game fisheries in Scotland: a review. Wildl. Biol. 14, 395–411.

Hatch, J.J., Weseloh, D.V., 1999. Double-crested cormorant (*Phalacrocorax auritus*). In: Poole, A., Gill, F. (Eds.), The birds of North America, No. 441. The birds of North America, Inc, Philadelphia, PA.

Hebert, C.E., Morrison, H.A., 2003. Consumption of fish and other prey items by Lake Erie waterbirds. J. Great Lakes Res. 29, 213–227.

Hennemann, W.W., 1983. Environmental influences on the energetics and behaviour of anhingas and double-crested cormorants. Physiol. Zool. 56, 201–216.

Hilton, G.M., Furness, R.W., Houston, D.C., 2000. A comparative study of digestion in North Atlantic seabirds. J. Avian Biol. 31, 36–46.

Johnson, J.H., Ross, R.M., McCullough, R.D., 2002. Little Galloo Island, Lake Ontario: a review of nine years of double-crested cormorant diet and fish consumption information. J. Great Lakes Res. 28, 182–192.

Keller, T.M., Visser, G.H., 1999. Daily energy expenditure of great cormorants *Phalacrocorax carbo* sinensis wintering at Lake Chiemsee, southern Germany. Ardea 87, 61–69.

Kendeigh, S.C., Stewart, D.J., Weininger, D., 1977. Avian energetics. In: Pinowski, J., Kendeigh, S.C. (Eds.), Granivorous birds in ecosystems. Cambridge University Press, London, pp. 127–205.

Kirby, J.S., Holmes, J.S., Sellers, R.M., 1996. Cormorants *Phalacrocorax carbo* as fish predators: an appraisal of their conservation and management in Great Britain. Biol. Conserv. 75, 191–195.

Leopold, M.F., van Damme, C.L.G., van der Veer, H.W., 1998. Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. J. Sea Res. 40, 93–107.

Madenjian, C.P., Gabrey, S.W., 1995. Waterbird predation on fish in western Lake Erie: a bioenergetics model approach. Condor 97, 141–153.

Martucci, O., 1997. Winter food habits of cormorants Phalacrocorax carbo in central Italy: some remarks. Ekol. Polska 45, 239–243.

Noordhuis, R., Marteijn, E.C.L., Noordhuis, R., Dirksen, S., Boudewijn, T.J., 1997. The trophic role of cormorants *Phalacrocorax carbo* in freshwater ecosystems in the Netherlands during the non-breeding period. Ekol. Polska 45, 249–262.

Platteeuw, M., Koffigberg, K., Dubbeldam, W., 1995. Growth of cormorant *Phalacrocorax carbo sinensis* chicks in relation to brood size, age ranking and parental fishing effort. Ardea 83, 235–245.

Privileggi, N., 2003. Great cormorants *Phalacrocorax carbo* sinensis wintering in Friuli-Venezia Giulia, Northern Adriaic: specific and quantitative diet composition. Vogelwelt 124 (Suppl), 237–243.

Ridgway, M.S., Pollard, J.B., Weseloh, D.V., 2006. Density-dependent growth of double-crested cormorant colonies on Lake Huron. Can. J. Zool. 84, 1409–1420.

Rudstam, L.G., Van de Valk, A.J., Adams, C.M., Coleman, J.T.H., Forney, J.L., Richmond, M.E., 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecol. Appl. 14, 149–163.

Schmid, D., Grémillet, D.J., Culik, B.M., 1995. Energetics of underwater swimming in the great cormorant (*Phalacrocorax carbo sinensis*). Mar. Biol. 123, 875–881.

Seefelt, N.E., Gillingham, J.C., 2008. Bioenergetics and prey consumption of breeding double-crested cormorants in the Beaver Archipelago, northern Lake Michigan. J. Great Lakes. Res. 34, 122–133.

Seiche, K., 2003. The conflicts between great cormorants *Phalacrocorax carbo sinensis* and carp fish farming: attempted resolution and strategy in Saxony, Germany. Vogelwelt (Suppl.) 124, 349–354.

Stempniewicz, L., Martyniak, A., Borowski, W., Goc, M., 2003. Fish stocks, commercial fishing and cormorant predation in the Vistula lagoon, Poland. In: Cowyx, I.G. (Ed.), Interactions between birds and fish: implications for management. Blackwell Science, Oxford, pp. 51–64.

Stewart, D.C., Middelemas, S.J., Gardiner, W.R., Mackay, S., Armstrong, J.D., 2005. Diet and prey selection of cormorants (*Phalacrocorax carbo*) at Lock Leven, a major stocked trout fishery. J. Zool. 267, 191–201.

Van De Valk, A.J., Adams, C.M., Ludstam, L.G., Forney, J.L., Brooking, T.E., Gerken, M.A., Young, B.P., Hooper, J.T., 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. Trans. Am. Fish Soc. 131, 27–39.

Wilson, B.R., Feltham, M.J., Davies, J.M., Holden, T., Britton, J.R., Harvey, J.P., Cowx, I.G., 2003. Increasing confidence in impact estimates—the Monte Carlo approach. Vogelwelt (Suppl.) 124, 375–387.

Wolter, C., Pawlizki, R., 2003. Seasonal and spatial variation in cormorant predation in a lowland floodplain river. In: Cowx, I.G. (Ed.), Interactions between birds and fish: implications for management. Blackwell Science, Oxford, pp. 178–186.