INTRASPECIFIC VARIATION IN EGG SIZE AND EGG COMPOSITION IN BIRDS: EFFECTS ON OFFSPRING FITNESS

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CONTENTS

I. INTRODUCTION

There is good evidence in many non-avian organisms for a positive relationship between egg or propagule size and the growth, survival or fecundity of offspring, e.g. plants (Howe & Richter, 1982; Stanton 1984), invertebrates (Capinera, 1979; Dixon 1985; but see Karlsson & Wiklund, 1984), vertebrates (Kaplan, 1980, 1992; Hutchings, 1991). Lack (1968) pointed out that the functional significance of egg-size variation (as distinct from clutch size) had been surprisingly neglected in avian studies, despite its obvious importance to avian reproductive strategies, a conclusion also reached more recently and almost 25 years later by Magrath (1992) and Arnold (1992). Nevertheless, many studies have concluded that good evidence also exists for a positive relationship between egg size and offspring growth and/or survival in birds. Clutton-Brock (1991), for example, stated that "in birds, positive relationships between egg size and chick survival are common", whilst Amundsen & Stokland (1990) concluded that a positive correlation between egg size and nestling growth or survival "has been found for most avian species studied". Mueller (1990) criticized many of the studies underlying these conclusions and claimed that there was no unequivocal evidence for a positive relationship between egg size and chick survival in birds (but see Bolton, 1991). One of his main criticisms was that earlier studies often failed to control for other characters which might be phenotypically correlated both with egg size and offspring fitness, e.g. female age or parental quality (Reid & Boersma, 1990; Bolton, 1991). In view of these contrasting opinions, the first aim of this paper is to review the evidence for a positive relationship between egg size and offspring fitness (growth and survival) in birds *at the intraspecific level*. In so doing I will not discuss clutch size, or intraclutch egg-size

Table 1. *Studies reporting a relationship between egg-size and chick growth and/or survival up to fledging.* o = *no significant relationship,* + = *positive relationship,* − = *no data. See text for details of* o/+ *studies.*

Species	Development[a]	Growth	Survival	Other factors[b]	Reference[c]
Eudyptes chrysolophus (macaroni penguin)	SA	o[d]	+[e]	—	1
Spheniscus magellanicus (Magellanic penguin)	SA	o	o	PQ	2
Phalacrocorax aristotelis (common shag)	A	o	—	PQ	3
Phalacrocorax atriceps (blue-eyed shag)	A	—	o	—	4
Puffinus puffinus (Manx shearwater)	SA	o	o	LD	5
Puffinus tenuirostris (short-tailed shearwater)	SA	—	o	PQ	6
Cygnus olor (mute swan)	P	+	—	OA	7
Cygnus olor (mute swan)	P	—	o	—	8
Anseranas semipalmata (magpie goose)	P	+[d]	—	—	9
Branta canadensis (Canada goose)	P	—	o	—	10
Branta canadensis (Canada goose)	P	—	o	—	11
Chen caerulescens (lesser snow goose)	P	o[d]	—	—	12
Chen caerulescens (lesser snow goose)	P	—	o[e]	PA/YR	13
Lagopus lagopus (red grouse)	P	—	+[d]	—	14
Numenius phaeopus (whimbrel)	P	—	o/+	—	15
Vanellus vanellus (northern lapwing)	P	—	o	—	16
Charadrius hiaticula (ringed plover)	P	—	o[f]	—	17
Catharacta skua (great skua)	SP	+	—	—	18
Catharacta skua (great skua)	SP	+	o	—	19
Larus argentatus (herring gull)	SP	—	o/+[ef]	—	20
Larus argentatus (herring gull)	SP	—	+	—	21
Larus fuscus (lesser black-backed gull)	SP	o[e]	+[e]	PQ	22
Larus occidentalis (western gull)	SP	—	o	PQ/YR	23
Rissa tridactyla (black-legged kittiwake)	SP	—	+	PA	24
Fratercula arctica (Atlantic puffin)	SA	—	o	—	25
Sterna caspia (Caspian tern)	SP	—	o/+	—	26

Table 1. *(cont.)*

Species	Development[a]	Growth	Survival	Other factors[b]	Reference[c]
Sterna hirundo (common tern)	SP	—	o/+	PQ	27
Sterna dougallii (roseate tern)	SP	+	o	PQ	28
Alca torda (razorbill)	SA	o	+[f]	—	29
Uria lomvia (thick-billed murre)	SA	+[f]	—	—	30
Columbus palumbus (wood pigeon)	A	—	o[f]	—	31
Apus apus (common swift)	A	o	+[ef]	—	32
Parus major (great tit)	A	+	o/+	—	33
Parus major (great tit)	A	—	o/+	—	34
Turdus merula (European blackbird)	A	+[f]	o	PQ	35
Ficedula hypoleuca (pied flycatcher)	A	—	o	—	36
Ficedula hypoleuca (pied flycatcher)	A	+	—	—	37
Cassidix major (boat-tailed grackle)	A	—	o	—	38
X. xanthocephalus (yellow-headed blackbird)	A	o	o	—	39
Sturnus vulgaris (common starling)	A	o	o	—	40
Melospiza melodia (song sparrow)	A	o	o	—	41

[a] SA = semi-altricial; P = precocial; SP = semi-precocial; A = altricial.
[b] PQ = parental quality; LD = laying date; OA = offspring age; PA = parental age; YR = year.
[c] 1, Williams (1990); 2, Reid & Boersma (1990); 3, Amundsen & Stokland (1990); 4, Shaw (1985); 5, Brooke (1978); 6, Meathrel *et al.* (1993); 7, Scott & Birkhead (1983); 8, Birkhead *et al.* (1983); 9, Whitehead *et al.* (1990); 10, LeBlanc (1987); 11, Lessells (1986); 12, Ankney (1980); 13, T. D. Williams, unpub. data; 14, Moss *et al.* (1981); 15, Grant (1991); 16, Galbraith (1988); 17, Pienkowski (1984); 18, Furness (1983); 19, Williams (1980); 20, Davis (1975); 21, Parsons (1970); 22, Bolton (1991); 23, Sydeman & Emslie (1992); 24, Thomas (1983); 25, Harris (1984); 26, Quinn & Morris (1986); 27, Nisbet (1973); 28, Nisbet (1978); 29, Lloyd (1979); 30, Birkhead & Nettleship (1982); 31, Murton *et al.* (1974); 32, O'Conner (1979); 33, Schifferli (1973); 34, Ojanen (1983); 35, Magrath (1992); 36, Ojanen (1983); 37, Jarvinen and Ylimauna (1984); 38, Bancroft (1984); 39, Richter (1984); 40, Greig-Smith *et al.* (1988); 41, Arcese & Smith (1988).
[d] Experimental studies.
[e] Species with marked intraclutch egg-size variation, where sequence is known to affect growth or survival.
[f] Hatching mass used instead of egg mass.

variation, explicitly (for which see e.g. Slagsvold *et al.*, 1984; Godfray, Partridge & Harvey, 1991), except where these influence the relationship between egg size and offspring fitness.

Next, given that some form of positive relationship between egg size and offspring fitness does indeed exist, I consider how large egg size benefits chicks. Larger eggs may

be advantageous for two reasons: (1) they may give rise to chicks which are structurally larger or which hatch at a more advanced stage of development, or (2) they may produce chicks which hatch with larger nutrient reserves, particularly reserves of lipid-rich yolk (Lack, 1968; O'Connor, 1979). The relative importance of these two different (though not necessarily mutually exclusive) effects of large egg size to offspring fitness may vary between species in relation to species-specific developmental or ecological patterns (Ricklefs, Hahn & Montevecchi, 1978). For example, Birkhead & Nettleship (1984) suggested that in species with intense sibling competition it would be advantageous for chicks to be structurally larger at hatching whereas, in species which lay only one egg, there would be little selection for increased structural size of the hatchling. In the second part of this paper, therefore, I consider the relationship between egg size and chick mass and size at hatching in order to determine, (a) whether large eggs produce larger or heavier chicks at hatching, and (b) if this varies systematically between species.

Thirdly, if there is species-specific variation in the mechanism by which egg size affects offspring fitness then this must reflect systematic relationships between the size and composition of eggs (Parsons, 1970; Ricklefs et al., 1978). This could give rise, in turn, to species-specific 'strategies' which might be adopted by laying females with regard to differential investment during egg formation. Females which are able to increase their total investment in egg production might make facultative adjustments to egg composition, increasing egg quality (Hepp et al., 1987; Arnold, 1992), and thus maximizing the benefits to their offspring of increased parental investment. For example, in species where chick structural size is important, females ought to invest more in the protein content of eggs (principally in albumen in altricial species) with increasing egg size (Boersma, 1982). Conversely, if reserves at hatching are important then females ought to invest more in the lipid (yolk) component of larger-sized eggs. Numerous studies have questioned whether egg size or egg quality determines offspring fitness, i.e. whether bigger eggs are better, but although there is a considerable literature on the relationship between egg size, egg composition and chick development at the interspecific level (e.g. Carey, Rahn & Parisi, 1980; Sotherland & Rahn, 1987), there has been little consideration of this relationship within species. In an attempt to address this question, the third part of this paper investigates whether there are general, or species-specific, relationships between egg size and egg composition (or quality) that relate to ecological or developmental aspects of offspring growth and/or survival. If such relationships exist then this would indicate which elements of the female reproductive system are likely to prove most fruitful for future research into the proximate, physiological mechanisms underlying egg production and egg-size variation in wild birds.

II. EFFECTS OF EGG SIZE ON OFFSPRING GROWTH AND SURVIVAL

(1) Chick growth and survival to fledging

Data were obtained from the literature for 40 studies (34 species, Table 1). In six studies no details of the analyses were presented, the author(s) simply stating that chick growth and/or survival was independent of egg size (Brooke, 1978; Birkhead, Bacon & Walter, 1983; Harris, 1984; Pienkowski, 1984; Lessells, 1986; Arcese & Smith, 1988). In a further five studies sample sizes were relatively small ($n \leqslant 20$ chicks), reducing the likelihood of these studies detecting a significant effect of egg size (Nisbet, 1978; Williams, 1980; Scott & Birkhead, 1983; Whitehead, Freel & Tschirner, 1990; Grant,

1991). Where the unit of egg size was reported ($n = 35$ studies), fresh egg mass was used in 18 cases and an index of egg volume (usually length × breadth²) in 17 cases. As egg volume and fresh egg mass are typically highly correlated ($r \geqslant$ 0·95, e.g. Reid & Boersma, 1990; Meathrel *et al.*, 1993) these measures were considered to be equally representative of egg size, and the term 'egg size' is used throughout this paper. Information on development patterns and fledging periods were obtained from the cited studies or from standard reference texts.

Of 20 studies, all on different species, nine (45 %) have reported a significant positive relationship between chick growth or chick size at fledging and egg size (seven studies) or hatching mass (two studies, Table 1); the remaining 11 studies found no significant effect of egg size on chick growth. Seven of these 20 studies controlled for one or more variables potentially correlated both with egg size and offspring growth: five for parental quality, one for laying date and one for offspring age (Table 1). Of these, only three found a residual effect of egg size on chick growth, two controlling for parental quality (roseate tern, Nisbet, 1978; European blackbird, Magrath, 1992) and one for offspring age (mute swan, Scott & Birkhead, 1983).

The relationship between chick growth and egg size seems more clear in precocial species, a significant effect of egg size being reported in 5 of 7 studies (71 %) compared to 4 of 13 (31 %) studies of altricial species. As the effect of egg size may be related to duration of the rearing period (see below), I compared the duration of the fledging periods between species where egg size was reported to have a positive effect on growth (44·2 ± 12·2 days) or no effect (41·7 ± 6·6 days). This result suggests that the effect of egg size on chick growth is independent of the length of the rearing period.

Thirty-four studies (on 31 species) have reported on the relationship between chick survival up to fledging and egg size (Table 1). In 13 of these (42 %, 11 species) chick survival was reported to be positively related to egg size (eight studies) or hatching mass (five studies). Ten of these 34 studies controlled for one or more correlated variables (nine for parental quality or age, one for laying date and two for annual variation, Table 1) and of these, only three found a residual effect of egg size on offspring survival, two controlling for parental quality (Nisbet, 1973, Bolton, 1991) and one for parental age (Thomas, 1983). Four of the 13 studies involved species which show marked intraclutch egg-size variation, hatching asynchrony or brood reduction. In the common swift, chicks from small eggs have a lower probability of survival because small eggs are most often last-laid C-eggs (O'Connor, 1978). Chicks from these eggs hatch significantly later and suffer higher mortality through brood reduction than chicks from larger, first-laid (A) and second-laid (B) eggs. Similarly, in the herring gull (Davis, 1975) and the lesser black-backed gull (Bolton, 1991) there is a positive relationship between egg size and chick survival only if all eggs are included in the analysis (i.e. pooling over laying sequences). In these (and other) gull species, third-laid C-eggs are again significantly smaller, hatch later and produce chicks which suffer disproportionate mortality through brood reduction compared to A- or B-eggs (Parsons, 1970; Bolton, 1991; Sydeman & Emslie, 1992). In these species, therefore, the effect of egg size on chick survival is confounded by the effect of laying (and hatching) sequence (the *Eudyptes* penguins represent an extreme example of this, see Williams, 1990).

Five other studies have reported 'inconsistent' results with respect to the relationship between chick survival and egg size (o/+ in Table 1). In the Caspian tern (Quinn & Morris, 1986) and common tern (Nisbet, 1973) chick survival correlated with egg size

only for A-eggs and C-eggs respectively, but not for eggs of other laying sequences. Chick survival was related to egg size for early broods in the great tit, but not for late broods (Schifferli, 1973), and in only two of five years (Ojanen, 1983). Finally, Grant (1991) showed that in the whimbrel, brood survival was positively correlated with mean egg volume per clutch, but chick survival to fledging within broods was not related to hatching mass. Of the four studies which show a consistent, positive relationship between egg size and offspring growth (not associated with intraclutch egg-size variation or hatching asynchrony), only one controlled for any correlated variable (parental age, Thomas 1983).

Chick survival was related to egg size in 8 of 17 studies (47 %) of precocial species compared to 5 of 17 studies (29 %) of altricial species. Mean duration of the fledging period was slightly shorter in species where a positive relationship between survival and egg size was reported ($33 \cdot 6 \pm 3 \cdot 8$ days), compared to no effect ($43 \cdot 0 \pm 6 \cdot 4$ days). In species where egg size was positively related to chick survival, the fledging period varied from 15 to 45 days in precocial species and from 18 to 60 days in altricial species.

To summarize these findings, although over 40 studies have described or commented on the relationship between egg size and offspring fitness, for 34 different avian species, less than half of these have demonstrated that chick growth or survival is dependent on the size of the egg from which the chick hatches. Furthermore, many studies suffer from weaknesses that mean they only provide, at best, equivocal support for the hypothesis of a positive relationship between egg size and offspring fitness. As Mueller (1990) pointed out, the confounding effect of intraclutch egg-size variation must either be controlled for, or effects of egg size must be compared among eggs of the same laying sequence. Intraclutch egg-size variation is often associated with hatching asynchrony and lower success of small, last-laid eggs may be due to differential mortality through brood reduction, rather than due to their small size *per se*. While this criticism can be levelled at several of the more commonly referenced studies (e.g. O'Connor, 1978; Davis, 1975; Bolton, 1991), this problem was often fully realized and discussed by these authors. Nevertheless, two studies have shown that chick survival is related to egg size independent of laying sequence effects (Parsons, 1970; Lundberg & Vaisanen, 1979). In contrast, in the lesser snow goose, variation in chick survival has been shown to be related to the effects of laying sequence, rather than to egg size *per se*, despite marked intraclutch egg-size variation (Williams, Lank & Cooke, 1993).

A more widespread criticism (and one which has been long realized, Nisbet, 1978; Birkhead & Nettleship, 1982) is the failure of many studies to consider the possible confounding effects of characters which may be correlated both with egg production and offspring fitness. Recently, several studies have investigated the importance of egg size on chick growth or survival, controlling for parental quality (e.g. Amundsen & Stokland, 1990; Reid & Boersma, 1990; Bolton, 1991; see also Nisbet, 1978). These have typically involved exchanging eggs of different sizes between small-egg (low-quality) and large-egg (high quality) parents. So far, only two studies have demonstrated a residual effect of egg size on offspring survival independent of sequence-specific mortality and controlling for parental quality (Nisbet, 1978; Magrath, 1992). Even here age effects were not considered (e.g. Croxall, Rothery & Crisp, 1992), nor were any possible effects of parental performance in early incubation (i.e. before exchange of eggs). Similarly, only three studies have reported a residual effect of egg size on chick survival controlling for parental quality (Nisbet, 1973; Bolton, 1991) or age (Thomas,

1983; but see below). A related criticism of some studies is the use of mean egg size per clutch in relation to mean chick size or whole-brood survival (Schifferli, 1973; Grieg-Smith *et al.*, 1988; Galbraith, 1988). Mean egg size is more likely to be more highly correlated with female quality than is individual egg size, increasing the likelihood that variation in parental quality will confound the interpretation of results. For example, Thomas (1983) found a positive relationship between mean egg volume and fledging success over all clutch sizes, but egg size did not affect probability of survival in single-egg clutches. If egg size, rather than parental quality, determines chick survival at the level of the individual chick it is individual egg size that is important not mean egg size. A within-clutch comparison is the most powerful way of testing for an effect of egg size on offspring fitness independent of female quality, but there have so far been few such analyses. As an example, mean egg volume in the whimbrel was positively correlated with brood survival, but chick survival was not related to individual hatching masses within broods (Grant, 1991). Similarly, in the lesser snow goose there was no difference in the mass of successful and unsuccessful eggs in a within-clutch analysis, either to hatching or fledging (T. D. Williams, unpublished data).

So far, all but one of the studies demonstrating an effect of egg size on offspring fitness in birds (controlling for parental quality) have been carried out on semi-altricial or semi-precocial seabirds and there is a need for additional studies on other species, in particular for true altricial species (e.g. passerines) or precocial species (e.g. waterfowl). Parental 'quality' may reflect both intrinsic factors, e.g. body size (De Steven, 1978), body condition (Murphy, 1986) or physiology, and extrinsic factors such as territory quality (Arnold, 1992). Further data are therefore also needed on other potential measures of female (or parent) quality in relation to egg size, preferably involving experimental studies (e.g. Hill, 1988; Bolton, Houston & Monaghan, 1992).

(2) *Chick growth and survival early in chick-rearing*

Twelve studies have reported on the relationship between egg size and chick growth and/or survival during the early stages of the chick-rearing period, prior to fledging (Table 2). Of these 8 of 10 (80%) and 4 of 5 (80%) studies, respectively, reported a positive relationship between egg size and offspring growth and survival. Three studies which showed a positive early effect of egg size on chick growth (Lloyd, 1979; Amundsen & Stokland, 1990; Reid & Boersma, 1991) failed to detect a significant effect of egg size at fledging (Table 2). Similarly, one of two studies found an effect of egg size on early chick survival but not when considering overall survival to fledging (Galbraith, 1988).

There are, therefore, more consistent data, though so far from fewer studies, which indicate the importance of egg size to chick growth or survival early in the chick-rearing period. Slower growth immediately after hatch, due to hatching from a smaller egg, may be compensated for later in the rearing period (Ojanen, 1983). However, early chick mortality can not be compensated for (even though the effect can be swamped by subsequent egg-size independent mortality, making its detection difficult or impossible). Future studies should therefore assess chick survival (and growth) at an early or intermediate stage between hatch and fledging (Jarvinen & Ylimaunu, 1984), in addition to controlling for correlated characters. Indeed it is conceivable that the effect of egg size on offspring fitness has been misinterpreted rather than over-estimated: egg size could be fundamentally important in determining the high levels of chick mortality

Table 2. *Studies reporting a relationship between egg-size and offspring growth and/or survival early in chick-rearing (relationship at fledging from the same study is given in brackets; see Table 1)*

Species	Development pattern[a]	Number of days	Growth	Survival	Reference[b]
Spheniscus magellanicus (Magellanic penguin)	SA	10	+ (o)	o (o)	2
Phalacrocorax aristotelis (common shag)	A	7	+ (o)	—	3
Branta canadensis (Canada goose)	P	25	o[cd]	—	42
Chen caerulescens (lesser snow goose)	P	4	—	+[c]	12
Lophodytes cucullatus (hooded merganser)	P	1–2	+	—	43
Numenius phaeopus (whimbrel)	P	7	+	—	15
Vanellus vanellus (northern lapwing)	P	10	—	+ (o)	16
Larus argentatus (herring gull)	SP	10–15	+	+ (o/+)	20
Larus ridibundus (black-headed gull)	SP	10	+	—	44
Sterna hirundo (common tern)	SP	3	+	—	27
Sterna hirundo (common tern)	SP	5	o	+	28
Alca torda (razorbill)	SA	5	+ (o)	—	29

[a] As for Table 1.
[b] 1–41, as for Table 1; 42, Thomas & Peach Brown (1988); 43, Kennemar *et al.* (1988); 44, Lundberg & Vaisenen (1979).
[c] Hatching mass used instead of egg mass.
[d] Experimental studies.

that occur soon after hatch in many species (Lack, 1968; Parsons, 1970; Howe, 1978; Clark & Wilson, 1981; Galbraith, 1988; Rhymer, 1988).

(3) Do egg-size effects vary between species?

Given at least partial support for a positive relationship between offspring fitness and increasing egg size in birds are any systematic differences evident between or within species? Magrath (1992) suggested that egg mass might have a greater effect on survival in precocial than altricial species, because there is relatively little investment in post-hatching feeding in precocial species and investment in egg production is proportionately greater. In contrast, in altricial species the cost of investment in egg production will be relatively minor compared to post-hatch investment. There is some support for this hypothesis in the literature: a positive relationship between egg size and survival has so far been reported for a greater proportion of studies of precocial species (47 %) compared to altricial species (29 %) and there is also some evidence that chick growth is more often related to egg size in precocial species (Section II). However, some of the most unequivocal evidence for increased survival of chicks from larger eggs

comes from studies of Laridae where, although chicks are nidifugous at hatching, they are dependent on parental feeding until fledging (Parsons, 1970; Thomas, 1983; Bolton, 1991). Even so, Amundsen & Stokland's study on the common shag and Magrath's (1992) study of the European blackbird remain the only ones so far that have attempted to control for the possible confounding effects of parental quality in true altricial species, so any conclusions are obviously premature. It might similarly be predicted that egg size would have a greater effect on chick growth and survival in species with shorter chick-rearing or fledging periods. First, as discussed above, the longer the rearing period the more time small chicks will have to undergo compensatory growth (Ojanen, 1983), provided the small chick disadvantage is not maintained by a dominance hierarchy amongst siblings in a brood. Secondly, in species with long fledging periods there is a greater chance that egg-size independent mortality effects (e.g. predation) will swamp the early effects of egg size. Despite this, there was no apparent difference in the duration of fledging periods for species where egg size was related to chick growth compared to those in which there was no effect. However, fledging periods of species where chick survival was related to egg size were somewhat shorter than in other species. More detailed studies of the timing of chick mortality in relation to egg-size and egg-independent factors are required in order to determine whether this is a biological or 'statistical' effect. It is worth noting however, that apparent effects of egg size on chick survival persisted for up to 40–45 days post-hatching in semi-precocial species (Parsons, 1970; Bolton, 1991) and 45 days post-hatch in one true altricial species (O'Connor, 1979).

If egg size influences offspring fitness through growth, resistance to starvation or chilling, then egg size effects should be more apparent in some years than others, e.g. in years of low food availability or adverse weather conditions. Indeed, Ankney & Bisset (1973) suggested that this sort of fluctuating selection for large egg size may be important in maintaining variation in egg size within populations. Unfortunately, very few studies have investigated the relationship between egg size and offspring fitness in more than one year, even though annual effects on egg size, independent of parental age and experience have been demonstrated in several species (Davis, 1975; Furness, 1983; Croxall *et al.*, 1992). Ojanen (1983) reported a positive relationship between egg size and chick survival in two of five years in the great tit, although he did not discuss differences in environmental conditions or food availability between years. Davis (1975) found a strong relationship between egg size and chick survival in 1 year of 2 years but suggested this was due to annual differences in age structure of the breeding population. In a long-term study of the fitness consequences of egg size in the lesser snow goose, eggs giving rise to fledged chicks were significantly larger than unsuccessful eggs in only one of 12 years, and this was unrelated to seasonal variation in weather conditions (T. D. Williams, unpublished data).

(4) *Other advantages and disadvantages of large egg size*

In addition to the direct provision of greater amounts of nutrients and energy for growth or resistance to starvation, larger eggs could enhance offspring fitness in a number of other ways, although these have generally received less attention. Rhymer (1988) showed that mallard ducklings which hatched from larger eggs were better able to maintain homeothermy at low temperatures due to their having larger body mass and

Table 3. *Relationship between egg-size and the wet weight and size of offspring at hatching*

Species	Development[a]	Variation explained by egg-size (%)				
		Mass	Wing	Tarsus/foot	Culmen ±head	Ref[b]
Spheniscus magellanicus (Magellanic penguin)	SA	30, 28[cd]	5, 5[ce]	18, 14[ce]	4, n.s.[ce]	2
Spheniscus demersus (jackass penguin)	SA	94	—	—	—	45
Phalacrocorax aristotelis (common shag)	A	77	—	—	—	46
Branta canadensis (Canada goose)	P	40	—	—	—	42
Chen caerulescens (lesser snow goose)	P	94	—	26	n.s.	12
Chen caerulescens (lesser snow goose)	P	76	—	—	—	47
Anas platyrhynchos (mallard)	P	76	—	—	—	48
Anas platyrhynchos (mallard)	P	66	—	—	—	49
Anas acuta (pintail)	P	89	—	—	—	50
Aix sponsa (wood duck)	P	49	—	—	—	51
Somateria mollissima (common eider)	P	86	—	—	—	52
Lagopus scoticus (red grouse)	P	53, 70[f]	—	—	—	14
Coturnix japonicus (Japanese quail)	P	69	n.s.	+	—	53
Fulica americana (American coot)	P	67	+	n.s.	n.s.	54
Fulica americana (American coot)	P	70	—	—	—	55
Fulica atrica (European coot)	P	90	—	—	—	56
Vanellus vanellus (northern lapwing)	P	50	—	n.s.	23	16
Pluvialis dominica (lesser golden plover)	P	36	—	—	—	57
Charadrius semipalmatus (semipalmated plover)	P	60	—	—	—	57
Eudromias morinellus (Eurasian dotteral)	P	42	—	25	n.s.	58
Numenius phaeopus (whimbrel)	P	74–79[g]	—	14–38	18–38	15
Numenius phaeopus (whimbrel)	P	62	—	—	—	57
Limosa haemastica (Hudsonian godwit)	P	75	—	—	—	57
Tringa flavipes (lesser yellowlegs)	P	n.s.	—	—	—	57

Table 3. (*cont.*)

Species	Development[a]	Variation explained by egg-size (%)				Ref[b]
		Mass	Wing	Tarsus/ foot	Culmen ±head	
Caladris minutilla (least sandpiper)	P	n.s.	—	—	—	57
Calidris alpina (dunlin)	P	21	—	—	—	57
Micropalama himantopus (stilt sandpiper)	P	59	—	—	—	57
Lobipes lobatus (northern phalarope)	P	n.s.	—	—	—	57
Catharacta skua (great skua)	SP	61–72[g]	—	—	—	18
Larus argentatus (herring gull)	SP	83	—	—	—	21
Larus fuscus (lesser black-backed gull)	SP	69	—	39	—	22
Larus atricilla (laughing gull)	SP	72	n.s.	n.s.	—	53
Larus ridibundus (black-headed gull)	SP	52, 65[h]	—	—	—	44
Sterna caspia (Caspian tern)	SP	—	—	—	16, n.s.	26
Uria lomvia (thick-billed murre)	SA	16[d]	n.s.[e]	—	—	30
Apus apus (common swift)	A	n.s.[d]	12	—	—	32
Corvus cornix (hooded crow)	A	87	63	n.s.	62	59
Parus major (great tit)	A	53	—	—	—	33
Ficedula hypoleuca (pied flycatcher)	A	+[d]	n.s.[e]	—	—	37
Turdus merula (European blackbird)	A	94	80[j]	—	—	35
Molothrus ater (brown-headed cowbird)	A	92	—	—	—	60
X. xanthocephalus (yellow-headed blackbird)	A	+	—	+	+	39

[a] As for Table 1.

[b] 1–41, as for Table 1; 42–44 as for Table 2; 45, Cooper & Williams (1984); 46, Stokland & Amundsen (1988); 47, Newell (1988); 48, Rhymer (1988); 49, Batt & Prince (1979); 50, Duncan (1987); 51, Hepp *et al.* (1987); 52, G. J. Robertson personal communication; 53, Ricklefs *et al.* (1978); 54, Hill (1988); 55, Alisauskas (1986); 56, Horsfall (1984); 57, Ricklefs (1984*a*); 58, Byrkjedal & Kalas (1985); 59, Rofstad & Sandvik (1989); 60, Nolan & Thompson (1978).

[c] For first-laid (A) and second-laid (B) eggs respectively.

[d] Controlling for body size.

[e] Controlling for body mass.

[f] For wild and captive birds respectively.

[g] In different years.

[h] For first-laid (A) and last-laid (C) eggs respectively.

[j] PC1 for tibia and gape.

n.s., not significant.

lower mass-specific cooling rates. Similarly, in species where eggs are temporarily left unattended in the nest for periods during incubation large eggs should in theory take longer to cool down, due to their smaller surface area:volume ratio and, therefore, may be better able to withstand chilling (e.g. Procellariformes, Lack, 1968; aerial insectivores, O'Connor, 1979). Several studies have also shown that large eggs may be less vulnerable to predation. In the glaucous-winged gull, *L. glaucescens*, small eggs are taken more often by avian predators, possibly because they are easier to handle (Verbeek, 1988). Similarly, in an experimental study of egg predation behaviour, Montevecchi (1976) concluded that in natural situations predation pressure would be greater on small eggs than on large eggs.

In contrast to the positive effects of large egg size considered so far, large egg size may also be disadvantageous, e.g. if larger eggs take longer to produce (although there is no evidence that this is the case within species; large eggs may be produced by better quality females which can maintain higher rates of yolk, albumen or shell production). In thick-billed murres, Birkhead & Nettleship (1982) showed that 'growth rates' of eggs average 4 g/day compared to 9 g/day in chicks. In this species it is more advantageous for a female to lay early and invest more time in chick rearing than to delay egg-laying in order to produce a larger egg. Birkhead & Nettleship (1982) therefore suggested that small egg size might be adaptive in allowing birds to lay early. Related to this, numerous studies have suggested that egg size may be proximately constrained either by the extent of body reserves available to the laying female (e.g. Slagsvold & Lifjeld, 1989; Nilson & Svensson, 1993) or by rate-limiting steps during the different stages of egg production (Shaw, 1990; Williams, 1990; Bolton, 1991). If resources for egg-production are finite then, theoretically, laying larger eggs should also result in a smaller clutch size (Smith & Fretwell, 1974). Evidence for such a trade-off between egg size and clutch size within-species is so far lacking in birds however (Arcese & Smith, 1988; Rohwer, 1988; Lessells, Cooke & Rockwell, 1989; Magrath, 1992). Finally, Lack (1968) proposed that laying larger eggs would increase the total duration of the laying period and, thus, the length of time that laying females and eggs were at risk from predation (see also Clark & Wilson, 1981).

III. EGG SIZE AND OFFSPRING MASS AND SIZE AT HATCHING

In order to address the question of whether large eggs give rise to larger or heavier chicks at hatching data were obtained from the literature for 33 studies on 38 species (Table 3). Hatching mass was significantly correlated with egg size for all but three species (and in these species sample sizes were very small, Ricklefs, 1984 a). Similar results have previously been reported for six domesticated species (Shanawany, 1987). On average, egg size explained $65.9 \pm 20.8 \%$ (range 16–94%, $n = 35$) of the variation in hatching mass, and this value was very similar in altricial and precocial species (67.8%, range 16–94%, $n = 8$ vs. 65.3%, range 21–94%, $n = 27$). Within species, values appear to be broadly similar in different studies (e.g. compare Alisauskas, 1986 and Hill, 1988; Batt & Prince, 1979 and Rhymer, 1988) and in different years in the same study (Furness, 1983; Grant, 1991), although data on this are very limited. In the Magellanic penguin, which lays similar-sized eggs within a clutch, egg size explained a similar amount of the variation in hatching mass in first- and second-laid eggs (Reid & Boersma, 1990). In contrast, in the black-headed gull, the correlation between egg

size and hatching mass increased with laying sequence, being highest for the last-laid C-egg (Lundberg & Vaisanen, 1979).

Overall, chick size at hatching was less highly correlated with egg size than was hatching mass (Table 3); combining all size data, egg size explained $30.4 \pm 22.9\%$ (4–80%, $n = 18$) of the variation in chick size (t-test on arcsine transformed data for comparison with hatching mass, $t = 4.89$, $P < 0.001$). This was also true within-species: in all cases egg size was more highly correlated with hatching mass than with hatching size (e.g. Rofstad & Sandvik, 1989; Reid & Boersma, 1990; Bolton, 1991; Grant, 1991). There were insufficient data to determine whether different body structures were more or less highly correlated with egg size, although there is clearly considerable variation in this relationship, e.g. wing length 5–63%, tarsus length 14–39%.

The significantly higher correlation obtained between egg size and hatching mass, compared with other measures of hatchling size, suggests that large eggs give rise to heavier chicks (i.e. chicks with more nutrient reserves) rather than structurally larger chicks (cf. Grant, 1991). Four studies controlled for the effect of body size in the analysis of egg size:hatching mass and in three of these hatching mass remained significantly correlated with egg size (Birkhead & Nettleship, 1982; Jarvinen & Ylimaunu, 1984; Reid & Boersma, 1990), although the value of the partial correlation coefficient for mass decreased. That is, for a given body size, large eggs produced heavier chicks. Conversely, controlling for hatching mass, in two species there was no residual correlation between egg size and hatching size: for a given hatching mass large eggs did not give rise to structurally larger chicks (Birkhead & Nettleship, 1982; Jarvinen & Ylimaunu, 1984). In the swift, O'Connor (1979) found no correlation between egg size and hatching mass controlling for body size (wing length) and concluded that large eggs yield large chicks rather than heavy chicks. However, in this study egg size was not significantly correlated with wing length when body mass was controlled for. In the Magellanic penguin, hatching size was still correlated with egg size controlling for hatching mass, but egg size explained less of the variation in size compared to mass (4–18% vs. 30%, Table 3). Reid & Boersma (1990) similarly concluded that in this species the most significant effect of egg size was on the reserves available to the chick at hatching, rather than on the chick's structural size.

To summarize, most studies to date support the hypothesis that chicks from larger eggs are heavier at hatching rather than structurally larger, i.e. that they hatch with more nutrient (yolk) reserves. Although heavier chicks may also be larger, only a few studies have controlled for body size effects. Those studies that have tended to find a strong residual effect of egg size on chick mass but a weaker or non-significant effect of egg size on chick size when controlling for body mass. The importance of egg size to the nutrient reserves of the chick at hatching has been demonstrated directly in several species. In the altricial hooded crow, weight of the yolk sac at hatching was positively related to egg volume and chicks hatching from larger eggs tended to have proportionately larger yolk sac masses (Rofstad & Sandvik, 1987). Similarly, in semi-altricial alcids (Birkhead & Nettleship, 1984) and in the precocial Canada goose (Thomas & Peach Brown, 1988), weight of the yolk sac retained at hatch increases with increasing egg size (see also Parsons, 1970). It is important to note however, that there have so far been no studies of species where siblicide is common (e.g. large raptors, gannets, boobies, herons, egrets) or of parasitic species (e.g. cuckoos, cowbirds) where

Table 4. *Allometric relationships between egg components and fresh egg mass. Values are the slopes (b) of log–log regressions (following Ricklefs et al. 1978), except for those in parentheses which are for linear regressions*

Species	Developmental pattern[a]	Albumen		Yolk					Ref[b]
		Wet	Dry	Wet	Dry	Water	Lipid	Protein	
Podilymbus podiceps (pied-billed grebe)	SP	1·24*	0·93	0·68	0·45*	1·19*	0·46*	0·73	61
Podiceps auritus (horned grebe)	SP	1·21	1·55	0·43	0·43	1·01	0·41	1·04	61
Diomedea immutabilis (Laysan albatross)	SA	(>1)	—	(<1)	—	—	—	—	62
Puffinus griseus (sooty shearwater)	SA	(>1)	—	(<1)	—	—	—	—	62
Sula bassanus (northern gannet)	SA	(1·36)	—	—	—	—	—	—	63
Pelecanus onocrotalus (white pelican)	SA	1·17	—	0·53*	—	—	0·55*	—	64
Phalacrocorax atriceps (blue-eyed shag)	A	(>1)	—	(<1)	—	—	—	—	4
Cygnus olor (mute swan)	P	0·85*	—	1·13*	—	—	1·21*	—	65
Chen caerulescens (lesser snow goose)	P	—	1·17	—	1·08	—	—	—	12
Branta leucopsis (barnacle goose)	P	1·00	—	1·03	—	—	—	—	66
Aix sponsa (wood duck)	P	0·94	0·78*	1·10	1·11	1·10	—	—	51
Anas platyrhynchos (mallard)	P	0·59*	—	1·30*	—	—	—	—	67
Anas discors (blue-winged teal)	P	0·95	0·70*	1·07	1·15*	0·97	1·22*	—	68
Coturnix japonicus (Japanese quail)	P	(1·03)	—	1·14	—	—	—	—	53
Fulica atra (European coot)	P	(1)	—	(1)	—	—	—	—	56
Fulica americana (American coot)	P	0·82*	—	1·43*	1·28*	0·81*	1·31*	—	55
Fulica americana (American coot)	P	(>1)	—	(<1)	—	—	—	—	54

Species									Ref[b]
Vanellus vanellus (northern lapwing)	P	1·24*	1·08	0·62*	1·17	1·27*	0·47*	—	16
Larus atricilla (laughing gull)	SP	(1)	—	0·80*	—	(1)	(1)	—	53
Larus delawarensis (ring-billed gull)	SP	1·28*	1·16*	0·66*	0·76*	1·10	—	—	69
Larus argentatus (herring gull)	SP	1·18	0·99	0·63	0·51	1·20	0·520	0·85	70
Sterna hirundo (common tern)	SP	(>1)	—	(<1)	—	—	(<1)	—	27
Uria aalge (common guillemot)	SA	1·12	—	0·80	—	—	—	—	71
Alca torda (razorbill)	SA	0·96	—	1·05	—	—	—	—	71
Fratercula arctica (Atlantic puffin)	SA	1·29*	—	0·51*	—	—	—	—	71
Ficedula hypoleuca (pied flycatcher)	A	(>1)	—	(<1)	—	—	(<1)	—	36
Tyrannus tyrannus (Eastern kingbird)	A	—	1·07	—	0·72*	—	0·94	0·95	72
Pica pica (magpie)	A	1·62*	1·59*	0·57*	—	1·10*	0·68*	1·26*	73
Parus major (great tit)	A	(1)	—	(1)	—	—	(1)	—	36
Sturnus vulgaris (common starling)	A	1·12	1·20	0·55	1·04	—	0·51	0·99	74
Agelaius phoeniceus (red-winged blackbird)	A	1·02	0·60	1·08	0·96	1·05	0·91	—	75
X. xanthocephalus (yellow-headed blackbird)	A	1·50*	1·24	0·82	0·79	1·03*	—	1·07	39
Quiscalus major (boat-tailed grackle)	A	1·78*	—	—	—	—	—	—	76
Molothrus ater (brown-headed cowbird)	A	0·52*	0·62*	1·11*	1·12	1·05*	0·62	—	77

[a] As for Table 1.

[b] 1–60 as for Tables 1–3; 61, Arnold (1989); 62, Warham (1983); 63, Ricklefs and Montevecchi (1979); 64, Jones (1979); 65, Birkhead (1984); 66, Owen and West (1988); 67, Birkhead (1985); 68, Rohwer (1986); 69, Meathrel and Ryder (1987); 70, Meathrel *et al.* (1987); 71, Birkhead and Nettleship (1984); 72, Murphy (1986); 73, Clarkson (1984); 74, Ricklefs (1984b); 75, Muma and Ankney (1987); 76, Bancroft (1985); 77, Ankney and Johnson (1985).

* Slope significantly different from 1.

chicks evict host young from the nest after hatching. It is likely that it is in these species that selection for large structural size of chicks at hatching will be greatest.

IV. QUALITY AND COMPOSITION OF EGGS IN RELATION TO EGG SIZE AND OFFSPRING FITNESS

In the Caspian tern, increased reproductive investment in egg production occurs disproportionately between different eggs within a clutch: variance in total clutch weight is due primarily to differences in the weight of the first-laid egg. Quinn & Morris (1986) suggested that the 'reproductive value' of the second-laid egg was lower, because success of this egg was constrained by hatching asynchrony and brood reduction. It is therefore less advantageous for the female to increase investment in the second-laid egg, i.e. the female invests more in the most viable egg. In the lesser snow goose, Williams *et al.* (1993) also found some support for the hypothesis that females allocate nutrients to eggs within a clutch according to the fitness that each egg has by virtue of its position in the laying sequence. These studies imply that females have the ability to adjust some aspect(s) of egg production and to allocate reserves differentially to eggs within (and possibly between) clutches. Neither of the above two studies considered the relationship between egg composition and egg size, and the possible physiological mechanisms underlying such differential investment in egg production are unknown. A knowledge of how egg composition varies with egg size might indicate which elements of the female reproductive system are involved in this process. As outlined in the Introduction, several authors have also suggested that females may be able to adjust egg composition facultatively to maximize the benefits of increased egg size with respect to offspring fitness (Boersma, 1982; Alisauskas, 1986; Hepp *et al.*, 1987).

Ricklefs *et al.* (1978) pointed out the difficulty of comparing changes in egg composition as a function of egg size in different species using linear regression statistics, because differences in mean egg size and composition influence the slopes of such relationships. The following section therefore concentrates on studies which present log:log regressions of egg components on egg size (although studies where only linear regression analyses or correlations are reported have been included in Table 4). With this method of analysis slopes with a value significantly greater than 1 or less than 1 indicate a proportional increase and decrease, respectively, in the egg component with increasing egg size; values not significantly different from 1 indicate that components change in direct proportion (isometrically) to variation in egg size. Restricting the data in this way makes comparisons complicated because relatively few studies ($n = 11$, Table 4) have so far reported on all or most components of eggs within individual species. In addition, variation in egg composition as a function of egg size within species (as indicated by 95 % confidence limits for values of slopes) appears to be very marked (e.g. Alisauskas, 1986; Arnold, 1989, 1992). Nevertheless some tentative generalizations can be drawn from the data presented in Table 4.

In the majority of studies larger eggs contain an absolutely greater mass of dry components, compared to small eggs, even when the percentage content of components varies isometrically with egg size (Table 4). In this respect larger eggs are therefore 'better' eggs and do not simply have a higher water content (Ankney, 1980; Ojanen, 1983). Large eggs also have an absolutely higher energy content compared to small eggs in both precocial species (Hepp *et al.*, 1987; Meathrel & Ryder, 1987) and altricial

species (Ojanen, 1983; Murphy, 1986; Muma & Ankney, 1987; Arnold, 1992). In the American coot (Alisauskas, 1986) and boat-tailed grackle (Bancroft, 1985), large eggs actually contain proportionately more energy, i.e. they have a higher energy density. This suggests that in most species egg size is a relatively good measure of egg quality (but see Ricklefs, 1977). In addition to this general relationship between egg size and egg quality, however, is there any evidence for differential changes in the proportional composition of eggs with respect to variation in egg size?

In approximately half the species so far studied egg composition varies in direct proportion to changes in egg size, e.g. wet albumen, 10 of 20 (50 %) studies, dry albumen, 9 of 14 (64 %), wet yolk, 12 of 22 (55 %) and dry yolk, 8 of 13 (62 %). These studies include species with all four patterns of chick development (Table 4). Wet albumen content increased disproportionately with increasing egg size in seven species but in three of these (Galbraith, 1988; Arnold, 1989, 1992) larger eggs also contained proportionately more water, and dry albumen content increased isometrically with egg size. In only two species, the ring-billed gull (Meathrel & Ryder, 1987) and the magpie (Clarkson, 1984), is there a disproportionate increase in dry albumen content (which is 95 % protein) with increasing egg size. There is some evidence for a general trend toward increasing albumen content and decreasing yolk content with increasing egg size in seabirds (Ricklefs & Montevecchi, 1970; Jones, 1979; Montevecchi *et al.*, 1983; Warham, 1983; Birkhead & Nettleship, 1984; Shaw, 1985; Meathrel, Ryder & Termaat, 1987) although this is so far largely based on linear regressions of wet albumen content. It has previously been suggested that variation in egg size in gulls (Laridae) is largely due to changes in albumen content (Parson, 1970; Ricklefs *et al.*, 1978; Bolton, 1991) and it appears that this may also be the case in other species, particularly in seabirds. As albumen mainly comprises protein and water the difference in albumen content must involve changes in one or both of these components. Variation in egg size in these species must, therefore, be mainly determined post-ovulation through processes occurring in the oviduct, rather than in the ovary (Ricklefs *et al.*, 1978; Bolton, 1991). Albumen contains on average 46 % and 71 % of the total egg protein in precocial and altricial species respectively (Carey *et al.*, 1980) and as albumen is entirely used up by hatching (cf. yolk) it is protein in the albumen that limits structural growth of the chick (Freeman & Vince, 1974). Despite this there is little evidence for any disproportionate increase in this component associated with increasing reproductive investment in larger eggs. It is the wet albumen component that is largely responsible for variation in egg size, and this reflects an increase in relative water content (rather than dry albumen or protein, Meathrel *et al.*, 1987; Galbraith, 1988; Arnold, 1989, 1992). This indicates that an increase in egg size may involve addition of greater amounts of water to the egg either in the magnum or during 'plumping' in the shell gland or uterus (Johnson, 1986). Arnold (1992) argued that changes in water content are not adaptive because water has no nutritional value and some species at least can tolerate wide variations in water content. However, if a high water content is retained by the neonate this may be adaptive in species, such as seabirds, which have a high salt content in their diet (Ricklefs *et al.*, 1978). The fact that there appears to be a positive relationship between egg size and offspring survival in those species where variation in egg size involves variation in the wet albumen or water component of eggs (e.g. Parsons, 1970; Bolton, 1991) supports the idea that these changes are adaptive.

In four species large eggs contain more wet yolk and in one of these, and in one

additional species, dry yolk content is proportionately greater in larger eggs (Table 4). Three of these five species are waterfowl (Birkhead, 1984, 1985; Rohwer, 1986) and there is some evidence for a similar trend toward increasing yolk content and decreasing albumen content, with increasing egg size, in the wood duck (Hepp *et al.*, 1986) and American coot (Alisauskas, 1986), though not in two *Podiceps* species (Arnold, 1989). In three species where large eggs contain relatively more yolk, there is also a disproportionate increase in lipid content with increasing egg size (Birkhead, 1984; Alisauskas, 1986; Rohwer, 1986). Similarly, in three species where relative yolk content decreases with increasing egg size, egg lipid content also decreases (Jones, 1979; Galbraith, 1989; Arnold, 1989). Changes in the yolk component of eggs, as a function of egg size, therefore reflect real differences in the nutrient or energy content of eggs, i.e. in egg 'quality' (cf. albumen). This supports Lack's (1968) original contention that large eggs would be most advantageous if they contained proportionately more yolk. In addition to containing all the egg lipid, yolk provides 60–90 % of the embryo's total energy requirement (Freeman & Vince, 1974; Ojanen, 1983) and contains 54 % of the total egg protein in precocial species (though only 29 % in altricial species, Carey *et al.*, 1980). Increased yolk content could therefore benefit both structural growth of the chick as well as its stored nutrient reserves. However, variation in yolk content in different-sized eggs mainly involved changes in lipid content rather than in protein content (Alisauskas, 1986; Rohwer, 1986; Galbraith, 1988; Arnold, 1989). This is consistent with the fact that large eggs give rise to chicks which retain larger nutrient reserves (yolk) at hatching, rather than being structurally larger, and with the positive relationship between egg size and offspring survival in these species, at least over the first few days after hatching (e.g. Ankney, 1980; Galbraith, 1988). Yolk lipid is synthesized in the liver, transported by the blood system to the ovary, and then taken up by the developing ovarian follicles. Changes in lipid content with increasing egg size could be regulated at any, or all, of these stages of yolk production.

Again, surprisingly little data is available for true altricial species and there is no consistent pattern of egg composition with respect to egg size. In four species wet albumen content increases and/or wet yolk content decreases with increasing egg size (Ojanen, 1983; Clarkson, 1984; Richter, 1984; Bancroft, 1985). However, in one species the opposite pattern occurs (Ankney & Johnson, 1985) and in three species egg composition varies isometrically with egg size (Ojanen, 1983; Ricklefs, 1984b; Muma & Ankney, 1985). Both wet and dry albumen content vary with egg size in two species (Clarkson, 1984; Ankney & Johnson, 1985), and although water content varies disproportionately with egg size in three out of five species, the values of the slopes for this relationship are very close to one (cf. other species such as seabirds). As in other species, however, changes in wet yolk content are generally reflected in similar changes in dry yolk or lipid content, rather than protein content (Table 4), although the magpie provides an exception to this (Clarkson, 1984).

To conclude, there is little evidence so far that birds facultatively adjust the protein content of eggs, with increased investment in larger eggs, to enhance structural development of their chicks. This is consistent with the fact that larger eggs more often give rise to heavier, but not larger chicks. In semi-altricial and semi-prococial seabirds, increased egg size appears to mainly reflect increased water content of eggs. In precocial species, larger eggs generally contain more yolk and this is reflected in increased egg

lipid content consistent with large eggs giving rise to chicks with increased nutrient reserves at hatching. These differential changes in egg composition with increasing egg size may reflect facultative adjustments made by the laying female in order to maximize offspring fitness.

V. CONCLUSIONS AND CONSIDERATIONS FOR FUTURE RESEARCH

This review has highlighted the paucity of data which unequivocally support the widely held view that egg size and offspring fitness are positively related in birds. More studies are required, particularly for altricial species, where the confounding effects of other parental traits that might also affect offspring fitness are controlled for (e.g. age, parental quality). In addition, the influence of other factors such as annual variation, and female body size and condition should be investigated. The complexity of the many different factors that could potentially be correlated with both egg size and offspring fitness, point to the value of laboratory studies (on non-domesticated species) where these variables can be more easily controlled. There is also a need for more data on egg composition, particularly for chemical components of eggs (protein and lipid, rather than yolk and albumen), and for species with different chick-rearing patterns e.g. siblicidal and parasitic species. Magrath (1992) and Bolton *et al.* (1992) have suggested that birds may have requirements for specific nutrients (vitamins, minerals or amino acids) during egg formation and that these may constrain egg size. With the exception of calcium as yet very little is known about these aspects of egg production in wild birds. Another element of the relationship between egg composition and offspring fitness is how variation in egg components relates to composition of the neonate. Several studies have shown that there can be marked variation in the way different individual embryos utilize egg components, e.g. Ankney (1980), Vleck & Vleck (1987), Thomas & Peach Brown (1988).

Future research into the causes and consequences of egg-size variation in wild birds is likely to prove most fruitful through an experimental approach in three main areas. First, although many studies have reported the effect of supplemental feeding on clutch size very few of these have considered effects on egg size (Bolton *et al.*, 1992). Providing birds with supplemental food of different compositions (e.g. high protein or lipid content), particularly in relation to the species-specific predictions outlined in Section IV, would allow determination of the potential nutrient constraints on egg production. A similar approach could be taken for energy requirements as energy expenditure during egg formation can also be experimentally manipulated (Nager & van Noordwijk, 1992; Yom-Tov & Wright, 1993). Secondly, it is likely that new techniques can be applied to the non-destructive determination of the composition of intact eggs, which could then be allowed to hatch and develop normally. For example, Hutchison *et al.* (1992) used magnetic resonance imaging to examine the inner structure of hen's eggs. This provides information on the relative size of yolk and albumen and, in addition, reveals the ring structure of yolk (Grau, 1976) allowing the timing and pattern of yolk formation to be determined. Small animal body composition analyzers, which have recently been applied to studies of live birds and mammals (e.g. Walsberg, 1988; Roby, 1991), might also be used to estimate lipid content of intact eggs. Thirdly, experimental manipulation of egg size or composition offers a way to directly test predictions about how these factors affect offspring fitness (review: Bernardo, 1991). These techniques

include manipulation of follicle development, either directly or hormonally, before laying (Sinervo & Licht, 1991) and modification of egg composition following laying, typically by decreasing the proportion of one or more egg component, e.g. by removal of yolk or albumen (Sinervo & Huey, 1990; Maramatsu *et al.*, 1990; Hill, 1993). Al-Murrani (1982) reported that injection of amino acids into the yolk sac increased growth rates in domestic chicks, a technique not yet applied to wild birds. Finally, the adaptive significance of the increased water content of larger eggs, found particularly in seabirds, could be investigated by experimentally manipulating rates of water loss during incubation (see e.g. Carey, 1986).

As a final general point, variation in egg size at the individual level appears to be very marked in bird populations, even though such information is rarely reported. For example, in the song sparrow mean egg mass varied from 2·20 g to 3·75 g (70 %) and the total mass of three-egg clutches frequently equalled that of four-egg clutches (Arcese & Smith, 1988). Similarly, in geese there is often considerable overlap in total clutch masses for different clutch sizes (Ankney & Bisset, 1973; Flint & Sedinger, 1992). Despite this marked variation in egg size within-species egg production in birds has generally been considered to be a conservative process (e.g. Grau, 1984; Astheimer & Grau, 1985) and most attention has focused on differences between species (Carey *et al.*, 1980; Sotherland & Rahn, 1987). As this review has shown there can also be marked variation in egg composition between individuals of the same species as well as between species. Experimental studies have shown that this may reflect differences in condition of individual females (Alisauskas, 1986) or in territory quality (Arnold, 1992). Egg composition can also vary within individuals between clutches in the same year (Owen & West, 1988) or between years (Hatchwell & Pellatt, 1990) and recent studies have demonstrated significant intraspecific variation in the duration of the period of rapid yolk development in gulls (Meathrel, 1991) and auks (Hatchwell & Pellatt, 1990). Although Lack's (1968) comment about the neglect of avian egg size is obviously not as valid today, the ecological significance of variation in egg size (and composition) particularly at the individual and intraspecific level, and the proximate, physiological mechanisms underlying this, remain poorly understood in wild birds.

VI. SUMMARY

1. There is little unequivocal evidence to date in support of a positive relationship between egg size and offspring fitness in birds. Although 40 studies (of 34 species) have considered the effect of variation in egg size on chick growth and/or survival up to fledging only 12 studies have controlled for other characters potentially correlated both with egg size and offspring fitness. Of these only two have reported a significant residual effect of egg size on chick growth (in the roseate tern and European blackbird) and three a residual effect on chick survival (all in seabirds: common tern, lesser black-backed gull and kittiwake).

2. More consistent evidence exists, though from fewer studies, for a positive relationship between egg size and offspring fitness early in the chick-rearing period; chick growth and chick survival being dependent on egg size in 8 of 10 studies and 4 of 5 studies respectively. It is suggested that the most important effect of variation in egg size might be in determining the probability of offspring survival in the first few days after hatching.

3. Egg size explains on average 66 % of the variation in chick mass at hatching

($n = 35$ studies) but only 30 % of the variation in chick body size ($n = 18$). When effects of hatchling body size are controlled for chick mass remains significantly correlated with egg size, though the reverse is not true. This supports the hypothesis that large eggs give rise to heavier chicks at hatching, i.e. chicks with more nutrient (yolk) reserves, rather than structurally larger chicks.

4. Egg composition increased isometrically with increasing egg size in about half the studies so far reported ($n \approx 20$). However, in seabirds, and some passerines, larger eggs contain disproportionately more albumen, whilst in some waterfowl percentage yolk content increases with increasing egg size. Changes in albumen content largely reflect variation in the water content of eggs, but changes in yolk content involve variation in lipid content, and therefore in egg 'quality'. The adaptive significance of variation in egg composition is considered; females may adjust egg composition facultatively to maximise the benefits to their offspring of increased reproductive investment.

5. Considerations for future research are discussed with particular emphasis on experimental studies and the application of new techniques.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

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