A comparative analysis of early growth in forty-eight species of hand-reared raptor chicks

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Abstract

Raptor (*Falconiformes* and *Strigiformes*) chicks experience a rapid growth rate in the initial twenty days after hatching. Relative growth rate has shown to be influenced by a number of developmental and ecological factors, although the difference across taxonomy has rarely been investigated. This project focused on the weight gain, daily intake and relative growth rate of forty-eight species of raptor, across six families, which were hand-reared in captivity at the International Centre for Birds of Prey, Newent, Gloucesteshire. Significant relationships between age, weight gain, daily intake, and relative growth rate, were established. Taxonomical differences were also significant across all variables, except order against relative growth rate. This could have been due to the limitation of the model as a result of restricted data availability.

This project provides the first taxonomical analysis of weight gain, daily intake and relative growth rate of raptors in captivity. The results give a basis for raptor ecological research and should be expanded on to provide a more thorough dataset that would be applicable to wild raptor populations.

Key words:

Bird of prey; body weight; chick; development; growth; raptor

Introduction

Raptors, commonly known as birds of prey, are generally the apex predator of the ecosystem they reside in. Therefore, their population numbers directly impact the populations of the species that they prey upon (Both et al 2009). This trophic effect has led to an interest in their conservation. Anthropogenic influences such as pesticide use and physical disturbance during nesting periods are key elements to declining raptor populations (Arrogo and Razin 2006; Martinez-Lopez et al 2007). Despite the interest in raptor ecology few have studied the taxonomic differences between early stages of development in chicks (Penteriani et al 2005). Raptor chicks experience a rapid growth rate relative to their body size in the initial 20 days of life (Olsen et al 1982). For example, great horned owls (*Bubo virginianus*) gain 18% of their bodyweight every 48 hours during the first 20 days after hatching (Turner and McClanahan 1981). As with many organisms, bird relative growth rate generally decreases with body size after the initial growth to approximate adult size (Ricklefs 1973).

Chick development can be influenced by a variety of factors. For example, it has been argued that male chicks have a faster relative growth rate than female chicks due to competition pressures created by their species sexual dimorphism, where the female is usually larger (Delannoy and Cruz 1988). Sexual dimorphism is thought to occur as females typically have a shorter embryonic period compared to males. Therefore, females hatch earlier and are able to assert dominance over other siblings due to their larger size (Blanco et al 2003). Boulet et al (2001) suggested that both male and female chicks have similar food intake in the first 21 days after hatching. After this period male chick development rate reduces. Female growth

rate does not alter as their growth efficiency and metabolic rate is significantly greater than males (Krijsveld 1998). For example, female chicks of marsh harriers, *Circus aeruginosus*, can grow up to 45% heavier than males that occupy the same nest (Krijsveld 1998). Therefore, this evidence suggests that competition pressure between siblings is not a relevant factor for the rapid growth rates observed in the initial 20 days of a chick's life (Olsen et al 1982; Bortolotti 1984; Bortolotti 1986; Schaadt and Bird 1993).

It is generally agreed that the high energy demand from chicks must impact development, and that relative growth rate decreases as energy demands increase (Bortolotti 1986; Green and Yelenberg 1994). Therefore, it could be assumed that energy demands increase with brood size, thus decreasing the relative growth rate of chicks (Saether 1994; Haley 2002). However, there has been little empirical support for this relationship (Gard and Bird 1992). For example, Moss (1979) showed that Sparrow-hawk (*Accipiter nisus*) chick growth rates were independent of brood size, although there were correlations between growth rate and hatching order. Hatching asynchrony occurs when the female parent lays the eggs at different intervals which results in various aged chicks in the brood, thus creating a decrease in daily energetic demands on the parents (Mock and Schwagmeyer 1990; Vinuela 2000). Synchronised hatching is when the female lays all the eggs of a clutch in a single sitting. Therefore, chicks hatch at approximately the same time which often results in high daily energetic demands on parents, especially for those that possess large broods. Synchronised hatching generally leads to depressed growth rates of chicks if demands are not met, for example due to poor prey abundance (Vinuela 2000). Hussell (1972) proposed the peak load reduction hypothesis. This suggested that hatching asynchrony occurs as a result of selective

pressures to decrease daily energetic demands on parents, therefore making brood demands more achievable. However, this hypothesis has been challenged as studies suggest the benefit to parents is minor and the only way the hypothesis could be true is if these benefits have a disproportionate value to parents. This seems unlikely as numerous studies provide evidence that suggests asynchronised hatching occurs due to a variety of interconnected selective pressures including competition, prey availability and habitat quality (Moss 1979; Mock and Schwagmeyer 1990; Gard and Bird 1992; Vinuela 2000). For example, younger siblings of asynchronised broods in the Egyptian vulture (*Neophron percnopterus*) show a decreased growth rate as a result of competition with older sibling's that dominate the brood and have high energetic demands (Donazar and Ceballos 1989). McDonald et al (2005) provided evidence that in less abundant prey habitats the gender of the last chick to hatch in a brood of brown falcons, *Falco berigora*, determines its' survival probability. Male chicks are more likely to survive as they are the smaller sex, thus energetic demands are lower than that of the female and basic requirements are more likely to be met. Therefore, parental investment in the less energetically demanding sex increases the fitness of the parent. Brood reduction in altricial raptors is an adaptive response to prey availability and habitat quality (Saether 1994; Haley 2002).

Size, weight gain and food consumption significantly influence relative growth rate of raptor chicks (Fernie et al 2006). Food consumption levels of chicks are impacted by prey abundance, which consequently is positively correlated with relative growth rate (Masterov 2000). For example, bald eagle (*Haliaeetus leucocephalus*) nestlings experience an increased growth rate due to highly profitable prey abundance in mesohaline habitats in comparison to depressed growth rates from low calorific prey

in tidal-fresh salinity zones (Marham and Watts 2000). Therefore, habitat quality significantly impacts relative growth rate. This is also supported by habitats that are chemically contaminated as they generally have a negative correlation with prey abundance - consequently, contaminants have a negative effect on the relative growth rate of chicks in affected areas (Woodford et al 1998; Gill and Elliot 2003; Fernie et al 2006). Contrary to these findings, however, Donazar and Ceballos (1989) and Saether (1994) found that chick growth rate was independent of prey abundance. Negro et al (1994) continued to support this with their experiments on hand reared chicks. They raised raptor chicks with abundant and restricted diets. Their results showed that raptors that had a reduced diet continued to grow on all growth parameters measured, despite temporary starvation, and all chicks re-gained the weight lost in two to four days. This showed that raptor chicks are not affected by prey availability alone as chicks would survive, relatively unaffected, during times of temporary low prey abundance.

The majority of the research conducted on raptor chicks has focused on wild populations and the factors that affect survival rates, with some indication of factors affecting growth rate in species (Wiklurd 1990; Arrogo and Razin 2006; Penteriana et al 2007). Raptor chicks experience a rapid growth rate in the initial stages of life but there has been little research on development of relative growth rate across a taxonomic range of species of raptor chicks (Penteriani et al 2005).

This investigation therefore aims to elucidate the variability of growth across a wide sample of raptor species reared in captivity. In addition to an improvement in our understanding of the likely relevance of taxonomic differences, this information may also help to improve hand-rearing practices. The information employed for this

research comes from hand rearing records kept by the International Centre for Birds of Prey in Newent, Gloucestershire.

<u>Methods</u>

The International Centre for Birds of Prey (ICBP) has recorded the weights of hand-reared chicks since 1978. Records are paper based and range across various families of raptors including *Falconidae*, *Accipitridae*, *Strigidae*, *Tytonidae*, *Sagittariidae* and *Cathartidae*. Chicks are typically fed a standard diet four times a day and kept separate but under similar conditions when rearing. Chicks are weighed before and after feeding and amount of days reared range from 1 to 55 days.

The paper records were transferred onto an electronic format in Microsoft Excel (Microsoft Excel version 14 2010). Only records that contained more than two daily records on chick bodyweight were placed into the database. Records were also rejected if feeding data were limited or inconsistent. The database recorded taxonomy, medical information, age, morning weights, weight gain per day and daily food intake, but not all the information was complete enough to be included in the analyses here presented. Relative growth rate (RGR) of individual chicks was calculated from their daily weight data according to the formula:

$$RGR = \frac{\log(w_2) - \log(w_1)}{t_2 - t_1}$$

Where w_1 and w_2 are the weight data at the beginning (t_1) and the end (t_2) of each sampling interval; this interval was usually a day, but the formula allows for varying time intervals, which occasionally occurred when, for example, a day's record was missed.

Data analysis was conducted in the statistical program SPSS (IBM SPSS version 19.0.0 2010) and consisted of fits of general liner models and univariate analyses of response variables, weight, intake or RGR with age as covariant and taxonomic level (order, family or species) as fixed factors.

Results

Size increased along protracted sigmoid curves (Fig. 1) and the (linear) effect of age on size was significant (P <0.00; Table 1). At the order level *Falconiformes* chicks had a larger average body size than *Strigiformes* chicks (Fig. 1a and b). There were also significant differences in size at the family level (Fig. 1c and d; Table 2). Families are ranked from heaviest to lightest in the order: *Sagittariidae*, *Cathartidae*, *Accipitridae*, *Strigidae*, *Falconidae*, and *Tytonidae*. Finally there were also significant differences among species (Fig. 1e and f; Table 3).

Table 1. Analysis of covariance of raptor chicks' morning weight (log-transformed) vs. age classified by order (fixed factor) with a significance of P <0.00 and variance of r^2 = 0.59

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	295.962[a]	2	147.981	2390.263	.000
Intercept	2928.987	1	2928.987	47310.436	.000
Age	264.909	1	264.909	4278.943	.000
Order	27.262	1	27.262	440.347	.000
Error	205.665	3322	.062		
Total	10384.268	3325			
Corrected Total	501.627	3324			

Table 2. Analysis of covariance of raptor chicks' morning weight (log-transformed) vs. age classified by family (fixed factor) with a significance of P <0.00 and variance of r^2 = 0.692

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	347.166[a]	6	57.861	1242.919	.000
Intercept	741.533	1	741.533	15928.963	.000
Age	194.166	1	194.166	4170.901	.000
Family	78.466	5	15.693	337.106	.000
Error	154.461	3318	.047		
Total	10384.268	3325			
Corrected Total	501.627	3324			

Table 3. Analysis of covariance of raptor chicks' morning weight (log-transformed) vs. age classified by species (fixed factor) with a significance of P <0.00 and variance of r^2 = 0.935

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	469.479[a]	48	9.781	996.711	.000
Intercept	1541.765	1	1541.765	157113.004	.000
Age	161.405	1	161.405	16447.956	.000
Species	200.779	47	4.272	435.326	.000
Error	32.148	3276	.010		
Total	10384.268	3325			
Corrected Total	501.627	3324			

Fig. 1 Growth trajectories of recently hatched chicks at the International Centre for Birds of Prey organised by taxonomic level order (a & b), family (c & d) and species (e & f) and either as individual chick data (a, c & e) or taxonomic level averages at 5.75 days (b, d & f)

Daily intake also increased along protracted sigmoid curves (Fig. 2) and the (linear) effect of age on intake was significant (P <0.00; Table 4). At the order level *Falconiformes* chicks had higher intake than *Strigiformes* chicks (Fig. 2a and b). There were also significant differences in daily intake at the family level (Fig. 2c and d; Table 5). Families are ranked from highest intake to least in the order: *Cathartidae, Sagittariidae*, *Accipitridae*, *Falconidae*, *Strigidae* and *Tytonidae*. Finally there were also significant differences among species (Fig. 2e and f; Table 6).

Table 4. Analysis of covariance of raptor chicks' daily intake (log-transformed) vs. age classified by order (fixed factor) with a significance of P <0.00 and variance of r^2 = 0.497

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	379.832[a]	2	189.916	1619.709	.000
Intercept	515.458	1	515.458	4396.107	.000
Age	346.724	1	346.724	2957.056	.000
Order	39.901	1	39.901	340.297	.000
Error	383.535	3271	.117		
Total	4832.316	3274			
Corrected Total	763.367	3273			

Table 5. Analysis of covariance of raptor chicks' daily intake (log-transformed) vs. age classified by family (fixed factor) with a significance of $P <0.00$ and variance of $r^2 = 0.537$

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	410.368[a]	6	68.395	632.991	.000
Intercept	173.449	1	173.449	1605.263	.000
Age	335.330	1	335.330	3103.470	.000
Family	70.437	5	14.087	130.378	.000
Error	352.999	3267	.108		
Total	4832.316	3274			
Corrected Total	763.367	3273			

Table 6. Analysis of covariance of raptor chicks' daily intake (log-transformed) vs. age classified by species (fixed factor) with a significance of $P <0.00$ and variance of $r^2 = 0.682$

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	524.477[a]	48	10.927	147.508	.000
Intercept	315.301	1	315.301	4256.538	.000
Age	291.434	1	291.434	3934.338	.000
Species	184.546	47	3.927	53.008	.000
Error	238.890	3225	.074		
Total	4832.316	3274			
Corrected Total	763.367	3273			
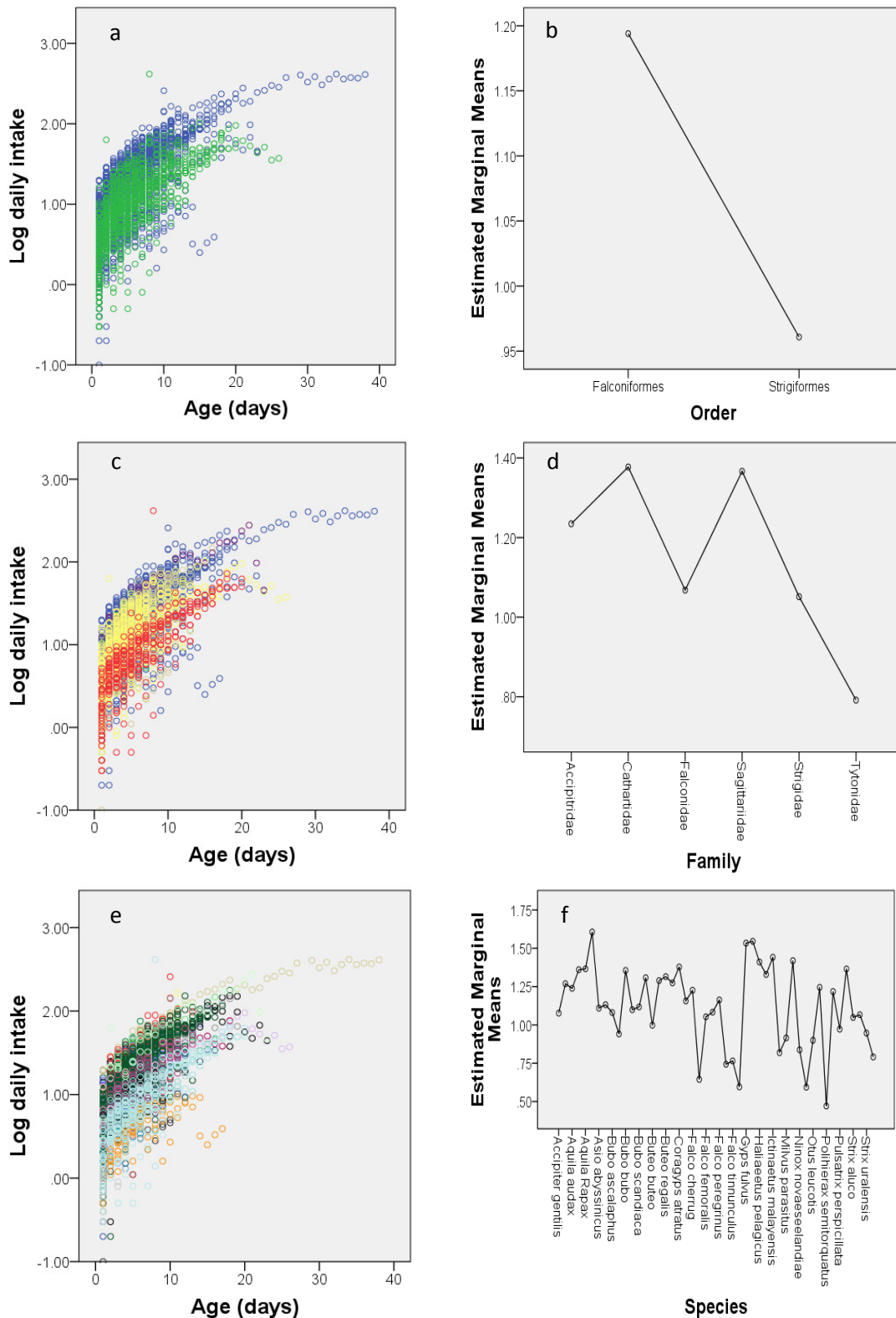
Fig. 2 Logarithmic daily intake of recently hatched chicks at the International Centre for Birds of Prey organised by taxonomic level order (a & b), family (c & d) and species (e & f) and either as individual chick data (a, c & e) or taxonomic level averages at 5.41 days (b, d & f)

Relative growth rate decreased along protracted sigmoid curves (Fig. 2) and the effect of age on growth rate was significant (P <0.00; Table 7). At the order level *Falconiformes* chicks had a higher relative growth rate compared to *Strigiformes* chicks (Fig. 3a and b) however, this was not significant at a 5% confidence level (P =0.512; r^2 = 0.02; Table 7). On the other hand relative growth rate was significant at family level (Fig. 3c and d; Table 8). Families are ranked from highest growth rate to least in the order: *Falconidae, Tytonidae, Strigidae, Accipitridae, Cathartidae and Sagittariidae.* Finally there were also significant differences among species (Fig. 3e and f; Table 9).

Table 7. Analysis of covariance of raptor chicks' relative growth weight vs. age classified by order (fixed factor) with no significant value of P =0.512 and 2% variance (r^2 = 0.02)

| Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	.377[a]	2	.188	31.549	.000
Intercept	17.340	1	17.340	2905.793	.000
Age	.374	1	.374	62.697	.000
Order	.003	1	.003	.430	.512
Error	17.938	3006	.006		
Total	66.009	3009			
Corrected Total	18.314	3008			

Table 8. Analysis of covariance of raptor chicks' relative growth weight vs. age classified by family (fixed factor) with a significance value of $P < 0.00$ and a variance of $r^2 = 0.055$

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.037[a]	6	.173	30.033	.000
Intercept	2.662	1	2.662	462.519	.000
Age	.737	1	.737	127.995	.000
Family	.663	5	.133	23.044	.000
Error	17.277	3002	.006		
Total	66.009	3009			
Corrected Total	18.314	3008			

Table 9. Analysis of covariance of raptor chicks' relative growth weight vs. age classified by species (fixed factor) with a significance value of $P < 0.00$ with a variance of $r^2 = 0.084$

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.815[a]	51	.036	6.378	.000
Intercept	6.885	1	6.885	1233.960	.000
Age	.803	1	.803	143.906	.000
Species	1.441	50	.029	5.166	.000
Error	16.499	2957	.006		
Total	66.009	3009			
Corrected Total	18.314	3008			
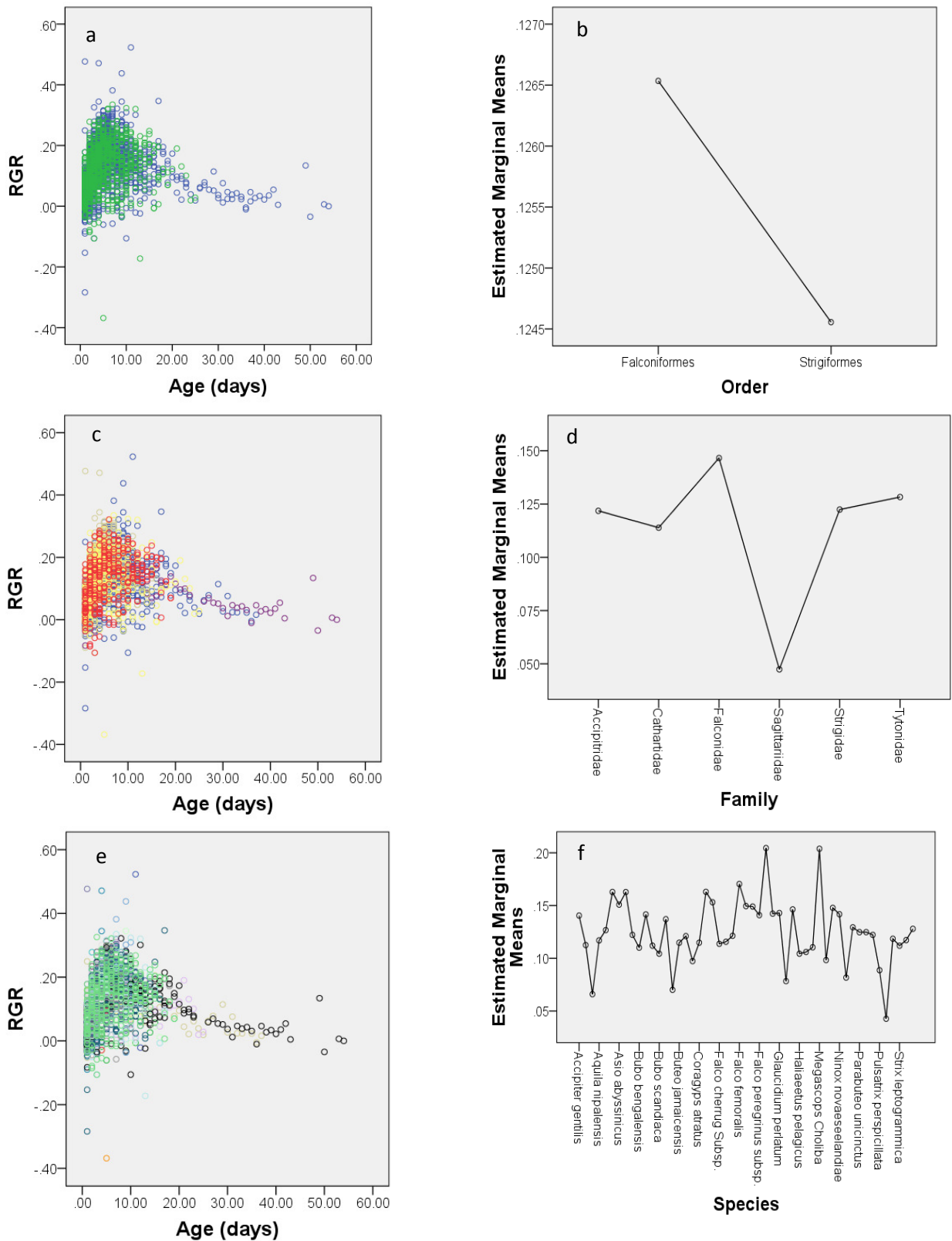
Fig. 3 Relative growth rates of recently hatched chicks at the International Centre for Birds of Prey organised by taxonomic level order (a & b), family (c & d) and, species (e & f) and either as individual chick data (a, c & e) or taxonomic level averages at 5.2419 days (b, d & f)

Discussion

The linear relationship found between bodyweight of young raptor chicks and age was consistent with previous findings (Collopy 1986; Komen 1991; Durrant and Handrich 1998; Nagarajan et al 2002). However, there was not enough data relating to older chicks present to explain the bell-shaped curve of bodyweight gain that was cited by Komen (1991) and Durrant and Handrich (1998). They suggested chick bodyweight exceeds that of adults, possibly due to competition pressures within the brood - therefore, a decrease in bodyweight to equal that of adult bodyweight is necessary before fledging is possible. Although the data analysed does not demonstrate a bell shaped curve, it is clear that the data reaches a plateau at approximately 20-25 days old (Fig. 1a). Passed this age, the amount of available data begins to decrease, and therefore no conclusive trends can be determined. Hatch weight significantly varied across the taxonomic scale observed (order, family and, species) and differences in initial hatch weights were maintained with age. Similarly, daily intake was correlated with age and significantly varied across the aforementioned taxonomic scales. In particular, the results suggested *Falconiformes* had a significantly higher intake and thus increased body mass in comparison to *Strigiformes* (Fig. 1a and b; Fig. 2a and b). Interestingly, results of the relative growth rates between the orders *Falconiformes* and *Strigiformes* showed no significant difference, with only 2% variance at the 5% confidence interval (Fig. 3a and b; Table 7). On the other hand, relative growth rate at the family and species taxonomic level were significantly different (Fig. 3d and f; Table 8 and 9). Results typically showed an initial increase in relative growth rate followed by a decrease. The results demonstrate that relative growth rate was highest in the families that contained smaller species. *Falconidae* had the highest

average relative growth rate followed by both the families in the order *Strigiformes*. Typically, smaller species have a faster metabolism and therefore convert calories into metabolic processes, such as tissue formation for repair and growth, at an increased rate in comparison to larger species of raptor (Fevold and Craighead 1958; Wasser 1986; Nagy 1987). Although order level was not significant at the 5% confidence interval it provides some evidence to support Duke et als' (1975) findings on *Falconiformes*. They showed that *Falconiformes* had a higher basal metabolic rate and consequently increased relative growth rate in comparison to *Stirgiformes*. They suggested this was due to a more efficient digestive tract as *Falconiformes* gut contains more gastric juice that efficiently breaks down food, thus preventing energy loss when pellets are produced. Pellets typically contain the less calorific products of prey items that are more difficult to digest such as hair, feathers and, bone (Duke et al 1975).

Growth rates are typically associated with ecological and developmental factors such as prey availability, competition, and habitat quality (Gard and Bird 1992; Blanco et al 2003; Markham and Watts 2008). Contrary to this, Royle et al (1999) suggested that evolutionary time-scales had a strong influence on the relative growth rates of raptor chicks. Royle et al (1999) proposed that relative growth rate would be higher in broods that contained non-direct kin (half-sisters or brothers). Therefore, polygamous avian species would be expected to have a high relative growth rate. Although raptors are traditionally considered to be strictly monogamous, there is growing evidence of polygamy in raptor species in recent years (Kimball et al 2003). The highest relative growth rates of raptor chick families in this study were found in *Falconidae,* followed by *Tytonidae,* and then *Strigidae.* Each of these families has species that have been shown to be either polyandrous or polygynous

through cooperative breeding, including the lesser kestrel (*Falco naumanni*), European eagle owl (*Bubo bubo*), tengmalams owl (*Aegolus fenereus*), flammulated owl (*Otus flammeolus*) and the barn owl (*Tyto alba*) (olheim 1983; Marti 1990; Tella et al 1996; Martinez et al 2005; S; Linkhart et al 2008;). There has been no evidence of polyandry for the slowest growing raptor family, *Sagittariidae*, that was found in this study. Polygamy is thought to occur in raptors due to increased benefits from group living when prey and nesting availability are limited and predation rates are high (Solheim 1983). Therefore, these results support the evolutionary theory of growth rate in raptor chicks as the highest relative growth rate was found in families that have the potential to be polyandrous, thus broods could contain chicks of non-direct kin.

The data presented were restricted by the amount of data recorded at the time of the chicks' rearing. Interpretation of these results must be carefully undertaken as the data could have been skewed by age bias. Age bias occurred due to the limited period over which chick weights were recorded - data generally consisted of chicks up to 25 days old. Only two species of chicks, the wedge-tailed hawk (*Aquila* audrax) and the secretary bird (*Sagittarius serpentarius*), provided data in excess of 30 days. As well as the age bias, gender differences could have skewed results as the effect of relative growth rate has been shown to significantly differ between sexes (Krijgsveld et al 1998; Boulet et al 2001; Blanco et al 2003). Female raptor chicks typically have a more efficient growth and metabolism rate in comparison to male chicks (Krijgsveld et al 1998; Boulet et al 2001). On the other hand, male chicks are significantly smaller than females in sexually dimorphic species, therefore generally reach fledging rate faster (Richner 1991). The data are also based on captive birds, and so stressors such as prey availability, predation,

habitat contamination, precipitation, wind, and competition, are not present although some stressors such as anthropogenic activity, humidity, and temperature, are still applicable to hand reared raptor chicks (Donazar and Ceballos 1989; Woodford et al 1998; Masterov 2000; Vinuela 2000; Gill and Elliot 2003; Sanchez et al 2004; Kontiatien et al 2009). Hand reared chicks and wild chicks have been shown to have little variance in their growth parameters, and therefore, these results could be applied to a wild population (Collopy 1986, Bird and Lague 1982). However, caution should be taken when applying these results to both captive raptors and wild raptor populations as the univariate statistical analyses assume a straight line of best fit through the data, which could potentially lead to misinterpretation and false conclusions.

Conclusion

These results provide the first insight into taxonomical variations between bodyweight, daily consumption, and relative growth rates of newly hatched raptor chicks that until now has rarely been studied across such a diverse sample size. They add valuable datasets to the growing knowledge of raptor ecology. Results showed significant relationships between age and body mass; intake; and growth rate. As well as this, significant differences were found between all variables across the taxonomy, with the one exception between order (*Falconiformes* and *Strigiformes*) and relative growth rate. Relative growth rate results for family taxonomy provided some supportive evidence for evolutionary theories of growth rates in raptor chicks, although to confirm this evolutionary phylogeny should be investigated (Royle et al 1999).

The production of linear graphs of age against daily intake and body mass may increase the understanding of hand-rearing practices, as there are few datasets available that suggest daily intake values of different species of raptors. The graph of species relative growth rate against age may also provide a basis of how fast different species grow in the short time frame for those who practice chick hand-rearing.

Although these models provide a comprehensive analysis of raptor chick growth rate, many complicating variables, such as gender and temperature, were not included due to lack of information. Further research should focus on a precise and consistent dataset that includes ages up to and including fledging age. This would allow better interpretation between taxonomies of body mass and intake with a progressing age. Including variables in the model such as gender, clutch size and

environmental factors, as well as taking several measurements of growth parameters including body weight, tarsus size, cranium size, and feather development, could provide a more comprehensive representation of growth rate and the factors that determine it.

Acknowledgements

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