Lipid reserves, fasting capability and the evolution of nestling obesity in procellariiform seabirds

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Several alternative explanations have been proposed to account for the evolution of nestling obesity in a variety of avian groups. These predict quite different patterns of fat accumulation, storage and use by chicks of different ages. Yet surprisingly few studies have measured changes in body composition during chick development. We tested the applicability of these hypotheses for fulmars, *Fulmarus glacialis*, by direct measurement of changes in water, lipid and lean dry mass in growing chicks. Lipid and lean dry mass increased until ca. 70% of the way through chick rearing, but then levelled off. Total body water also increased until the same stage, but gradually declined thereafter, and it was this change rather than fat metabolism that resulted in mass recession. The observed pattern of a continued increase in stored lipid, and most importantly, its maintenance all the way through the mass-recession phase until chicks reach fledging, is incompatible with many of the proposed hypotheses. We suggest that the most likely ultimate explanation for large fat deposits is to fuel chicks during the initial critical period away from the nest site while they learn to forage effectively.

Keywords: fat stores; mass recession; post-fledging survival

1. INTRODUCTION

Birds exhibit a remarkably broad spectrum of developmental patterns from hatching to fledging (Starck & Ricklefs 1998). For instance, the proportion of body fat accumulated during the first half of the nestling period varies from 10% to 60% of dry body mass (Taylor & Konarzewski 1989). Despite a considerable research effort, the adaptive significance of this extensive variation remains poorly understood.

Accumulation of body fat is especially marked in procellariiform seabirds (albatrosses, shearwaters and petrels). Chicks reach a peak mass of, on average, 136% of adult body mass about 70% of the way through chick-rearing, but then gradually lose mass until fledging (Warham 1990). Other taxonomic groups, including oilbirds (*Steatornis caripensis*), birds of prey (Falconiformes), swallows (Hirundinidae) and various pelagic seabirds such as tropicbirds (Phaethontidae), some auks (Alcidae) and gannets (Sulidae), also show this characteristic type of growth pattern, but generally to a lesser extent than is seen in the Procellariiformes.

A number of hypotheses have been proposed to explain the evolution of such high levels of nestling obesity. (i) Large stores of body fat ensure the survival of chicks during prolonged fasts resulting from occasional periods of bad weather or otherwise poor foraging conditions experienced by parents at sea (Lack 1968). (ii) Fat reserves provide an insurance against stochastic variation

in foraging success of individual parents, over and above the effects of temporal or spatial variation in food supply for the colony as a whole (Ricklefs 1990; Ricklefs & Schew 1994). In this case, routine overfeeding of chicks arises because each parent forages independently of its partner and has limited capacity to regulate food delivery according to nestling energy requirements. (iii) Chicks deposit lipid during early chick rearing when their energy requirements are comparatively low, and use these stores to subsidize greater metabolic costs later in development. (iv) Parents oversupply chicks with prey that are energy-rich but nutrient-poor, and fat reserves therefore act as an energy sink (Ricklefs 1979). (v) Fat accumulated during the nestling period is crucial for survival after fledging, while fledglings develop foraging skills (Perrins *et al.* 1973). (vi) Fat stores have evolved to fuel chick metabolism in the period shortly before fledging to allow adults to commence post-breeding migration sooner than they could otherwise (Brooke 1990). However, in the majority of cases, chicks are apparently not abandoned by adults during the mass-recession phase, although they are visited less frequently, and so this last hypothesis can apply only in a few species (Warham 1990).

Previous studies of nestling obesity have focused on natural and experimentally induced variation in feeding frequencies, meal sizes and mass changes of chicks (Ricklefs *et al.* 1985, 1987; Schaffner 1990; Hamer & Hill 1993, 1994, 1997; Bolton 1995; Hamer *et al.* 1997*a,b*). This type of approach has limitations, because changes in the amounts of fat stored by chicks can be inferred only indirectly from fluctuations in body mass, and is therefore potentially confounded both by variation in mass of

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stomach contents, and by changes in body composition during growth. For example, it is generally assumed that the pre-fledging mass recession of chicks mainly results from the metabolism of fat once provisioning rates decline. Yet, this need not necessarily be the case, as chick tissues continue to lose water until they reach full functional maturity.

A few studies have monitored changes in body components of pelagic seabird chicks until part-way through development (see, for example, Ricklefs *et al.* 1980; Montevecchi *et al.* 1984; Navarro 1992), but to our knowledge only one has included procellariiform chicks in the mass recession phase (Obst & Nagy 1993). In the current study, we examine temporal changes in body composition directly in northern fulmar (*Fulmarus glacialis*) chicks. This is one of the most abundant procellariiforms in the Northern hemisphere, and also had the advantage that comprehensive data were already available on provisioning rates and diet (Hamer *et al.* 1997a; Phillips & Hamer 1999; Phillips *et al.* 1999). The purpose of the current study was to relate changes in stored reserves and fasting capability of chicks to variation in feeding frequency, and so distinguish between several of the above hypotheses, which predict quite different patterns of fat accumulation, storage and use by chicks during development.

2. METHODS

(a) *Body composition analysis*

The northern fulmar is a robust, surface-nesting species, with an adult mass of *ca.* 800 g. Both incubation and chick-rearing periods are prolonged, and chicks fledge at a mean age of 57 days (see §3). A sample of 23 fulmar chicks aged from ten to 60 days was collected under license from Fair Isle, Shetland (59°32' N, 1°38' W) in July–September 1997 and stored frozen until analysis. Chick age was estimated from wing length (maximum wing chord) by means of a logistic curve fitted to changes in wing with age of a sample of chicks of known age. With this approach for the known-age sample, the mean difference ($\pm$ s.e.) between predicted and observed age was -0.17 ± 0.13 d. A further 49 chicks at the colony were weighed daily or every five days from hatching to fledging to provide data on changes in mass during growth.

Chicks collected for analysis were plucked, then dissected into eight major body components: pectoral muscles, leg muscles, heart, liver, kidney, gut (contents removed), skin, and remaining carcass. To obtain fresh and dry masses, feathers and tissues were weighed, dried initially at 40 °C for two to three weeks, and then transferred and dried to constant mass at 40 °C in a vacuum oven. Drying at 40 °C minimizes potential loss of volatile lipids. Dried tissues were homogenized in an electric blender and subsamples removed for lipid extraction. Lipid content was determined by using a refluxing soxhlet apparatus with petroleum ether as the solvent.

(b) *Fasting capability*

Minimum potential fasting durations, i.e. the number of days that chicks of a particular age can survive following a meal, were estimated as follows. The maximum energy available from stored lipid was calculated assuming a calorific density of 38 kJ g^{-1} (Ricklefs 1974) and that lipid mass equivalent to a lipid index (lipid/lean dry mass) of 0.1 cannot be metabolized as an energy source (Taylor & Konarzewski 1989; Navarro 1992).

Figure 1. Changes in body mass of fulmar chicks with age ($n = 1747$ measurements from 49 chicks).

Energy assimilated from chick meals was calculated from the product of (i) mean meal mass in each of ten-day age classes, estimated with a periodic weighing protocol (Phillips & Hamer 1999); (ii) the published value for mean caloric density of prey delivered to chicks (6.2 kJ g^{-1}) (Hamer *et al.* 1997a); and (iii) an assumed assimilation efficiency of 83% (Hilton *et al.* 1999). Chicks' daily energy requirements (mass-specific resting metabolic rate, RMR) were estimated in two ways according to equations presented in Weathers & Siegel (1995): (i) from the power relationship, $\text{RMR (kJ h}^{-1}\text{)} = aM^b$ where M is chick mass, and a and b are species-specific scaling coefficients calculated from adult mass (800 g), with b reduced by 39% for fasting chicks; and (ii) by using a quadratic regression fitted to the relationship between log RMR and log chick mass in 27 species of bird. It should be noted that even approach (i) may provide only minimum values for potential fasting duration, as over the longer term, starving chicks begin to lose mass, reducing their total energy expenditure. Petrel chicks may also save energy by allowing their body temperature to drop and going into partial torpor (Boersma 1986). In addition, because fulmar chicks contain so much lipid, which has a lower maintenance energy requirement than lean tissue, they may have lower mass-specific RMRs than the species that provided data for the above generic equations.

3. RESULTS

(a) *Changes in mass during development*

Chicks increased in mass rapidly after hatching, reaching a mean mass of 950 g by 40–45 days old (figure 1). Chicks then underwent a period of mass recession until fledging at around adult mass. Mean fledging age was 57.1 ± 2.4 d (range 52–61 days, $n = 15$ chicks).

(b) *Body composition*

Changes in different components of chick mass (water, lipid and lean dry mass) can be considered in several ways, (i) in terms of absolute mass, and (ii) as a proportion of total chick mass (excluding gut contents).

The total water content of chicks increased from 140 g at ten days to over 600 g by 40–45 days old, but then declined to 400 g by 60 days old (figure 2a). In contrast, total lipid mass increased from only 10 g at 10 days old, to *ca.* 300 g by 45 days old, and then began to level off (figure 2b). Lean dry mass (including feathers) showed a similar pattern,

Figure 2. Changes in total (a) water mass, (b) lipid mass and (c) lean dry mass of fulmar chicks with age ($n = 23$ chicks).

increasing from *ca.* 30 g at ten days old to *ca.* 230 g at 40–45 days old before it also levelled off (figure 2c).

Expressed as a proportion of total chick mass (excluding gut contents), water showed a linear decline from 77% at ten days old to 42% at 60 days old, and lipid concentration a linear increase from *ca.* 6% at 10–16 days old to 34% at 60 days old (figure 3a,b). Lean dry mass also increased in a broadly linear fashion, from a mean of around 19% at 10–25 days of age, to 23% in chicks older than 50 days (figure 3c). The greater degree of scatter in this last graph is presumably attributable to the simultaneous changes in water and lipid content, which together constitute a much greater proportion of overall chick mass.

(c) *Fasting capability*

Total energy content of lipid reserves available for energy generation increased from 230 kJ in chicks aged

Figure 3. Changes in the proportion of (a) water, (b) lipid and (c) lean dry mass in fulmar chicks with age ($n = 23$ chicks).

ten days to over 11 000 kJ in chicks approaching fledging (table 1). After taking account of assimilation efficiency, the energy content of the average meal fed to chicks increased by far less, from 265 kJ in the youngest chicks to 630–650 kJ in chicks aged over 40 days (table 1). In terms of usable energy, a meal therefore represented 54% of the total available until the next feed for chicks aged ten days, compared with under 6% of the total energy available for chicks aged over 40 days.

Minimum age-specific fasting capabilities for chicks with RMRs calculated by the two different approaches (see § 2), and relying either on lipid stores alone, or on lipid reserves plus the energy contained in their last meal, are shown in figure 4. With an empty gut, a chick aged ten days could survive for at least a further one to two days on its fat stores alone. By contrast, a chick with the same mass of stored fat that had just been fed could survive for three

Table 1. *Estimated energy content of lipid reserves and chick meals compared with resting metabolic rates (RMR)*

(See text for details of methodology.)

age class (days)	mean chick mass (g)	lipid index	mean stored lipid (g)	lipid available for energy generation (g)	energy available from stored lipid (kJ)	mean meal mass (g)	meal energy content (kJ)	total available energy from reserves and last meal (kJ)	RMR ^a (kJ d ⁻¹)	RMR ^b (kJ d ⁻¹)
10	209	0.29	9.2	6.0	230	51.3	265	495	135	194
11–20	394	0.36	24.4	17.6	668	75.9	392	1060	196	317
21–30	681	0.59	73.2	60.8	2312	109.1	564	2876	270	467
31–40	896	0.76	148.9	129.3	4912	122.1	631	5544	317	563
41–50	924	1.28	299.8	276.3	10 500	126.4	653	11 153	323	574
> 50	825	1.40	312.8	290.4	11 037	123.8	639	11 676	302	533

^a Calculated from equations (2) and (5); ^b calculated from equation (7) of Weathers & Siegel (1995).

Figure 4. Minimum estimated fasting capability of fulmar chicks of different ages. Lines fitted by least-squares method.

to four days (figure 4). Chicks aged 11–20 days could survive for slightly longer, at least two to three days on their fat stores alone, and three to five days following a meal. Minimum fasting capability increased markedly in older chicks, with those aged 21–30 days able to survive for 6–11 days, depending on their RMR, and those aged over 40 days able to survive for 18 days at the very least.

4. DISCUSSION

(a) *Comparison with adult fulmars*

Our results indicate that, during fulmar chick development, both lean dry mass and total lipid mass gradually increase until chicks reach 40–45 days old, after which no obvious further changes take place (figure 2*b,c*). The asymptotic lean dry mass of chicks (*ca.* 230 g; figure 2*c*) is remarkably similar to the mean value of 224 g for adult fulmars collected at St Kilda, which were analysed for lean dry and lipid, but not water content, by Osborn & Harris (1984). By comparison, the asymptotic lipid mass of chicks (*ca.* 300 g; figure 2*b*) is much greater than the mean of 113 g for adults (Osborn & Harris 1984). Adult fulmars clearly store much less fat than fledglings; this observation is in keeping with the results of other seabird

studies (Ricklefs *et al.* 1980; Montevecchi *et al.* 1984; Roby 1991; Navarro 1992).

(b) *Mass recession*

The increase in lean dry mass with age corresponds to growth of feathers and structural tissue (internal organs, skin, bone and cartilage), which had mostly ceased by the time chicks started to lose mass (see figure 1). This might be considered surprising given that flight feathers continue to develop until at least fledging. However, secondary feathers, wing coverts and body feathers have already reached maximum dry mass by 45 days old, and although the lengths of primary feathers increase considerably from 45 days old to 60 days old (by 50 mm for the longest primary), this represents an increase in total dry mass of only 2 g, which is tiny in comparison with an overall plumage mass at fledging of *ca.* 77 g (R. A. Phillips and K. C. Hamer, unpublished data).

In contrast to lipid and lean dry content, total body water also increased until 40–45 days post-hatching, but gradually declined thereafter (figure 2*a*). It is primarily this decrease in water mass that appears to be responsible for the pre-fledging mass recession seen in fulmars. However, a caveat should be noted that the oldest chicks also weigh less on average because they are less likely to have been fed recently, as only 35% of chicks older than 50 days are fed per day, compared with a mean of 89% earlier in chick rearing (R. A. Phillips and K. C. Hamer, unpublished data). In chicks of the barn swallow (*Hirundo rustica*), the northern gannet (*Morus bassanus*) and the Cape gannet (*M. capensis*), the observed mass recessions are also attributable mainly or entirely to loss of water (Ricklefs 1968; Navarro 1992; W. A. Montevecchi, unpublished data). In contrast, in the only comparable study on a procellariiform, Wilson's storm petrel (*Oceanites oceanicus*), chicks were found to metabolize a substantial portion of their lipid stores, as well as to lose water, during the mass-recession phase (Obst & Nagy 1993). The mechanism responsible for mass recession appears therefore to differ within the Procellariiformes, and data on more species are clearly required.

(c) *Evolutionary explanation for large fat reserves*

In comparison with later in chick rearing, young fulmar chicks possess small lipid stores. By 11–20 days

post-hatching, they have accumulated *ca.* 24 g, which represents just 8% of total chick mass (figure 2*b*). From then on, the size of the fat reserve increases fairly steadily until it reaches a peak mass of 300 g when chicks are around 45 days old, which is maintained until fledging.

Lipid reserves of young fulmar chicks, albeit much smaller than later in development, are crucial in extending by one or two days the period they can survive without feeding (see §3) and clearly convey a considerable selective advantage. In fulmars, as in other surface-nesting Procellariiformes, there is an initial period after hatching when chicks are brooded, followed by a further 'guard' phase when one adult is normally in attendance (Warham 1990). This lasts usually until 10–14 days in fulmars, which corresponds with the time taken to accumulate sufficient energy reserves to survive between meals without a 'top-up' feed by an attending adult (see also Roby 1991). From the observed pattern of chick mortality at the colony, it is during this early stage that chicks are most vulnerable to starvation and hypothermia. Predation rates are low, and most young chicks that survive this initial critical period usually survive to fledging (R. A. Phillips and K. C. Hamer, unpublished data).

By comparison, older chicks have fat stores more than sufficient to last them from one meal until the next. The maximum observed intervals between feeding events for young chicks (under 25 days old) during two-week periods at St Kilda (Outer Hebrides) in 1994, and St Kilda and Foula (Shetland) in 1995, were 80 h, 48 h and 32 h, respectively (Hamer *et al.* 1997*a*). There are no data on maximum feeding intervals for fulmar chicks at Fair Isle, but the average of 89% of chicks fed per day (until 50 days of age), is only slightly lower than feeding frequencies at the above colonies (K. C. Hamer, unpublished data). The likelihood of chicks at Fair Isle having to endure more than a few days without a meal is therefore equally low, given that the probability of a chick not being fed on a particular day is 0.11, and hence, assuming independence of feeding by both adults, the probability of not being fed, for example, on any four days is only one in 10 000. In fact, the probability of not being fed on consecutive days is far lower than this, as adults that have not returned one day are more likely to return the next.

In line with results of other studies in which lipid reserves were measured directly, estimated fasting capabilities of fulmar chicks were much greater than the probable maximum time between meals (Ricklefs *et al.* 1980; Montevecchi *et al.* 1984; Taylor & Konarzewski 1989; Roby 1991; Navarro 1992; this study). With the exception of short-tailed shearwaters (*Puffinus tenuirostris*), which may occasionally have to survive for up to 13 nights between feeds, observations indicate that most procellariiform chicks are rarely without food for more than three or four days (Ricklefs *et al.* 1985; Hamer & Hill 1993; Bolton 1995; Hamer *et al.* 1997*b*). This has generally been interpreted as supporting the idea that fat stores act as a buffer against stochastic variation in food delivery to individual chicks, as suggested by Ricklefs & Schew (1994), rather than as insurance against occasional periods of poor feeding conditions (Lack 1968). To a certain extent, however, measured lipid reserves and fasting capability of fulmar chicks aged over 40 days are far greater than

would be anticipated on the basis of Ricklefs & Schew's model, even allowing for a degree of chronic overfeeding to reduce the probability of chance starvation. More importantly, this hypothesis predicts a relationship between size of energy reserves and variability in provisioning rate, yet there is no correspondence between lipid mass, which increases a great deal as chicks grow, and the coefficient of variation (CV) of either the proportion of chicks fed per day or the mean number of meals per day in chicks aged up to 50 days at Fair Isle (CVs of 30–48 and 51–66, respectively, depending on the age category; R. A. Phillips and K. C. Hamer, unpublished data). Taken together, these suggest that stochasticity in adult feeding rates do not provide the ultimate explanation for the accumulation of such large lipid stores in fulmars.

There was no evidence in this study that fat stored early in chick rearing subsidizes higher energy requirements later in development, because the mass of deposited lipid was much higher, rather than lower, in older compared with younger fulmar chicks. Similar results were obtained in other studies of pelagic species (Ricklefs *et al.* 1980; Montevecchi *et al.* 1984; Navarro 1992; Roby 1991; Obst & Nagy 1993). Nor did the accumulation pattern provide support for the 'energy-sink' hypothesis. Taylor & Konarzewski (1992) suggested that calcium might be limiting for the little auk (*Alle alle*), a planktivorous alcid. The diet of ancestral, high-latitude fulmar populations was probably also pelagic zooplankton, but at the majority of breeding sites, including Fair Isle, contemporary diets consist predominantly of discarded whitefish, juvenile Gadidae, sand-eel (*Ammodytidae*) or capelin (*Mallotus villosus*) (Phillips *et al.* 1999). It is difficult to see how calcium could be in short supply in a piscivorous diet, or why it would result in nestling obesity in fulmars when many inshore seabirds also eat fish but do not accumulate massive lipid stores. One possibility could be, as Taylor & Konarzewski (1992) suggest, that insoluble calcium soaps may form in the proventriculus of birds with high-lipid diets. In any event, what counts heavily against the 'energy-sink' hypothesis is that very large fat stores are maintained by fulmar chicks well beyond the time when addition of lean dry tissue, including virtually all feather formation, has ceased. The end of lean tissue growth is presumably indicative of a reduction in nutrient requirements, and if nutrient limitation was ultimately responsible for nestling obesity we would anticipate that chicks would begin to metabolize their lipid stores from an age of 45 days onwards to reduce wing loading and improve flight efficiency at fledging, which was not the case.

One other possibility is that fat storage functions primarily to enhance survival during the initial critical period away from the colony. Most studies of seabirds have shown that individual chicks in better condition during rearing or that weighed more at fledging have higher post-fledging survival (Perrins *et al.* 1973; Jarvis 1974; Sagar & Horning 1998; Phillips & Furness 1998) and that these are heritable traits (Brooke 1986; Phillips & Furness 1998). Fledglings clearly derive a substantial benefit from being able to use stored energy after departure from the nest site, when they must learn to forage independently and efficiently. Presumably, large reserves are particularly important for Procellariiformes that

fledge during unfavourable weather, which could include either stormy or particularly calm conditions. It is this last hypothesis that is best supported by the observed pattern of lipid accumulation in fulmars, in which fat stores increase throughout development and, most importantly, are maintained right through until fledging. Further research is necessary before it is possible to judge its applicability to other species in which nestlings have similarly evolved unusually high levels of obesity.

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