

Avian egg size: variation within species and inflexibility within individuals

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ABSTRACT

Egg size is a widely-studied trait and yet the causes and consequences of variation in this trait remain poorly understood. Egg size varies greatly within many avian species, with the largest egg in a population generally being at least 50% bigger, and sometimes twice as large, as the smallest. Generally, approximately 70% of the variation in egg mass is due to variation between rather than within clutches, although there are some cases of extreme intra-clutch egg-size variation. Despite the large amount of variation in egg size between females, this trait is highly consistent within individuals between breeding attempts; the repeatability of egg size is generally above 0.6 and tends to be higher than that of clutch size or laying date. Heritability estimates also tend to be much higher for egg size (> 0.5) than for clutch size or laying date (< 0.5). As expected, given the high repeatability and heritability of egg size, supplemental food had no statistically significant effect on this trait in 18 out of 28 (64%) studies. Where dietary supplements do increase egg size, the effect is never more than 13% of the control values and is generally much less. Similarly, ambient temperature during egg formation generally explains less than 15% of the variation in egg size. In short, egg size appears to be a characteristic of individual females, and yet the traits of a female that determine egg size are not clear. Although egg size often increases with female age (17 out of 37 studies), the change in egg size is generally less than 10%. Female mass and size rarely explain more than 20% of the variation in egg size within species. A female's egg size is not consistently related to other aspects of reproductive performance such as clutch size, laying date, or the pair's ability to rear young. Physiological characteristics of the female (e.g. endogenous protein stores, oviduct mass, rate of protein uptake by ovarian follicles) show more promise as potential determinants of egg size. With regards to the consequences of egg-size variation for offspring fitness, egg size is often correlated with offspring mass and size within the first week after hatching, but the evidence for more long-lasting effects on chick growth and survival is equivocal. In other oviparous vertebrates, the magnitude of egg-size variation within populations is often as great or greater than that observed within avian populations. Although there are much fewer estimates of the repeatability of egg size in other taxa, the available evidence suggests that egg size may be more flexible within individuals. Furthermore, in non-avian species (particularly fish and turtles), it is more common for female mass or size to explain a substantial proportion of the variation in egg size. Further research into the physiological basis of egg-size variation is needed to shed light on both the proximate and ultimate causes of intraspecific variation in this trait in birds.

Key words: age, egg mass, food, intraspecific variation, optimal egg size theory, phenotypic plasticity, physiology, reproductive performance, temperature.

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I. INTRODUCTION

How much should parents invest in each of their progeny? Some life-history models predict that there is an optimum amount of effort that organisms should invest in each offspring (e.g. Smith & Fretwell, 1974; McGinley, Temme & Geber, 1987). However, propagule size, one component of the effort expended per offspring, often shows tremendous variation within species (Bernardo, 1996). Intraspecific variation in propagule size could be due to differences in optima between individuals and environments, or to temporal changes in the optimum effort-per-offspring. Alternatively, nutritional or physical limitations might constrain the amount of resource invested in each offspring (e.g. Congdon & Gibbons, 1987). However, to date the ubiquitous variation in propagule size within populations remains unexplained (Bernardo, 1996).

The development of better models of parental investment in offspring will require knowledge of the patterns of variation within species (e.g. whether variation occurs within or between individuals; whether variation is related to resource availability), and of the aspects of maternal phenotype that influence propagule size (Bernardo, 1996). In these respects, the ornithological literature provides a rich resource. Perhaps more than in any other taxonomic group, most aspects of egg-size variation have been extensively documented: variation within and between clutches, repeatability between clutches produced by an individual female, heritability,

response to food supplementation, correlations with female phenotypes, and correlations with offspring growth and survival. In this review, I examine the patterns of intraspecific egg-size variation within avian populations and draw attention to (a) the large intraspecific variation in egg size within avian populations, (b) the lack of plasticity in egg size within individual females, and (c) our lack of understanding of the proximate or ultimate causes of intraspecific egg-size variation.

I begin by summarizing the variation in egg size within avian populations, as well as repeatability and heritability estimates of this trait. Repeatability of egg size could be due to the repeatability of environmental conditions within individuals (e.g. food supply), and so I review the effects of environmental factors (food and temperature) on egg size. Next, I summarize relationships between female characteristics (e.g. age, size) and egg size, giving special attention to physiological traits of the female that, although less intensively studied, are crucial to understanding variation in reproductive performance (Bernardo, 1996). The proximate causes and ultimate consequences of intraspecific egg-size variation are then considered. Finally, to assess the extent to which the observed patterns are unique to birds, I briefly review intraspecific egg-size variation in other taxonomic groups.

I have not included studies of domesticated species in this review because the causes of intraspecific variation present in natural populations may have been obscured or eliminated by the long history of

artificial selection on reproductive traits. However, studies of captive, non-domesticated birds have been included since such populations commonly exhibit patterns of egg-size variation similar to those observed in nature (e.g. Williams, 1996a). Due to the enormous number of studies that have reported data on avian egg size, I have focused on variation in egg size between individuals, and generally do not consider the pattern of variation within clutches since this variation is small compared to the variation between clutches (see below) and has been reviewed elsewhere (Slagsvold *et al.*, 1984). Throughout, I use the term egg size to refer to egg mass or volume, which are highly correlated (generally $r^2 > 0.8$; e.g. Duncan, 1987; Reid & Boersma, 1990; Arnold, 1992; Magrath, 1992a; Meathrel *et al.*, 1993a; Smith, Ottosson & Ohlsson, 1993; Nol, Blanken & Flynn, 1997; Viñuela, 1997; but see Flint & Grand, 1999); where authors have provided data on both mass and volume, I use the former. Although I do not explicitly consider variation in egg quality, fresh egg mass is generally correlated with the dry

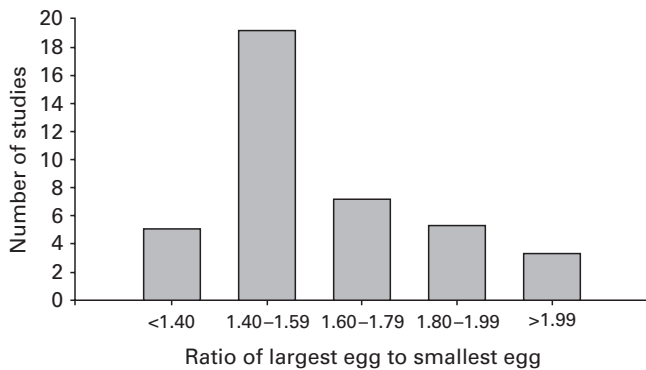


Fig. 1. The ratio of the size of the largest egg in the population to that of the smallest in 39 studies; mean egg size of the clutch was used where provided. Data are from Montevecchi *et al.* (1983); Bancroft (1984); Birkhead (1984); Nol *et al.* (1984); Murphy (1986a); Duncan (1987); Muma & Ankney (1987); Arcese & Smith (1988); Eldridge & Krapu (1988); Järvinen & Pyl (1989); Leblanc (1989); Amundsen & Stokland (1990); Coleman & Whittall (1990); Wiggins (1990); Hendricks (1991); Martin & Arnold (1991); Pehrsson (1991); Croxall *et al.* (1992); Flint & Sedinger (1992); Swennen & Meer (1992); Meathrel *et al.* (1993a); Nilsson & Svensson (1993a); Potti (1993); Robertson & Cooke (1993); Smith *et al.* (1993); Arnold (1994); Simmons (1994); Amundsen (1995); Wiebe & Bortolotti (1995); Amundsen *et al.* (1996); Dufva (1996); Weidinger (1996); Williams (1996a); Williams *et al.* (1996); Ashkenazi & Yom-Tov (1997); Blomqvist *et al.* (1997); Erikstad *et al.* (1998); Smith & Bruun (1998); Reed *et al.* (1999).

components of the yolk and albumen (e.g. St. Clair, 1996; Kennamer, Alsum & Colwell, 1997; Flint & Grand, 1999) and thus is a good measure of quality in terms of macronutrient composition (see Williams, 1994 and Hill, 1995 for reviews).

II. INTRASPECIFIC VARIATION IN EGG SIZE

Within many species of birds, there is a large range in egg size. The largest egg in a population is generally at least 50% bigger, and sometimes twice as large, as the smallest (Fig. 1). This variation is also seen in species with one-egg clutches, where egg size is the only means by which females can adjust the amount of nutrients and energy invested in eggs (e.g. Montevecchi *et al.*, 1983; Croxall, Rothery & Crisp, 1992; Meathrel *et al.*, 1993a; Amundsen, 1995; Amundsen, Lorentsen & Tveraa, 1996; Weidinger, 1996). Generally, approximately 70% of the variation in egg size is due to variation between rather than within clutches (Fig. 2). Notable exceptions to this pattern are found in the crested penguins (*Eudyptes* spp.) that exhibit extreme egg-size dimorphism, with differences of 30–60% between eggs within a clutch (Williams, 1990; St. Clair, 1996).

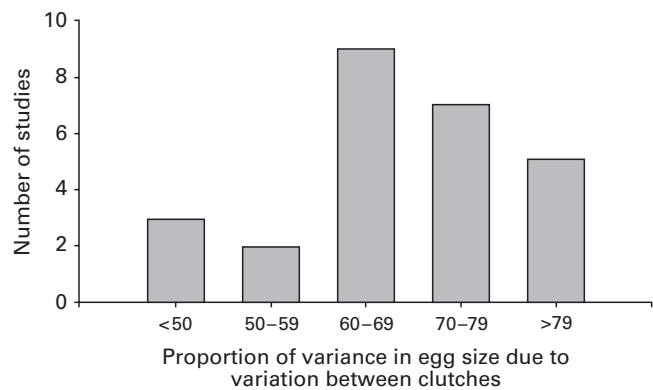


Fig. 2. Proportion of variance in egg size due to variation between rather than within clutches in 26 studies. Where more than one estimate was provided per species per study, I selected the lowest. Data are from Grant (1982); Zach (1982); Järvinen & Väisänen (1983); Bancroft (1984); Ricklefs (1984); Lank *et al.* (1985); Poole (1985); Redmond (1986); Rohwer (1986); Hepp *et al.* (1987); Muma & Ankney (1987); Galbraith (1988); Rohwer & Eisenhauer (1989); Amundsen & Stokland (1990); Coleman & Whittall (1990); Wiggins (1990); Grant (1991); Thompson & Hale (1991); Arnold (1992); Magrath (1992a); Swennen & Meer (1992); Nilsson & Svensson (1993a); Smith *et al.* (1993); Wiebe & Bortolotti (1995); Nol *et al.* (1997); Erikstad *et al.* (1998).

Table 1. *Repeatabilities of egg size, clutch size and laying date between breeding attempts*

Latin name	Common name	Repeatability	Reference
Egg size			
<i>Aegolius funereus</i>	Tengmalm's Owl	0.51	Hakkarainen & Korpimäki (1994)
<i>Anas acuta</i>	Northern Pintail	0.61	Duncan (1987)
<i>Anas acuta</i>	Northern Pintail	0.89	Flint & Grand (1996)
<i>Anas platyrhynchos</i>	Mallard	0.62	Batt & Prince (1979)
<i>Aythya marila</i>	Greater Scaup	0.36	Flint & Grand (1999)
<i>Branta bernicla nigricans</i>	Black Brant	0.78	Flint & Sedinger (1992)
<i>Branta canadensis</i>	Canada Goose	0.92	Leblanc (1989)
<i>Charadrius semipalmatus</i>	Semipalmated Plover	0.68	Nol <i>et al.</i> (1997)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.80	Lessells <i>et al.</i> (1989)
<i>Falco sparverius</i>	American Kestrel	0.71	Wiebe & Bortolotti (1995)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.61	Potti (1993)
<i>Haematopus palliatus</i>	American Oystercatcher	0.35	Nol <i>et al.</i> (1984)
<i>Lagopus lagopus scoticus</i>	Red Grouse	0.73–0.77	Moss & Watson (1982)
<i>Parus major</i>	Great Tit	0.58–0.72	Noordwijk (1987)
<i>Parus major</i>	Great Tit	0.64	Hörak <i>et al.</i> (1995)
<i>Parus major</i>	Great Tit	0.68	Dufva (1996)
<i>Stercorarius parasiticus</i>	Arctic Skua	0.63, 0.73	Phillips & Furness (1998)
<i>Sturnus vulgaris</i>	European Starling	0.76	Smith <i>et al.</i> (1993)
<i>Sturnus vulgaris</i>	European Starling	0.76	Christians & Williams (2001 <i>b</i>)
<i>Tachycineta bicolor</i>	Tree Swallow	0.77	Wiggins (1990)
<i>Taeniopygia guttata</i>	Zebra Finch	0.74	Williams (1996 <i>a</i>)
<i>Tringa tetanus</i>	Redshank	0.73, 0.87	Thompson & Hale (1991)
Clutch size			
<i>Anas platyrhynchos</i>	Mallard	0.54	Batt & Prince (1979)
<i>Branta bernicla nigricans</i>	Black Brant	0.14	Flint & Sedinger (1992)
<i>Bucephala albeola</i>	Bufflehead	0.55	Gauthier (1989)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.26	Findlay & Cooke (1987)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.15	Lessells <i>et al.</i> (1989)
<i>Falco tinnunculus</i>	Kestrel	0.19	Meijer <i>et al.</i> (1988)
<i>Geospiza fortis</i>	Darwin's Medium Ground Finch	0.08	Gibbs (1988)
<i>Parus major</i>	Great Tit	0.51	Perrins & Jones (1974)
<i>Parus major</i>	Great Tit	0.30–0.54	Noordwijk (1987)
<i>Parus major</i>	Great Tit	0.86	Dufva (1996)
<i>Taeniopygia guttata</i>	Zebra Finch	0.59	Williams (1996 <i>a</i>)
Laying date			
<i>Accipiter nisus</i>	Eurasian Sparrowhawk	0.18, 0.26 ^a	Newton & Marquiss (1984)
<i>Anas platyrhynchos</i>	Mallard	0.57	Batt & Prince (1979)
<i>Bucephala albeola</i>	Bufflehead	0.57	Gauthier (1989)
<i>Charadrius semipalmatus</i>	Semipalmated Plover	0.00 ^b	Nol <i>et al.</i> (1997)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.22	Hamann & Cooke (1989)
<i>Falco tinnunculus</i>	Kestrel	0.00	Meijer <i>et al.</i> (1988)
<i>Fulica atra</i>	European Coot	0.32	Perdeck & Cavé (1992)
<i>Haematopus palliatus</i>	American Oystercatcher	0.73	Nol <i>et al.</i> (1984)
<i>Parus major</i>	Great Tit	0.19–0.44	Noordwijk (1987)
<i>Stercorarius parasiticus</i>	Arctic Skua	–0.16, 0.50	Phillips & Furness (1998)
<i>Uria aalge</i>	Common Murre	0.20	Sydeman & Eddy (1995)

^a Corrected values from Lessells & Boag (1987).^b Repeatability of clutch completion date, not laying date.

Table 2. Heritability estimates for egg size, clutch size and laying date

(NS = heritability estimate was not significantly different from zero and was not provided.)

Latin name	Common name	Heritability	Reference
Egg size			
<i>Anas acuta</i>	Northern Pintail	NS	Duncan (1987)
<i>Anas platyrhynchos</i>	Mallard	0.55	Prince <i>et al.</i> (1970)
<i>Branta leucopsis</i>	Barnacle Goose	0.67	Larsson & Forslund (1992)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.53	Lessells <i>et al.</i> (1989)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	NS	Potti (1993)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.55	Potti (1999)
<i>Lagopus lagopus scoticus</i>	Red Grouse	0.66	Moss & Watson (1982)
<i>Parus major</i>	Great Tit	0.86	Ojanen <i>et al.</i> (1979)
<i>Parus major</i>	Great Tit	0.66–0.86	Noordwijk (1987)
<i>Parus major</i>	Great Tit	0.81	Hörak <i>et al.</i> (1995)
Clutch size			
<i>Anas platyrhynchos</i>	Mallard	0.46	Prince <i>et al.</i> (1970)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.20	Findlay & Cooke (1987)
<i>Chen caerulescens</i>	Lesser Snow Goose	0.17	Lessells <i>et al.</i> (1989)
<i>Ficedula albicollis</i>	Collared Flycatcher	0.33	Schluter & Gustafsson (1993)
<i>Ficedula albicollis</i>	Collared Flycatcher	0.35	Merila & Sheldon (2000)
<i>Geospiza fortis</i>	Darwin's Medium Ground Finches	NS	Gibbs (1988)
<i>Parus major</i>	Great Tit	0.48 ^a	Perrins & Jones (1974)
<i>Parus major</i>	Great Tit	0.25–0.50	Noordwijk (1987)
<i>Sturnus vulgaris</i>	European Starling	0.34	Flux & Flux (1982)
Laying date			
<i>Accipiter nisus</i>	Eurasian Sparrowhawk	NS	Newton & Marquiss (1984)
<i>Ficedula albicollis</i>	Collared Flycatcher	0.41	Merila & Sheldon (2000)
<i>Fulica atra</i>	Coot	0.02	Perdeck & Cavé (1992)
<i>Parus major</i>	Great Tit	–0.08–0.45	Noordwijk (1987)

^a Cited in Hailman (1986).

Despite such extreme dimorphism, the masses of the first- and second-laid eggs are correlated within clutches in the Macaroni Penguin (*E. chrysochome*; Williams, 1990), i.e. females still differ from one another in the size of egg they produce.

Egg size is highly consistent within individual females between breeding attempts. Repeatability is a measure of 'the proportion of variance in a character that occurs among rather than within individuals' (Lessells & Boag, 1987: p. 116; see also Falconer & Mackay, 1996) and is generally higher for egg size (> 0.6) than for clutch size or timing of egg laying (< 0.6; Table 1), as observed by Boag & Noordwijk (1987) and Lessells, Cooke & Rockwell (1989). Based on the data from Table 1, the mean repeatabilities for egg size, clutch size and timing of laying are 0.68, 0.40 and 0.35, respectively. Even in

the Macaroni Penguin, a species that shows extreme egg-size variation within clutches, the masses of the first- and second-laid eggs are positively correlated with the respective egg masses of the same female in the subsequent year ($r^2 = 0.27\text{--}0.67$; Williams & Croxall, 1991).

Estimates of heritability, the proportion of phenotypic variation due to additive genetic variance (Falconer & Mackay, 1996), also tend to be higher for egg size (> 0.5) than for clutch size or timing of egg laying (< 0.5; Table 2) (see also Hailman, 1986; Boag & Noordwijk, 1987; Lessells *et al.*, 1989). Based on the data from Table 2, the mean heritabilities for egg size, clutch size and timing of laying are 0.66, 0.35 and 0.24, respectively. It should be noted that there are a number of potential problems associated with measuring heritability in

the wild (Hailman, 1986). For example, offspring may tend to experience similar environmental conditions as their parents, and this will inflate the apparent heritability of a trait. Thus, the heritability values provided in Table 2 may be overestimates in many cases. However, given that the heritability estimates for egg size are consistently higher than those for clutch size and laying date, it seems likely that the general pattern is robust (see also Section VI.2).

III. ENVIRONMENTAL EFFECTS ON EGG SIZE

The high repeatability and heritability of egg size described above could be due to consistent or inherited environmental conditions such as food supply (e.g. due to foraging skills, social dominance, territory quality). Therefore, it is instructive to examine whether environmental factors such as food and ambient temperature can affect egg size.

(1) Food supplementation

Price (1998) and Meijer & Drent (1999) summarized the effects of food supplementation experiments and found that supplemental food leads to an advancement of laying date more often than to an increase in egg size or clutch size. I update these reviews with a focus on egg size and the magnitude of the effect of supplemental food on this trait. Only studies that report egg-size data are included, and I consider only experimental manipulations. Studies of captive birds are included, and thus “supplemental” food may actually refer to a higher quality diet, rather than extra food. In the few studies where more than one type of diet was provided, I report the largest effect size, i.e. there is a slight bias towards large effects.

Considering only statistically significant effects, 36% of studies (10/28) found that supplemental food or enhanced food quality increased egg size (Table 3). Clutch size was increased by supplemental food in 63% (15/24) of studies, and the timing of laying was advanced in 57% (12/21) (Table 3). The increase in egg size due to food supplementation was never more than 13% of the control values and was generally much less (Högstedt, 1981: 8%; Hill, 1988: 5%; Hiom *et al.*, 1991: 5–11%; Pehrsson, 1991: 12%; Källander & Karlsson, 1993: 4%; Wiebe & Bortolotti, 1995: 7%; Selman & Houston, 1996: 13%; Williams, 1996*b*: 12%; Ramsay & Houston, 1997: 7%; Eldridge & Krapu, 1988 did

not provide data on the magnitude of the effect). The effect of supplemental food on reproductive parameters is likely to depend on the type of food supplied, e.g. high-protein supplements have been found to have a greater effect than lipid supplements (Williams, 1996*b*; Ramsay & Houston, 1997).

In contrast to the large number of food supplementation studies, there have been relatively few food restriction experiments, and these have found no effect on egg size in Northern Bobwhite Quail (*Colinus virginianus*), Scaled Quail (*Callipepla squamata*) (Giuliano, Lutz & Patiño, 1996) and European Starlings (*Sturnus vulgaris*) (Meijer & Langer, 1995).

(2) Temperature

Only one study has experimentally examined the effect of temperature during egg production on egg size: Great Tits (*Parus major*) roosting in cooled nestboxes laid eggs 14% smaller than those roosting in heated nestboxes (Nager & Noordwijk, 1992). Correlations between ambient temperatures during egg formation and egg size yield mixed results including positive (Ojanen, 1983; Järvinen & Pyl, 1989; Järvinen, 1991; Magrath, 1992*b*; Nager & Zandt, 1994) and negative (Williams & Cooch, 1996) relationships, as well as no effect (Murphy, 1983; Robertson, 1995). Even within a species, there may be significantly positive and significantly negative relationships (Ojanen, Orell & Väisänen, 1981). Generally, temperature explains at most 10–15% of the egg-size variation (and often much less; but see Nager & Noordwijk, 1992). Given the lack of consistent results in the observational studies described above, more experimental studies of the effects of temperature on egg production are necessary.

IV. FEMALE CHARACTERS

(1) Age and experience

Saether (1990) reviewed variation in reproductive performance with age, and I update this work with a focus on egg size (i.e. only studies that report egg size data are included) and the magnitude of the changes in this trait. Although egg size appears to be a characteristic of individual females, it does increase slightly with age in many species; a statistically significant increase in egg size with age or experience was found in almost half (17/37) of the studies

Table 3. *Effects of supplemental food or enhanced food quality on egg size, clutch size and laying date* (○ = no significant effect (i.e. $P > 0.05$), + = positive effect (i.e. increase in egg or clutch size or advancement of laying date), - = negative effect, ND = no data. More than one symbol indicates variation in the effect, e.g. between years or sites.)

Latin name	Common name	Egg size	Clutch size	Laying date	Reference
<i>Aegolius funereus</i>	Tengmalm's Owl	○	+	+	Korpimäki (1989)
<i>Anas platyrhynchos</i>	Mallard	+	+	○	Eldridge & Krapu (1988)
<i>Anas platyrhynchos</i>	Mallard	+	+	ND	Pehrsson (1991)
<i>Circus ranivorus</i>	African Marsh Harrier	○	+	ND	Simmons (1994)
<i>Corvus monedula</i>	Jackdaw	○	+	+, ○	Soler & Soler (1996)
<i>Falco sparverius</i>	American Kestrel	+	ND	ND	Wiebe & Bortolotti (1995) ^a
<i>Ficedula hypoleuca</i>	Pied Flycatcher	○	+	○	Sanz & Moreno (1995)
<i>Fulica americana</i>	American Coot	+	-	○	Hill (1988)
<i>Fulica americana</i>	American Coot	○	+	+	Arnold (1994)
<i>Fulica atra</i>	European Coot	○	ND	○	Horsfall (1984) ^b
<i>Lanius collurio</i>	Red-backed Shrike	○	+	ND	Carlson (1989)
<i>Larus fuscus</i>	Lesser Black-backed Gull	+, ○	+, ○	○	Hiom <i>et al.</i> (1991)
<i>Larus fuscus</i>	Lesser Black-backed Gull	○	○	○	Bolton <i>et al.</i> (1992) ^c
<i>Melospiza melodia</i>	Song Sparrow	○	+	+	Arcese & Smith (1988)
<i>Pandion haliaetus</i>	Osprey	○	ND	ND	Poole (1985)
<i>Parus caeruleus</i>	Blue Tit	○	ND	ND	Nilsson & Svensson (1993 <i>a</i>)
<i>Parus caeruleus</i>	Blue Tit	○	○	+	Nilsson & Svensson (1993 <i>b</i>)
<i>Parus caeruleus</i>	Blue Tit	○	○	+	Nilsson (1994) ^a
<i>Parus caeruleus</i>	Blue Tit	+	○	+	Ramsay & Houston (1997)
<i>Parus caeruleus</i>	Blue Tit	○	+	○ ^d	Ramsay & Houston (1998)
<i>Parus major</i>	Great Tit	○	+	+	Nager <i>et al.</i> (1997)
<i>Pica pica</i>	Black-billed Magpie	+	+ ^e	+ ^e	Högstedt (1981)
<i>Pica pica</i>	Black-billed Magpie	○	○ ^d	+, ○	Hochachka & Boag (1987)
<i>Sturnus vulgaris</i>	European Starling	+, ○	○	+	Källander & Karlsson (1993)
<i>Taeniopygia guttata</i>	Zebra finch	+	+	○	Selman & Houston (1996) ^a
<i>Taeniopygia guttata</i>	Zebra finch	+	+, ○	ND	Williams (1996 <i>b</i>)
<i>Turdus merula</i>	Blackbird	○	○ ^d	+	Magrath (1992 <i>b</i>)
<i>Xanthocephalus xanthocephalus</i>	Yellow-headed Blackbird	○	○	○ ^d	Arnold (1992)

^a Supplemental/enhanced food was provided prior to egg laying only. In all other studies, supplemental/enhanced food was provided prior to and during egg laying.

^b No effect on mean egg size but there were effects on intra-clutch egg-size variation.

^c No effect on mean egg size but there were effects on egg composition.

^d Marginally non-significant effect ($0.05 < P < 0.1$).

^e Significant in paired comparisons within females only.

examined (Table 4). For comparison, statistically significant effects of age are observed more often with clutch size and timing of breeding (69%, 9/13 and 88%, 14/16, respectively; Table 4). Of the studies I examined that reported a statistically significant increase in egg size, the difference between the most extreme age classes was generally very small (Gratto, Cooke & Morrison, 1983: 5%; Lequette & Weimerskirch, 1990: 9%; Wiggins,

1990: 2%; Weimerskirch, 1990: 10%; Järvinen, 1991: 1%; Robertson *et al.*, 1994: 5%; Hōrak *et al.*, 1995: 2%; Flint & Grand, 1996: 3%; Viñuela, 1997: 5%; Ollason & Dunnet, 1986 and Flint & Sedinger, 1992 provided no data on the magnitude of the effect), although Hipfner, Gaston & Forest (1997) found a difference of approximately 17%. Of studies that presented the data as correlations, age or experience explained only a small amount of the

Table 4. *Changes in egg size, clutch size and laying date with age (or experience, where noted)*
 (~ = increase with age with a decline in the oldest age classes. Other symbols are as in Table 3.)

Latin name	Common name	Egg size	Clutch size	Laying date	Reference
<i>Aegolius funereus</i>	Tengmalm's Owl	○	ND	ND	Hakkarainen & Korpimäki (1994)
<i>Aix sponsa</i>	Wood Duck	○	ND	ND	Hepp <i>et al.</i> (1987)
<i>Anas acuta</i>	Northern Pintail	○	ND	ND	Duncan (1987)
<i>Anas acuta</i>	Northern Pintail	+	ND	ND	Flint & Grand (1996)
<i>Branta bernicla nigricans</i>	Black Brant	+	+	+	Flint & Sedinger (1992)
<i>Branta canadensis</i>	Canada Goose	○	ND	ND	Leblanc (1989)
<i>Calidris pusilla</i>	Semipalmated Sandpiper	+	○	+ ^a	Gratto <i>et al.</i> (1983)
<i>Chen caerulescens caerulescens</i>	Lesser Snow Goose	○	+	+	Cooch <i>et al.</i> (1992)
<i>Chen caerulescens caerulescens</i>	Lesser Snow Goose	+	ND	ND	Robertson <i>et al.</i> (1994)
<i>Corvus corone cornix</i>	Hooded Crow	○	+	+	Loman (1984) ^b
<i>Cygnus olor</i>	Mute Swan	○	+	+	Birkhead <i>et al.</i> (1983)
<i>Diomedea exulans</i>	Wandering Albatross	+	ND	○ ^a	Lequette & Weimerskirch (1990) ^b
<i>Diomedea exulans</i>	Wandering Albatross	+	○	ND	Croxall <i>et al.</i> (1992)
<i>Diomedea exulans</i>	Wandering Albatross	~	ND	○	Weimerskirch (1992)
<i>Ficedula albicollis</i>	Collared Flycatcher	○	ND	ND	Cichon (1997)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	+	ND	ND	Järvinen (1991)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	-	ND	ND	Potti (1993)
<i>Fulica americana</i>	American Coot	○	+	+	Crawford (1980)
<i>Fulmarus glacialis</i>	Fulmar	+	○	ND	Ollason & Dunnet (1986) ^b
<i>Fulmarus glacialisoides</i>	Antarctic Fulmar	+	ND	+ ^a	Weimerskirch (1990) ^b
<i>Lagopus lagopus alexandrae</i>	Willow Ptarmigan	○	ND	ND	Sandercock & Pedersen (1994)
<i>Larus glaucescens</i>	Glaucous-winged Gull	-	+	+	Reid (1988)
<i>Larus occidentalis</i>	Western Gull	~	ND	ND	Sydeman & Emslie (1992)
<i>Milvus migrans</i>	Black Kite	+	+	+	Viñuela (1997) ^b
<i>Pandion haliaetus</i>	Osprey	+	○	+	Poole (1985)
<i>Parus caeruleus</i>	Blue Tit	○	ND	ND	Nilsson & Svensson (1993a)
<i>Parus major</i>	Great Tit	○	ND	ND	Ojanen <i>et al.</i> (1979)
<i>Parus major</i>	Great Tit	○	ND	ND	Järvinen & Pryn (1989)
<i>Parus major</i>	Great Tit	○	ND	ND	Nager & Zandt (1994)
<i>Parus major</i>	Great Tit	+	ND	ND	Hörak <i>et al.</i> (1995)
<i>Parus major</i>	Great Tit	○	ND	ND	Dufva (1996)
<i>Passerculus sandwichensis</i>	Savannah Sparrow	○	+	+	Wheelwright & Schultz (1994)
<i>Sturnus vulgaris</i>	European Starling	○	ND	ND	Smith <i>et al.</i> (1993)
<i>Tachycineta bicolor</i>	Tree Swallow	+	ND	ND	Wiggins (1990)
<i>Tachycineta bicolor</i>	Tree Swallow	○	+	+	Wheelwright & Schultz (1994)
<i>Tringa totanus</i>	Redshank	+	ND	+, ○ ^a	Thompson & Hale (1991) ^b
<i>Uria lomvia</i>	Thick-billed Murre	+	ND	+	Hipfner <i>et al.</i> (1997)

^a Some measure of timing of breeding other than laying date (i.e. date of clutch completion or date of hatching).

^b Effect of experience, not age.

variation in some studies (Thompson & Hale, 1991: 4–12%; Croxall *et al.*, 1992: 6%), but explained 34–44% in others (Poole, 1985; Hipfner *et al.*, 1997). In some species, egg size increases from young to intermediate ages and then decreases, the greatest changes being 12–13% (Sydeman & Emslie, 1992; Weimerskirch, 1992), whereas in others only a decline with age is evident (Reid, 1988; Potti, 1993). Many of these studies simply compared reproductive parameters between birds of different age classes, and so apparent changes in egg size could be artifacts of selection (i.e. if survival was related to egg size). However, a few studies have also observed a change in egg size within individuals (e.g. Reid, 1988; Robertson *et al.*, 1994).

(2) Female mass and size

Given that egg size varies little within individuals, what factors determine a female's egg size? An intuitively attractive hypothesis is that bigger females lay bigger eggs. Table 5 lists the coefficients of determination (i.e. the square of the correlation coefficients) for statistically significant relationships between egg size and female mass, size (i.e. linear measures such as tarsus, wing chord and culmen length) and "condition" (mass standardized by size using residuals as described by Bennett, 1987, or mass divided by size) in a variety of species. The coefficients of determination provide an estimate of the proportion of the variation in egg size explained by these traits (Sokal & Rohlf, 1995). Significant positive correlations between egg size and at least one trait were observed in 33 of 50 studies and species, and a significant negative correlation was observed in only two (Redmond, 1986; Simmons, 1994). Female mass, size or condition generally explain less than 20% of the variation in egg size and the coefficient of determination was greater than 0.3 in only five studies. Furthermore, these strong relationships are not always consistent within species or even within studies (e.g. see data from *Numenius americanus*, *Taeniopygia guttata* and *Vanellus vanellus* in Table 5; note that Hegyi & Sasvári (1998) found no relationship in *Vanellus vanellus* despite a substantial sample size, $N = 64$).

(3) Reproductive performance

Female age, mass and size provide weak indices of a female's ability to produce large eggs. Is a female's egg size related to her 'quality' as judged by other measures of reproductive performance such as clutch

size, timing of laying and ability to rear young? A survey of the literature (Table 6) indicates that egg size is generally unrelated to clutch size; no relationship was found in 40 of 63 studies and species examined. Fifteen studies found a positive relationship between clutch size and egg size, whereas only five found a negative relationship. Similarly, most studies found no relationship between egg size and laying date (40 out of 69 studies and species). In those that did find a statistically significant effect, a seasonal decline in egg size was observed frequently (20 studies), but only six studies found an increase in egg size throughout the season. Decreases in egg size with laying date may be due to younger birds laying smaller eggs later (e.g. Hipfner *et al.*, 1997; Viñuela, 1997), rather than an effect of laying date *per se*.

A number of studies have cross-fostered eggs (i.e. randomly switched eggs among pairs) and examined the subsequent growth and survival of the chicks. The primary goal of such studies has been to study the effects of egg size on offspring growth and survival, independent of parental quality. However, these experiments also provide an opportunity to examine the relationship between the size of egg that a female produces and the ability of the pair to raise offspring, independent of the quality of egg from which the offspring hatch. A number of such experimental studies have found no relationship between the egg mass of the foster parents and the subsequent growth and survival of the chicks they raise (Magrath, 1992*c*; Smith, Ohlsson & Wettermark, 1995; Amundsen *et al.*, 1996; Hipfner & Gaston, 1999; Hipfner & Gaston, 1999; Reed, Turner & Sotherland, 1999; Styrsky, Eckerle & Thompson, 1999; see also Meathrel *et al.*, 1993*a*, although this study only compared large-egg females rearing small eggs and vice versa, and did not include large-egg females rearing large eggs and small-egg females rearing small eggs). Amundsen (1995) found no relationship between chick mass and foster-parent egg size, although sample sizes were relatively small ($N = 17$ total) and females that attended chicks for a longer period of time tended to have laid larger eggs ($P = 0.07$; Amundsen, 1995).

A few experimental studies have found positive correlations between the size of egg a female laid and the pair's chick-rearing abilities, including effects on chick survival (Reid & Boersma, 1990; Bolton, 1991; Blomqvist, Johansson & Götmark, 1997; Risch & Rohwer, 2000) and chick size (e.g. wing length, tarsus length) but not mass (Amundsen & Stokland, 1990; Reid & Boersma, 1990; Risch & Rohwer, 2000). In the Herring Gull (*Larus*

Table 5. Coefficients of determination for relationships between egg size and female mass, size and condition (mass standardized by size); all relationships are positive except where noted (Symbols are as in Table 3.)

Latin name	Common name	Mass	Size	Condition	Reference
<i>Actitis macularia</i>	Spotted Sandpiper	○	ND	ND	Lank <i>et al.</i> (1985)
<i>Aix sponsa</i>	Wood Duck	0.41	ND	ND	Hepp <i>et al.</i> (1987)
<i>Anas acuta</i>	Northern Pintail	0.11	ND	ND	Duncan (1987)
<i>Anas acuta</i>	Northern Pintail	○ ^a	ND	ND	Flint & Grand (1996)
<i>Anas clypeata</i>	Northern Shoveler	ND	○	ND	Rohwer (1988)
<i>Anas discors</i>	Blue-winged Teal	ND	0.06	ND	Rohwer (1988)
<i>Anas platyrhynchos</i>	Mallard	ND	○	ND	Rhymer (1988)
<i>Aythya marila</i>	Greater Scaup	ND	○	ND	Flint & Grand (1999)
<i>Branta canadensis</i>	Canada Goose	ND	○	0.18	Leblanc (1989)
<i>Charadrius semipalmatus</i>	Semipalmated Plover	0.26	○ ^b	0.16	Nol <i>et al.</i> (1997)
<i>Charadrius wilsonia</i>	Wilson's Plover	ND	○	ND	Bergstrom (1988)
<i>Chen caerulescens</i> <i>caerulescens</i>	Lesser Snow Goose	ND	○	ND	Cooch <i>et al.</i> (1992)
<i>Circus ranivorus</i>	African Marsh Harrier	ND	— ^c	ND	Simmons (1994)
<i>Corvus corone cornix</i>	Hooded Crow	0.24	0.26	○	Loman (1984)
<i>Daption capense</i>	Cape Petrel	ND	0.11, ○	○	Weidinger (1996)
<i>Falco sparverius</i>	American Kestrel	ND	○	+ ^d	Wiebe & Bortolotti (1995)
<i>Ficedula albicollis</i>	Collared Flycatcher	0.25–0.32	○	0.29, ○	Cichon (1997)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.07	0.04	ND	Ojanen <i>et al.</i> (1979)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.05, ○	○	ND	Järvinen & Väisänen (1983)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.08, ○	○	ND	Järvinen & Väisänen (1984)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	ND	ND	0.06–0.17	Slagsvold & Lifjeld (1989)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.1	0.03	ND	Järvinen (1991)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	0.08	0.02, 0.10	0.07	Potti (1993)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	ND	ND	0.12 ^e , ○ ^b	Potti (1999)
<i>Haematopus palliatus</i>	American Oystercatcher	0.22	0.26	ND	Nol <i>et al.</i> (1984)
<i>Larus fuscus</i>	Lesser Black-backed Gull	ND	0.18, 0.20	ND	Bolton <i>et al.</i> (1993)
<i>Limosa limosa</i>	Black-tailed Godwit	○	ND	ND	Hegyí & Sasvári (1998)
<i>Numenius americanus</i>	Long-billed Curlew	0.07–0.59 ^f	ND	0.12, 0.25	Redmond (1986)
<i>Numenius phaeopus</i>	Whimbrel	○	○	ND	Grant (1991)
<i>Pandion haliaetus</i>	Osprey	○	ND	ND	Poole (1985)
<i>Parus caeruleus</i>	Blue Tit	○ ^b	○	ND	Nilsson & Svensson (1993a)
<i>Parus cinctus</i>	Siberian Tit	0.25	0.18	ND	Järvinen (1991)
<i>Parus major</i>	Great Tit	0.05	○	ND	Ojanen <i>et al.</i> (1979)
<i>Parus major</i>	Great Tit	0.16	○	ND	Järvinen & Pryn (1989)
<i>Parus major</i>	Great Tit	0.12	0.05	ND	Nager & Zandt (1994)
<i>Parus major</i>	Great Tit	ND	○	0.14	Hörak <i>et al.</i> (1995)
<i>Parus major</i>	Great Tit	0.12	0.14	○ ^b	Dufva (1996)
<i>Puffinus tenuirostris</i>	Short-tailed Shearwater	ND	ND	○	Meathrel <i>et al.</i> (1993a)
<i>Stercorarius parasiticus</i>	Arctic Skua	ND	○	0.08	Phillips & Furness (1998)
<i>Sturnus vulgaris</i>	European Starling	○	ND	ND	Meijer (1992)
<i>Taeniopygia guttata</i>	Zebra Finch	0.43	ND	ND	Haywood & Perrins (1992)

Table 5. (cont.)

Latin name	Common name	Mass	Size	Condition	Reference
<i>Sturnus vulgaris</i>	European Starling	ND	○	0.09	Smith <i>et al.</i> (1993)
<i>Sturnus vulgaris</i>	European Starling	○	○	ND	Christians & Williams (2001b)
<i>Tachycineta bicolor</i>	Tree Swallow	0.07	○	0.05	Wiggins (1990)
<i>Taeniopygia guttata</i>	Zebra Finch	ND	○	0.08	Williams (1996a)
<i>Tringa totanus</i>	Redshank	0.06	0.06, 0.08	ND	Thompson & Hale (1991)
<i>Tyrannus tyrannus</i>	Eastern Kingbird	○	○	ND	Murphy (1986a)
<i>Vanellus vanellus</i>	Lapwing	0.35	○	0.31	Galbraith (1988)
<i>Vanellus vanellus</i>	Lapwing	0.29	0.15	0.21	Blomqvist & Johansson (1995)
<i>Vanellus vanellus</i>	Lapwing	○	ND	ND	Hegyí & Sasvári (1998)

^a Mass and size combined using principal component analysis.

^b Marginally non-significant ($0.05 < P < 0.1$).

^c No data on strength of relationship, but significantly negative.

^d Females whose eggs were above average size were in better condition.

^e Condition of females at 13 days of age.

^f Relationship was significantly positive in two years ($r^2 = 0.18, 0.59$) and significantly negative in a third ($r^2 = 0.07$).

argentatus), the rate of egg predation was related to the egg size of the foster parents, suggesting that egg size may be correlated with the quality of parental care during incubation (Brouwer & Spaans, 1994).

In summary, egg size is not consistently correlated with other aspects of reproductive performance such as clutch size, timing of laying, and ability to rear chicks, although positive relationships are observed in a few species. A comprehensive discussion of trade-offs between components of reproductive effort is beyond the scope of this review, but it should be noted that a lack of negative relationships between egg size and other reproductive parameters does not necessarily indicate the absence of trade-offs [Noordwijk & Jong, 1986; see Christians (2000) for an application of Noordwijk and Jong's (1986) model to egg size trade-offs]. Individuals may differ in the amount of resources they are able to invest in reproduction, e.g. high-quality females may be able to produce more eggs and larger eggs than low-quality females. Trade-offs can be observed when comparing females with a similar investment in eggs (e.g. total clutch mass); for instance, the finding that clutches of N large eggs weigh more than clutches of $N+1$ small eggs (Högstedt, 1981; Bancroft, 1984; Arcese & Smith, 1988; Rohwer & Eisenhauer, 1989; Flint & Sedinger, 1992; Cooke, Rockwell & Lank, 1995; Wiebe & Bortolotti, 1995; Flint & Grand, 1996) indicates that some females could increase

clutch size by laying smaller eggs. Alternatively, experimental manipulation can reveal trade-offs between clutch size and egg quality (Nager, Monaghan & Houston, 2000).

(4) Other aspects of female phenotype

Three studies have attempted to manipulate female condition experimentally by clipping flight feathers and have measured the size of eggs laid subsequently. Generally, handicapping reduced clutch size but had little (2–6%) or no effect on egg size (Slagsvold & Lifjeld, 1988, 1990; Winkler & Allen, 1995), even though there was some evidence that feather clipping reduced female condition as measured by breast-muscle thickness (Winkler & Allen, 1995). Thus, handicapping did not appear to manipulate the characteristics of the female responsible for determining egg size. Dufva (1996) investigated general measures of female health and found a significant positive relationship between egg size and blood levels of haemoglobin ($r^2 = 0.18$), but not haematocrit, in Great Tits. Furthermore, egg size was approximately 11% lower in females infected with *Trypanosoma* spp. than in females without this parasite (Dufva, 1996).

Houston, Jones & Sibly (1983) related female body composition to the macronutrient composition of the oviducal egg in Lesser Black-backed Gulls

Table 6. Correlations between egg size and other measures of primary reproductive performance (clutch size and laying date)

(~ = significant variation between clutches of different size but no linear pattern (clutch size) or a non-linear relationship (laying date). Other symbols are as in Table 3.)

Latin name	Common name	Clutch size	Laying date	Reference
<i>Acrocephalus scirpaceus</i>	Reed Warbler	ND	○	Øien <i>et al.</i> (1996)
<i>Aegolius funereus</i>	Tengmalm's Owl	○	○	Hakkarainen & Korpimäki (1994)
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	ND	○	Muma & Ankney (1987)
<i>Anas acuta</i>	Northern Pintail	○	○	Duncan (1987)
<i>Anas acuta</i>	Northern Pintail	○	○	Flint & Grand (1996)
<i>Anas clypeata</i>	Northern Shoveler	○	ND	Rohwer (1988)
<i>Anas discors</i>	Blue-winged Teal	○	ND	Rohwer (1988)
<i>Anas platyrhynchos</i>	Mallard	+	ND	Batt & Prince (1979)
<i>Anas platyrhynchos</i>	Mallard	○	○	Hill (1984)
<i>Anas platyrhynchos</i>	Mallard	○	ND	Pehrsson (1991)
<i>Aythya fuligula</i>	Tufted Duck	○	—	Hill (1984)
<i>Aythya marila</i>	Greater Scaup	○	ND	Flint & Grand (1999)
<i>Branta bernicla nigricans</i>	Brant	+	○	Rohwer & Eisenhauer (1989)
<i>Branta bernicla nigricans</i>	Black Brant	+	—	Flint & Sedinger (1992)
<i>Branta canadensis</i>	Canada Goose	○	○	Leblanc (1989)
<i>Branta canadensis minima</i>	Canada Goose	○	○	Rohwer & Eisenhauer (1989)
<i>Calidris mauri</i>	Western Sandpiper	+	—	Sandercock <i>et al.</i> (1999)
<i>Calidris pusilla</i>	Semipalmated Sandpiper	+	+, ○	Sandercock <i>et al.</i> (1999)
<i>Charadrius morinellus</i>	Dotterel	ND	○	Byrkjedal & Kålås (1985)
<i>Chen caerulescens caerulescens</i>	Lesser Snow Goose	○	ND	Lessells <i>et al.</i> (1989)
<i>Chen caerulescens caerulescens</i>	Lesser Snow Goose	—	ND	Cooch <i>et al.</i> (1992)
<i>Chen caerulescens caerulescens</i>	Lesser Snow Goose	○	ND	Williams, Lank & Cooke (1993)
<i>Chen caerulescens caerulescens</i>	Lesser Snow Goose	ND	○	Cooke <i>et al.</i> (1995)
<i>Chen canagica</i>	Emperor Goose	~	○	Rohwer & Eisenhauer (1989)
<i>Circus ranivorus</i>	African Marsh Harrier	○	○	Simmons (1994)
<i>Corvus monedula</i>	Jackdaw	○	—	Heeb (1994)
<i>Cygnus buccinator</i>	Trumpeter Swan	○	ND	Rohwer & Eisenhauer (1989)
<i>Cygnus olor</i>	Mute Swan	○	○	Birkhead <i>et al.</i> (1983)
<i>Cygnus olor</i>	Mute Swan	ND	— ^a	Scott & Birkhead (1983)
<i>Daption capense</i>	Cape Petrel	ND	—	Weidinger (1996)
<i>Egretta garzetta</i>	Little Egret	ND	—	Ashkenazi & Yom-Tov (1997)
<i>Eudyptes chrysolophus</i>	Rockhopper Penguin	ND	○	St. Clair (1996)
<i>Eudyptes chrysolophus</i>	Macaroni Penguin	ND	—, ○	Williams & Croxall (1991)
<i>Falco sparverius</i>	American Kestrel	~	—, ○	Wiebe & Bortolotti (1995)
<i>Ficedula albicollis</i>	Collared Flycatcher	—, ○	—, ○	Cichon (1997)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	○	○	Järvinen & Väisänen (1983)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	+, ○	○	Järvinen & Väisänen (1984)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	○	○	Järvinen (1991)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	+, —, ○	○	Potti (1993)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	ND	○	Sanz & Moreno (1995)
<i>Ficedula hypoleuca</i>	Pied Flycatcher	+, —, ○	ND	Järvinen (1996)
<i>Fulica americana</i>	American Coot	+	—, ○	Arnold (1994)
<i>Larus occidentalis</i>	Western Gull	ND	+	Sydeman & Emslie (1992)
<i>Lonchura striata</i>	Bengalese Finch	~	ND	Coleman & Whittall (1990)

Table 6. (cont.)

Latin name	Common name	Clutch size	Laying date	Reference
<i>Haematopus palliatus</i>	American Oystercatcher	○	–, ○	Nol <i>et al.</i> (1984)
<i>Lagopus lagopus scoticus</i>	Red Grouse	○	ND	Moss <i>et al.</i> (1981)
<i>Larus argentatus</i>	Herring Gull	+	ND	Hébert & Barclay (1988)
<i>Milvus migrans</i>	Black Kite	+	–	Viñuela (1997)
<i>Molothrus ater</i>	Brown-headed Cowbird	ND	~	Strausberger (1998)
<i>Numenius americanus</i>	Long-billed Curlew	ND	–, ○	Redmond (1986)
<i>Nycticorax nycticorax</i>	Black-crowned Night-Heron	ND	–	Ashkenazi & Yom-Tov (1997)
<i>Pagodroma nivea</i>	Snow Petrel	ND	○ ^a	Amundsen (1995)
<i>Pandion haliaetus</i>	Osprey	○	○	Poole (1985)
<i>Parus caeruleus</i>	Blue Tit	ND	○	Nilsson & Svensson (1993 <i>b</i>)
<i>Parus caeruleus</i>	Blue Tit	○	○	Nilsson & Svensson (1993 <i>a</i>)
<i>Parus caeruleus</i>	Blue Tit	○ ^b	○	Nilsson (2000)
<i>Parus cinctus</i>	Siberian Tit	○	○	Järvinen (1991)
<i>Parus major</i>	Great Tit	○	○	Järvinen & Pryn (1989)
<i>Parus major</i>	Great Tit	○	○	Järvinen (1991)
<i>Parus major</i>	Great Tit	ND	○	Nager & Zandt (1994)
<i>Parus major</i>	Great Tit	○	○	Dufva (1996)
<i>Parus major</i>	Great Tit	ND	○	Nager <i>et al.</i> (1997)
<i>Phoenicurus phoenicurus</i>	Redstart	○	○	Järvinen (1991)
<i>Pluvialis apricaria</i>	Golden Plover	ND	–	Byrkjedal & Kålås (1985)
<i>Puffinus tenuirostris</i>	Short-tailed Shearwater	ND	+	Meathrel <i>et al.</i> (1993 <i>b</i>)
<i>Pyrrhula pyrrhula</i>	Bullfinch	+	ND	Greig-Smith <i>et al.</i> (1988)
<i>Quiscalus major</i>	Boat-tailed Grackle	–	~	Bancroft (1984)
<i>Rissa tridactyla</i>	Kittiwake	ND	–	Runde & Barrett (1981)
<i>Sayornis phoebe</i>	Eastern Phoebe	ND	+, ○	Murphy (1994)
<i>Sialia sialis</i>	Eastern Bluebird	○	○	Pinkowski (1979)
<i>Somateria fischeri</i>	Spectacled Eider	○	ND	Rohwer & Eisenhauer (1989)
<i>Somateria mollissima sedentaria</i>	Common Eider	○	○	Robertson (1995)
<i>Somateria mollissima</i>	Common Eider	○	ND	Erikstad <i>et al.</i> (1998)
<i>Sterna hirundo</i>	Common Tern	ND	○	Moore, Williams & Morris (2000)
<i>Sturnus vulgaris</i>	European Starling	~	ND	Greig-Smith <i>et al.</i> (1988)
<i>Sturnus vulgaris</i>	European Starling	○	○	Meijer (1992)
<i>Sturnus vulgaris</i>	European Starling	+, ○	○	Smith <i>et al.</i> (1993)
<i>Tachycineta bicolor</i>	Tree Swallow	○	ND	Zach (1982)
<i>Tachycineta bicolor</i>	Tree Swallow	~	ND	Wiggins (1990)
<i>Taeniopygia guttata</i>	Zebra Finch	○	ND	Williams (1996 <i>a</i>)
<i>Troglodytes aedon</i>	House Wren	ND	+	Styrsky <i>et al.</i> (1999)
<i>Turdus merula</i>	Blackbird	+	ND	Greig-Smith <i>et al.</i> (1988)
<i>Turdus merula</i>	Blackbird	○	+	Magrath (1992 <i>b</i>)
<i>Turdus philomelos</i>	Song Thrush	○	ND	Greig-Smith <i>et al.</i> (1988)
<i>Tyrannus tyrannus</i>	Eastern Kingbird	○	○	Murphy (1983)
<i>Tyrannus tyrannus</i>	Eastern Kingbird	ND	~	Murphy (1986 <i>b</i>)
<i>Uria lomvia</i>	Thick-billed Murre	ND	–	Birkhead & Nettleship (1982)
<i>Uria lomvia</i>	Thick-billed Murre	ND	–, ○	Hipfner <i>et al.</i> (1997)
<i>Vanellus vanellus</i>	Lapwing	+, ○	○	Galbraith (1988)
<i>Vanellus vanellus</i>	Northern Lapwing	ND	–	Grønstøl (1997)
<i>Xanthocephalus</i>	Yellow-headed	○	○	Arnold (1992)
<i>xanthocephalus</i>	Blackbird			

^a Date of hatching, not laying date.^b Marginally non-significant effect ($0.05 < P < 0.1$).

(*Larus fuscus*); protein condition (the lean dry mass of the pectoral muscles divided by the cube of the flight muscle cord) was significantly correlated with various egg components whereas body lipid content was not. The relationship between egg size and a non-destructive measure of the protein condition (derived from the profile of the flight muscles over the keel) was marginally non-significant in this species ($r^2 = 0.12$; $P = 0.06$; Bolton, Monaghan & Houston, 1993). Protein condition (as defined by Houston *et al.*, 1983) was also positively related to egg size in Eastern Kingbirds (*Tyrannus tyrannus*), and the strength of this relationship ($r^2 = 0.21$; Murphy, 1986*b*) was relatively strong compared to most correlations between egg size and female mass (Table 5). These relationships may reflect the importance of the flight muscles as endogenous stores of protein and/or specific amino acids (Houston *et al.*, 1995*a*; Houston, Donnan & Jones, 1995*b*). However, no relationship was found between egg size and pectoral muscle mass in the European Starling (Christians & Williams, 2001*b*). Other measures of body composition such as the masses of the organs that make up the “metabolic machinery” (i.e. heart, lungs, kidneys, liver and digestive organs) also failed to explain egg-size variation in this study (Christians & Williams, 2001*b*). However, oviduct mass explained approximately 21% of the variation in albumen protein content (Christians & Williams, 2001*b*), suggesting that the physiological systems specific to egg production deserve further attention. For example, the rate of protein uptake into the ovarian follicles also explained a relatively large proportion ($r^2 = 0.24$ – 0.50) of the variation in yolk mass in Zebra Finches (*Taeniopygia guttata*; Christians & Williams, 2001*a*).

A few studies have attempted to use endocrinological techniques to manipulate the reproductive performance of breeding females to investigate the physiological basis of variation in egg size and number and to elucidate trade-offs between traits. Remarkably, exogenous estradiol failed to increase egg size in both European Starlings (Christians & Williams, 1999) and Zebra Finches (Williams, 1999), despite its roles in yolk precursor and albumen synthesis. Treatment with follicle-stimulating hormone (FSH), which is believed to stimulate ovarian follicular growth, actually reduced egg mass by approximately 10% in Zebra Finches (Christians and Williams, in press); exogenous hormone may have reduced endogenous FSH secretion *via* negative feedback in this experiment. The anti-estrogen tamoxifen also reduced egg size (15%), perhaps by

reducing the plasma concentration of yolk precursors below the level required to maintain normal yolk formation (Williams, 2000). No endocrinological technique has yet increased egg size in birds, although further studies with combinations of hormones may prove more successful (e.g. estradiol and FSH; Follett, Nicholls & Redshaw, 1968).

V. PROXIMATE CONSIDERATIONS

(1) What determines egg size?

Bernardo (1996) pointed out that a better understanding of propagule-size variation would require a more thorough consideration of maternal phenotype. Above, I have shown that a number of female characters that are commonly measured (i.e. female age, mass and size) generally explain little of the variation in egg size in birds (although there are a few exceptions). Similarly, supplemental food increased egg size in only one-third of the studies examined, and this effect was always small (< 15%) compared to the large variation between females. Furthermore, a large amount of variation in egg size is maintained on high-quality diets (Williams, 1996*b*). Thus, variation in the nutritional state of the female does not appear to be a general cause of egg-size variation.

Although each of the factors considered above explains at most a small proportion of the variation in egg size, it is possible that all of these factors together explain a substantial amount of the variation between females. Future work should address this possibility by analysing multiple traits simultaneously (e.g. using multiple regression) to determine the proportion of variation they explain collectively, rather than the pairwise analyses that are currently common (Bernardo, 1996). However, the factors discussed above are not completely independent (e.g. foraging skills or territory quality may improve with age, which could affect nutritional status and mass), and therefore it seems unlikely that the cumulative effect of these factors will equal the sum of their individual effects. Clearly, more work needs to be directed at the proximate causes of egg-size variation. Variation in egg size is likely to be explained, at least in part, by variation in the physiological systems involved in egg production (e.g. the production of yolk precursors by the liver and their uptake at the ovary), and yet this has received relatively little attention. Such work would enable greater physiological realism to be

incorporated into models of egg-size evolution (Bernardo, 1996). Furthermore, with a greater understanding of proximate mechanisms, manipulation of the endocrine systems involved in egg production may offer the potential to manipulate egg size experimentally and thus investigate the costs of producing larger eggs.

(2) Lack of plasticity within females

Egg size is relatively inflexible within individual female birds, despite large variation in this trait between individuals. Some species, notably the crested penguins, regularly show dramatic variation in egg size within clutches, and so it is not clear why individuals of other species do not alter the size of eggs they produce between clutches. Flexibility in egg size would be advantageous if females could increase egg size when environmental conditions favoured offspring from larger eggs, but decrease egg mass (and so increase the number of eggs or reduce reproductive expenditure) at other times, as in other taxa (e.g. Kaplan, 1998; Fox & Czesak, 2000; see below). The ability to adjust egg size between clutches would not be expected to be costly since the physiological mechanisms (e.g. yolk precursor production) and structures (i.e. ovary, oviduct) involved in egg formation themselves show great plasticity (Williams, 1998). Since reproductive physiology is upregulated so extensively, it is not clear why individuals could not vary the absolute extent of this upregulation in response to environmental conditions.

VI. ULTIMATE CONSIDERATIONS

(1) Consequences for offspring fitness

Williams (1994) reviewed the consequences of intraspecific variation in egg size for offspring fitness and concluded “there is little unequivocal evidence to date of a positive relationship between egg size and offspring fitness in birds”. However, relationships between chick growth and survival early in the chick-rearing period were more consistent, suggesting that the primary benefit of larger eggs might be to increase the chances of survival in the first few days after hatching (Williams, 1994). This review also pointed out that few studies had separated the effect of egg size *per se* from the effect of parental quality (Williams, 1994). Since then, a number of cross-fostering experiments have been

performed to disentangle these factors. In general, these studies confirm earlier work: egg size is often correlated with offspring mass and size within the first week after hatching (Amundsen, 1995; Smith *et al.*, 1995; Amundsen *et al.*, 1996; Reed *et al.*, 1999; Styrsky *et al.*, 1999). In some cases, this effect is not sustained throughout the chick-rearing period (Smith *et al.*, 1995; Amundsen *et al.*, 1996; Reed *et al.*, 1999; Styrsky *et al.*, 1999; Risch & Rohwer, 2000), whereas other traits and studies show more lasting effects (up to two weeks; Amundsen *et al.*, 1996; Erikstad, Tveraa & Bustnes, 1998; Hipfner & Gaston, 1999; Styrsky *et al.*, 1999; Hipfner, 2000; Hipfner, Gaston & Storey, 2001). The evidence for a relationship between egg size and offspring survival during the chick-rearing period is also equivocal (no effect: Smith *et al.*, 1995; Amundsen *et al.*, 1996; Styrsky *et al.*, 1999; positive effect: Blomqvist *et al.*, 1997; Risch & Rohwer, 2000), and there is little data regarding long-term consequences of egg size on offspring fitness (e.g. survival until breeding, Cooke *et al.*, 1995).

Overall, the results are consistent with the idea that larger eggs may only confer an advantage in harsh, low-quality environments (Smith *et al.*, 1995; Fox & Czesak, 2000). In good conditions, the extended parental care provided in many avian species might compensate for small eggs and enable small hatchlings to “catch-up” with offspring from larger eggs. However, further work is necessary to test this hypothesis explicitly (e.g. Einum & Fleming, 1999; Hipfner *et al.*, 2001).

(2) Consequences for maternal fitness

Traits closely linked to fitness generally have low heritabilities (Gustafsson, 1986; Mousseau & Roff, 1987). The high heritability of egg size, together with the equivocal evidence regarding the relationship between egg size and offspring fitness (see above) could be interpreted to mean that egg-size variation does not have important consequences for maternal fitness. While the existing evidence cannot rule out this possibility, this scenario would raise the question: why don't all females simply produce the smallest viable egg? Moreover, the relationship between a trait's heritability and its importance to fitness is complex (Price & Schluter, 1991; Merila & Sheldon, 2000), particularly since heritability incorporates a number of parameters. The narrow-sense heritability consists of the additive genetic variance divided by the phenotypic variance, the latter comprising both environmental and non-additive

genetic variance (Falconer & Mackay, 1996). Therefore, the high heritability of egg size could be due to relatively high additive genetic variance or relatively low environmental and non-additive genetic effects compared to other life-history traits. Furthermore, estimates of the heritability of egg size could be confounded with maternal effects to a greater extent than other traits (e.g. Potti, 1999). Even if the additive genetic variance for egg size is high, this variation could be maintained by temporally and/or spatially variable selection on egg size (Cooke *et al.*, 1995), antagonistic pleiotropy (i.e. genetic trade-offs between egg size and other traits; Cooke *et al.*, 1995) or frequency-dependent selection (Sinervo, Svensson & Comendant, 2000). Further work is needed to dissect the quantitative genetics of egg size to determine why the heritability of this trait is relatively high compared to that of clutch size and laying date (i.e. the relative roles of additive genetic, non-additive genetic and environmental variance and maternal effects). In addition, a better understanding of the mechanistic basis of egg-size variation will provide clues regarding trade-offs involving egg size, and whether egg size would be expected to be under relatively tight additive genetic control (and subject to less environmental variation *sensu* Price & Schluter, 1991).

VII. PATTERNS OF EGG-SIZE VARIATION IN OTHER TAXONOMIC GROUPS

(1) Other oviparous vertebrates

Egg size varies greatly within avian populations but little within individual females. Is this phenomenon unique to birds, or is it also true in other taxonomic groups? In other oviparous vertebrates, intraspecific variation in egg size is typically as great or greater than that observed in birds (e.g. *fish*: Heath & Blouw, 1998; Keckeis *et al.*, 2000; Teather, Boswell & Gray, 2000; *amphibians*: Crump, 1984; Kaplan, 1998; Cunnington & Brooks, 2000; *snakes*: Ford & Seigel, 1989; Seigel & Ford, 1991; *turtles*: Bjorndal & Carr, 1989; Iverson & Smith, 1993; Rowe, 1995; Iverson & Moler, 1997; Tucker & Janzen, 1998; Tucker, Paukstis & Janzen, 1998; *lizards*: Castilla & Bauwens, 2000; Ji & Brana, 2000; Shanbhag, Radder & Saidapur, 2000). Unfortunately, many studies of reptiles, amphibians and fish do not describe the extent of egg-size variation within females. Intraclutch coefficients of variation are sometimes reported, but it would be useful for future

studies to partition the variance into within- and between-clutch components to show explicitly whether the variation in egg size within females is large relative to that among females, and to facilitate comparison between studies. In most cases where the partitioning of variance is described, a large proportion is due to differences between clutches (i.e. females) in fish (Marsh, 1984: >50%; Benoit & Pepin, 1999: 83%; Morita *et al.*, 1999: 62%; Berg *et al.*, 2001: 95–97%; but see Teather *et al.* 2000: 30%) and amphibians (Beachy, 1993: 47–73%; Cunnington & Brooks, 2000: 70%). In reptiles, statistically significant variation in egg size between clutches produced by different females has been reported (Sinervo, 1990; Roosenburg & Kelley, 1996; Marco & Perez-Mellado, 1998; Tucker & Janzen, 1998; Steyermark & Spotila, 2001). Thus, this pattern of variation appears similar to that in birds. However, in a more extensive review of the patterns of variation in amphibians Kaplan (1998) concluded: “the intraclutch egg size variation of an individual can itself be a small to a substantial part of the overall egg size variation observed in a population” (Kaplan, 1998; see also Crump, 1984).

Another important level of variation is that which occurs between clutches produced by the same female, but there are few studies of non-avian oviparous vertebrates that describe this variation. The repeatability of egg size ranged from 0.14 to 0.27 in the frog *Bombina orientalis* (Kaplan, 1998) and 0.12 to 0.35 in the Atlantic Cod (*Gadus morhua*; Chambers & Waiwood, 1996; Kjesbu *et al.*, 1996). The relationship between egg size at first spawning and that at a subsequent spawning was significant ($r^2 = 0.13$) in the Brown Trout (*Salmo trutta*; Jonsson & Jonsson, 1999). Two studies of lizards measured multiple clutches per female and did not detect significant differences in egg size between females; the repeatability was not quantified (Castilla & Bauwens, 2000; Ji & Brana, 2000). However, significant differences in mean offspring size between females producing young in multiple breeding attempts were reported in three studies of viviparous snakes (Madsen & Shine, 1992; Luiselli, Capula & Shine, 1996; Bronikowski & Arnold, 1999). Bronikowski & Arnold (1999) estimated the repeatability of average offspring mass to be 0.43 and higher than that for litter size (0.20). Thus, although there are few studies on which to base a comparison, the consistency of egg size within individual females is not as striking in other taxa as it is in birds (see also Roosenburg & Dunham, 1997).

There are even fewer studies of the heritability of

Table 7. Relationships between egg size and female mass or size in oviparous vertebrates (number of studies that observed significant (SIG) or non-significant (NS) relationships). If both a significant and non-significant relationship were observed within a study (e.g. due to variation between years or populations), both types of relationship were counted (All significant relationships are positive except where noted.)

Taxonomic group	Female mass and egg size		Female size and egg size		References
	SIG	NS	SIG	NS	
Oviparous fish	3	3	4	7	Chambers & Waiwood (1996); Kjesbu <i>et al.</i> (1996); Lobón-Cervía <i>et al.</i> (1996); Tomasini <i>et al.</i> (1996); Morita & Takashima (1998); Ali & Wootton (1999a); Hendry <i>et al.</i> (1999); Jonsson & Jonsson (1999); Morita <i>et al.</i> (1999); Keckeis <i>et al.</i> (2000); Pampoulie <i>et al.</i> (2000); Tamate & Maekawa (2000); Teather <i>et al.</i> (2000)
Amphibians	6 ^a	6	2	1	Kuramoto (1978); Berven (1982, 1988); Williamson & Bull (1995)
Oviparous snakes	0	0	1	0	Seigel & Ford (1991)
Turtles	3	4	7	4	Bjorndal & Carr (1989); Congdon & Sels (1991); Iverson & Smith (1993); Rowe (1994, 1995); Iverson & Moler (1997); Roosenburg & Dunham (1997); Tucker <i>et al.</i> (1998); Wallis <i>et al.</i> (1999); Clark <i>et al.</i> (2001); Steyermark & Spotila (2001)
Lizards	6	2	6	10	Ferguson <i>et al.</i> (1990); Sinervo (1990); Ferguson & Talent (1993); Forsman & Shine (1995); Michaud & Echernacht (1995); Doughty (1996, 1997); Doughty & Thompson (1998); Marco & Perez-Mellado (1998); Abell (1999); Castilla & Bauwens (2000); Ji & Brana (2000); Ramirez-Bautista <i>et al.</i> (2000); Shanbhag <i>et al.</i> (2000)
Birds	22	12	14	24	See Table 5

^a One of these relationships is negative.

egg size in non-avian oviparous vertebrates; Sinervo & Doughty (1996) provide the only estimate from a natural, free-ranging population. The heritability of egg size in the Side-blotched Lizard (*Uta stansburiana*) was 0.61 whereas that of laying date was 1.0, although the latter estimate was confounded with maternal effects to a greater extent (Sinervo & Doughty, 1996). In a preliminary study of the heritabilities of egg size and number in a captive population of this lizard, the estimate for egg size (0.24) was lower than that for clutch size (1.0; Ferguson, Snell & Landwer, 1990). In captive rainbow trout (*Oncorhynchus mykiss*), one study estimated the heritabilities of egg size and number to be 0.52–0.60 and 0.55, respectively (Su, Liljedahl & Gall, 1997), whereas another estimated the heritability of both of these traits to be 0.2 (Gall, 1975). While heritability estimates differ between studies and species, it is interesting that egg size does not

stand out as more heritable than clutch size and laying date, as is the case in birds.

Of the potential causes of egg-size variation, female mass and size have received the most attention. Ford & Seigel (1989) found that egg size was positively related to female size in six of 12 (50%) species of turtles, seven of 16 (44%) species of oviparous lizard and one oviparous snake. In oviparous fish, positive correlations are slightly more common, accounting for 69% (67/97) of the relationships summarised by Heath & Blouw (1998); two relationships were significantly negative. I have updated these reviews (Table 7), distinguishing between female mass and linear measures of female size (e.g. snout-vent length, carapace length). In general, positive relationships between egg size and female mass or size are roughly as frequent in other oviparous vertebrates as they are in birds (Table 7). However, where relationships are significant, they

are often much stronger than those observed in avian species; coefficients of determination commonly exceed 0.3 (*cf.* ornithological studies, see above) and are sometimes much higher (e.g. *fish*: Kjesbu *et al.*, 1996; Heath & Blouw, 1998; Morita & Takashima, 1998; Hendry, Berg & Quinn, 1999; Jonsson & Jonsson, 1999; Morita *et al.*, 1999; Keckeis *et al.*, 2000; Tamate & Maekawa, 2000; *amphibians*: Kuramoto, 1978; *turtles*: Iverson & Smith, 1993; Rowe, 1994, 1995; Wallis, Henen & Nagy, 1999; Clark, Ewert & Nelson, 2001; *lizards*: Michaud & Echternacht, 1995; Doughty, 1996, 1997). In turtles, the size of physical apertures through which eggs must pass often limits egg size (Congdon & Gibbons, 1987; Iverson & Smith, 1993; Clark *et al.*, 2001), which may explain why female size is correlated with egg size more often than is female mass (Table 7). Physical limitations may also occur in some lizard species (Michaud & Echternacht, 1995). Female size and/or mass is also believed to play an important role in determining egg size in fish, and the variation between females is often attributed to differences to growth history (Morita *et al.*, 1999; Berg *et al.*, 2001; see also references in Elliott & Hurley, 1998). Since many species of oviparous vertebrates exhibit indeterminate growth, differences in female size may be due to age. Where age has been examined, it has been found to have a large effect on egg size in a variety of taxa (*fish*: Keckeis *et al.*, 2000; *frog*: Berven, 1988; *turtle*: Iverson & Smith, 1993).

Despite the importance of female size and mass in determining egg size, high-quality diets increase clutch size without affecting egg size in fish (Wootton, 1973; Ali & Wootton, 1999*b*) and snakes (Seigel & Ford, 1991), as is often the case in birds. However, in the frog *Bombina orientalis* the effect of food supply on egg size was substantial compared to the amount of variation between females (Kaplan, 1987).

In summary, the magnitude of egg-size variation within populations of various oviparous vertebrates is often as great or greater than that observed within avian populations. There are few data on the repeatability of egg size between different clutches produced by the same female, but the available evidence suggests that it is lower than in birds. Furthermore, egg-size plasticity is relatively well documented in amphibians (Kaplan, 1998). A further contrast with the patterns observed in avian species is that much of the variation in egg size is often explained by female mass or size, particularly in fish and turtles. The consequences of egg size for offspring fitness also tend to be more apparent in

oviparous vertebrates (*fish*: Heath & Blouw, 1998; Einum & Fleming, 1999, 2000; *amphibians*: Kaplan, 1998; *lizards*: Sinervo *et al.*, 1992), probably because there is less parental care in these species.

(2) Arthropods

Fox & Czesak (2000) recently reviewed patterns of progeny-size variation in arthropods and found some of the patterns to be similar to those observed in avian populations: egg size often changes with age (increasing in 11 species, decreasing in 28 and variable or not changing in 13), and there tends to be a positive relationship between egg size and female size (42 out of 79, or 53%, of the correlations examined were significantly positive), although this relationship is generally weak (Fox & Czesak, 2000). However, in terms of variation within females their general impression was that "For many arthropods, the variation in size among progeny produced by a single female may be as large as or larger than the variation among females within a population. Much of this variation is an effect of maternal age ... but in many arthropods there is substantial variation in egg size within individual clutches of eggs" (Fox & Czesak, 2000: p. 355).

Fox & Czesak (2000) also discuss numerous examples of plasticity in egg size in response to food, competition, predation risk and temperature, although the magnitude of the change in egg size in response to such factors is not described.

VIII. CONCLUSIONS

1. Egg size shows a great deal of variation within avian populations but varies little within individuals. Due to the paucity of data from other taxonomic groups, it is unclear whether this pattern is unique to birds. However, the available evidence suggests that in other oviparous vertebrates and arthropods egg size may be more flexible within individuals.

2. The causes of the differences between individual female birds remain largely unknown. Few factors appear to have strong effects on egg size in avian species, even though there is probably a bias in the literature towards reporting significant relationships.

3. As a result of our lack of understanding of the proximate causes of egg-size variation, the evolutionary significance of this variation also remains unclear. For instance, while variation could be due to differences in optimum egg size between indi-

viduals, we have no clues as to what aspects of female phenotype would determine this optimum, or why optima would vary greatly between females but not between breeding attempts within a female.

4. Further work on the physiological basis of intraspecific egg-size variation will therefore address not only mechanistic questions regarding how egg size is determined, but also ultimate questions regarding how and why intraspecific variation in life-history traits persists.

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