

Why don't all siblicidal eagles lay insurance eggs? The egg quality hypothesis

Robert E. Simmons

Department of Zoology, Uppsala University, Villavägen 9, S 752–36, Uppsala, Sweden

Several species of birds lay second eggs that are eliminated by the siblicidal behavior of the first-hatched chick. A widely accepted explanation for the occurrence of these second eggs is insurance against complete nest failure. However, if insurance is seen as an important breeding strategy for two-egg ($c/2$) layers, the question arises why single-egg species do not lay insurance eggs. The insurance-egg hypothesis predicts that extra eggs should occur where hatch failure is not trivial, which may be particularly prevalent in dense populations. Neither prediction was supported for siblicidal Wahlberg's eagles *Aquila wahlbergi*. Neither could food constraints or allometric relationships explain the small one-egg clutch ($c/1$) of this species. Instead, clutch size was experimentally shown to be related to optimal brood size: parents given two young were unable to rear them, and subsequent breeding opportunities were significantly curtailed. Since clutch and brood size are similarly related in $c/2$ eagles, insurance may be an exaptation of the second egg. One-egg species, however, appear to trade second (insurance) eggs for large, high-quality eggs, which enhance hatchability and chick viability. This was borne out by comparison of the world's $c/1$ eagles, which lay significantly ($p < .01$) larger eggs than $c/2$ eagles of the same body size. Large Wahlberg's eagle eggs also showed significantly ($p = .02$) greater hatchability than small eggs, and other studies show enhanced survival/quality for chicks from large eggs. Because only longer-lived eagles traded two eggs for single, large eggs, this is consistent with the idea of selection for offspring quality in long-lived species. I conclude that higher hatchability of single, large eggs decreases the need for an insurance egg and simultaneously enhances viability of resultant chicks in siblicidal eagles and possibly sulids. *Key words:* *Aquila wahlbergi*, brood manipulations, egg quality, insurance, siblicide, Wahlberg's eagle. [*Behav Ecol* 8:544–550 (1997)]

Siblicidal eagles (Accipitridae) that lay two-egg clutches ($c/2$), yet rear only one young, pose a fascinating puzzle: why are two eggs laid if both are never reared? Dorward (1962) and Meyburg (1974) postulated that the second (B) egg of such species helps to insure the success of the breeding attempt (reviewed by Mock et al., 1990). That is, egg B may hatch and produce a viable offspring, if and when the first egg does not hatch or fails later. Increasingly, both theoretical (Forbes, 1990, 1991) and empirical evidence for gulls, pelicans, and boobies (Anderson, 1990; Cash and Evans, 1986; Graves et al., 1984), is accruing for the idea of insurance offspring. However, little evidence is available for other species that never rear two young. For example, only 2.5% of 120 black eagle (*Aquila verreauxii*) nests and fewer macaroni, king and rockhopper penguin (*Eudyptes chrysolophus*, *E. schlegelii*, and *E. chrysocome*) nests were "saved" by the second egg (Brown et al., 1977; St Clair and St Clair, 1996; St Clair et al., 1995; Gargett, 1990; A.J. Williams, 1980a; T.D. Williams, 1989). This contrasts with 16–22% of nests in which a second egg insured success for pelicans and boobies (Anderson, 1990; Cash and Evans, 1986). The role of insurance in the evolution of two eggs in such species is also clouded because of a lack of focus on other ecological or lifetime factors that could influence clutch size.

Based on the poor evidence for second-egg insurance among eagles, Simmons (1988) suggested that the smaller second egg (B) may have been retained to enable parents to adaptively track population instability (see also Temme and Charnov, 1987): when population density is low, parents (particularly facultatively siblicidal species) can benefit by rearing two poorer quality offspring, while at population highs, selec-

tion for one high-quality offspring should occur. This differs slightly from Lack's (1954) brood reduction formulation in that it emphasizes quality, not merely numbers of surviving offspring, and is population density sensitive, not food sensitive. Hence, the offspring-quality hypothesis predicts that two nestlings should be reared more often in low-density populations, and longer-lived species should show the strongest selection for high-quality offspring.

Alternatively, the insurance hypothesis predicts that extra eggs should occur where hatch failure is not trivial and second eggs are inexpensive (Forbes, 1990). For example, Anderson (1990) postulated that because ground-nesting gannets (*Sula* spp.) showed increased hatch failure (due to high substrate temperatures), selection has favored a second egg. Single-egg boobies, however, nest in trees and have lower hatching failure and hence little need for insurance.

I experimentally and correlatively assessed other selective pressures and constraints such as poor food resources, body size/life span constraints, population density influences, and the ability and future costs (G.C. Williams, 1966) to parents in rearing a second nestling for the African Wahlberg's eagle (*Aquila wahlbergi*), which lays a single egg. Species of eagle that lay single eggs (when the insurance hypothesis predicts two eggs) provide one way of assessing the exaptation–adaptation problem (Gould and Vrba, 1982) because they are exceptions to the rule. If second eggs are inexpensive (Anderson, 1990; Ricklefs, 1974), and provide insurance in some species, the question arises why this and other species do not insure.

Wahlberg's eagle is a small (1300 g) African migrant that breeds at high densities throughout southern Africa. Breeding success (young reared/pair/year) and frequency is markedly density sensitive, both within and between populations in Africa (Simmons, 1993b). Pairs typically lay $c/1$, but can lay two eggs, so looking for patterns to the $c/2$ laying can unravel ecological factors promoting two eggs. (The opposite approach, seeking reasons for $c/1$ laying in $c/2$ species, is flawed because single eggs may be laid by young or old birds; New-

R. E. Simmons is currently at the Ministry of Environment and Tourism, P/Bag 13306, Windhoek, Namibia, Africa.

Received 8 October 1996; revised 10 February 1997; accepted 20 February 1997.

1045-2249/97/\$5.00 © 1997 International Society for Behavioral Ecology

Table 1
The incidence of two-egg clutches (c/2) in Wahlberg's eagle populations throughout Africa

Region (latitude)	No. of clutches	c/2	% c/2	Source
Uganda/Tanzania/Kenya (0–6° S)	31	3	9.7%	D. Loubser, L. Bennun ^a
Malawi (15° S)	6	1	16.7%	D. Loubser ^a
Zimbabwe (20° S)	724	18	2.5%	C. W. Hustler ^a
Transvaal, South Africa (23° S)	142	7	4.9%	Tarboton and Allan (1984)
Sabi Sand, South Africa (25° S)	88	2	2.3%	This study

^a Mainly from nest records at the Delaware Museum. Since these are egg collections, biases may arise from overrepresentation of c/2 clutches (i.e., prized clutches). This is unlikely, however, on the grounds that in the same museum sample, eggs collected from Zimbabwe in the 1930s (87 clutches, 2 c/2 clutches) show an identical proportion of c/2 laying (2.3%) as that found in the larger sample reported on nest record cards supplied by C. W. Hustler.

ton, 1979; Siegfried, 1968; Simmons, 1988). Wahlberg's eagles chicks exhibit intense sibling aggression given the chance (Simmons, 1991a), and population density is highly variable. The latter variation allows a comparison of egg-laying decisions under differing density-dependent conditions and thus ecological evaluations of insurance egg (Anderson, 1990; Mock et al., 1990) and offspring quality (Simmons, 1988) hypotheses. Here I present evidence from a 4-year study of Wahlberg's eagles showing that pairs can benefit when they lay a second egg, but most do not because the single, large egg provides its own form of hatchability insurance and chick viability. I then assess egg-size decisions in other c/1 and c/2 eagles.

STUDY AREA AND METHODS

Africa's highest known density of Wahlberg's eagles (23 pairs/100 km²; Simmons, 1994) occurs in the Sabi Sand Reserve of South Africa (24°48' S, 31°23' E). This wilderness area is a mosaic of woodland savanna and open grassland with many ephemeral rivers and extensive riverine vegetation. The area is underlain by granitic sandveld and clay soils and suffers little human impact. Annual rainfall in the study area averaged 620 mm. During a 4-year study, 88 breeding attempts were recorded in 135 pair-years in the 150 km² study area. Tree nests were monitored for egg, clutch, and brood size each year, using extendible mirror poles, and eggs and nestlings were measured with vernier calipers to the nearest 0.01 mm. Egg mass was measured to the nearest 0.1 g using a Salter 100 g scale, and egg volume (V), in cubic centimeters, was determined from $V = 0.51(\text{length})(\text{breadth})^2$.

The incidence of c/2 clutches from southern African populations (South Africa, Zimbabwe) were gathered from Tarboton and Allan (1984), Gargett (1968), and the nest record scheme in Zimbabwe. Data on equatorial populations were provided from nest records in Malawi and Kenya (see Acknowledgment). Further data on incidence of c/2 laying, hatchability, and population density were generously provided by W. Tarboton from a 10-year study on a 350 km² study area (Nylsvlei) in northern South Africa (see Tarboton and Allan, 1984).

Experimental data

To determine ecological constraints on c/2 laying, I assessed the ability of Wahlberg's eagle pairs to rear a second nestling by providing eight pairs with one extra young of about the

same age ($\bar{x} = 4.0 \pm 4.6$ days difference) once aggressive behavior had subsided (determined from laboratory studies; Simmons RE, unpublished data), when nestlings were older than 36 days. Although nestlings could not be assigned randomly because samples were limited by the availability of nestlings of similar age, introductions were both older and younger than residents. Five manipulations were performed in, 1988 and three in, 1989. Nests in, 1988 and, 1989 were checked continually up to the date of first flight for behavioral observations and growth measurements of doubled broods. Since single and doubled nests were visited equally, effects of disturbance should not differ between control and experimental nests. In, 1990 and, 1991, nests were only checked for egg laying and fledging success. For estimates of adult survival, I assumed nonreturning, patagially marked adults (Simmons, 1991b) had died because no marked birds missed in one year were ever seen in subsequent years, and all returning birds were 100% site faithful, even if they did not then breed (Simmons, 1993a). About half of all territorial birds were color marked ($N = 45$; Simmons, 1991b) and annually 80% returned to their old territories or were not seen again (Simmons, 1993a). I could thus gauge the costs of rearing two young on subsequent adult survival and breeding (i.e., residual reproductive value). I reevaluated experiments with prebreeding food supplements, reported elsewhere (Simmons, 1993b), to determine any food resource constraints before breeding. It should be borne in mind that sample sizes are naturally limited for eagles in relation to other siblicidal species because they are not colonial or annual breeders.

RESULTS

Incidence of c/2 clutches and insurance value

Two-egg clutches occurred twice (2.3%) in 88 breeding attempts and were laid by the same pair in consecutive years. This proportion accords with the incidence of c/2 clutches found elsewhere in southern Africa (2.8%; Table 1), but was significantly lower ($\chi^2 = 5.9$, $p = .01$) than their occurrence in equatorial Africa (10.8%). A density-sensitive relationship is implied from the lower population density in equatorial regions (Simmons, 1993b).

In 1990, at least one of the c/2 eggs hatched and fledged successfully. In 1991, the B egg hatched and fledged following the demise (hatched and lost) of the A egg; this example is provided to indicate that insurance can accrue to Wahlberg's eagles laying second eggs, although it is the first known ex-

Table 2
Clutch size, egg size (A eggs only), and body mass of the world's *Aquila* eagles

Species	Female mass (g)	Mean egg volume ^a (cm ³)	Mean clutch size (\bar{n})	Source
<i>Aquila chrysaetos</i>	5190	133	1.91 (—)	Edwards and Collopy (1983)
<i>A. verreauxii</i>	4380	144	1.8 (206)	Brown et al. (1977)
<i>A. audax</i>	4180	125	1.96 (140)	Cupper and Cupper (1981) Baker-Gabb (1984)
<i>A. heliaca</i>	3900	121	2.60 (—)	Meyburg (1987)
<i>A. nipalensis</i>	2987	103	?	Newton (1977)
<i>A. rapax</i>	2350	107	1.8 (104)	Huster and Howells (1986)
<i>A. clanga</i>	2135	101	1.37 (—)	Cramp and Simmons (1980)
<i>A. pomarina</i>	1610	84	1.78 (—)	Cramp and Simmons (1980)
<i>A. wahlbergi</i>	1500	76	1.03 (991)	This study

^a Egg volumes from Steyn (1982) and Cramp and Simmons (1980); clutch size data from sources indicated.

ample for this species. If an insurance function is apparent in the laying of a second egg, why don't all pairs (and other c/1 species) lay two eggs?

Incidence of hatching failure in Wahlberg's eagles

Hatching failure may be so rare that selection for insurance eggs has never occurred. However, nonhatching among c/1 nests accounted for 12.3% of 57 eggs that were not destroyed before hatch, a proportion slightly higher than that found in other carnivorous birds (10.6%; Koenig, 1982). Nonhatching could not be ascribed to pesticides because neither eggs nor chicks were affected (Simmons R, de Kock A, unpublished data). Nonhatching in a second Wahlberg's eagle population in southern Africa was similar at 12.5% ($n = 16$ eggs) in a nonpesticide-affected populations (Tarboton W, personal communication). Thus, insurance eggs could have aided about 12% of pairs in these population. As migrants they also have no chance of re-laying after the occurrence of nonhatching (Steyn, 1982); thus hatch failure terminates breeding.

Allometric relationships

Despite being the smallest of six species of well-studied *Aquila* eagles (*audax*, *chrysaetos*, *heliaca*, *rapax/nipalensis*, *verreauxii*, and *wahlbergi*), Wahlberg's eagle is the only species to lay regularly one egg (Steyn, 1982; Table 2). This is contrary to typical allometric body-mass-clutch-size relationships (Newton, 1977; Western and Ssemakula, 1982) or life-span-clutch-size relationships (Simmons, 1989; Zammuto, 1986), which are inversely related in birds. Allometric relations alone cannot explain this eagle's small clutch.

Food resources and energetic constraint on c/2 laying

Previous experiments (Simmons, 1995b) showed that of nine pairs provided extra food as they arrived back from migration, none laid larger (c/2) clutches. Thus pairs did not appear to be energy limited by poor early-season food resources. Corroboration is provided by oologist records: 45% of 11 Wahlberg's eagle pairs robbed of their clutches relaid (Lees, 1968), and did so within 9–13 days. Second eggs are thus possible, but do not occur for reasons unrelated to immediate food resources.

Experimental evidence for inability to rear two young

Experiments showed that of eight Wahlberg's eagle pairs given a second nestling, only one pair reared both. In all cases

in which an outcome was measurable ($n = 7$), subordinate nestlings rapidly lost condition while the other grew normally. The outcome in six cases was the death of the subordinate chick, presumed starved because of poor or negative weight gain, and in only one case (14%) did both young survive past first flight. In the latter case, the subordinate nestling gained only 50 g in over one month and at 770 g was about 20% lighter than his nest mate (at the same age) near first flight (66 days). Forty hours of observation at two nests with two chicks indicated that parents accepted the additional chicks, did not preferentially feed either nestling, and no overt nestling aggression occurred. Provisioning rates, however, were very low (one 50–100 g reptile/6.7 h) to twinned broods, and, unlike single chicks, the crops of twinned nestlings were never full and food remains were never found in such nests. All signs indicated that adult pairs were unable to provide sufficient food to rear extra nestlings and this may be sufficient to explain their single egg.

Adult survival and clutch size constraints

Of six pairs that reared two young for more than 10 days, all marked adults ($n = 9$) survived to the next year. Since 20% of the control (nonmanipulated) birds did not return, survival of experimental birds was unaffected. However, significantly ($p = .04$, Fisher's Exact test) fewer experimental pairs (16% of 6 pairs) bred in the subsequent year, relative to 64.5% of 31 nonmanipulated breeding pairs that returned. A cost to rearing two young is apparent.

Benefits of single eggs: size differences within eagles and other species

A different approach in evaluating the lack of insurance eggs is to pose an alternative question: what are the benefits of laying a single egg, assuming that the costs per se of B eggs are negligible? One benefit is that single eggs of c/1 layers may be larger than the first (A) eggs of c/2 layers, and large eggs may bring increased hatchability or chick survival.

Figure 1 indicates that the world's c/1 eagles lay eggs averaging 27–55% larger (by volume) than the largest A eggs produced by c/2 eagles of similar body mass (matched pair t test, $t = 6.33$, 3 df, $p < .01$). Based on age of adult plumage acquisition, significantly correlated with mean life span in falconiformes ($R^2 = .90$; Simmons, 1989), each c/1 species was also the longest-lived eagle within its body mass category. Similar results are apparent in sulidae: single eggs were 26.3% larger by volume than the largest (A) egg of c/2 species in

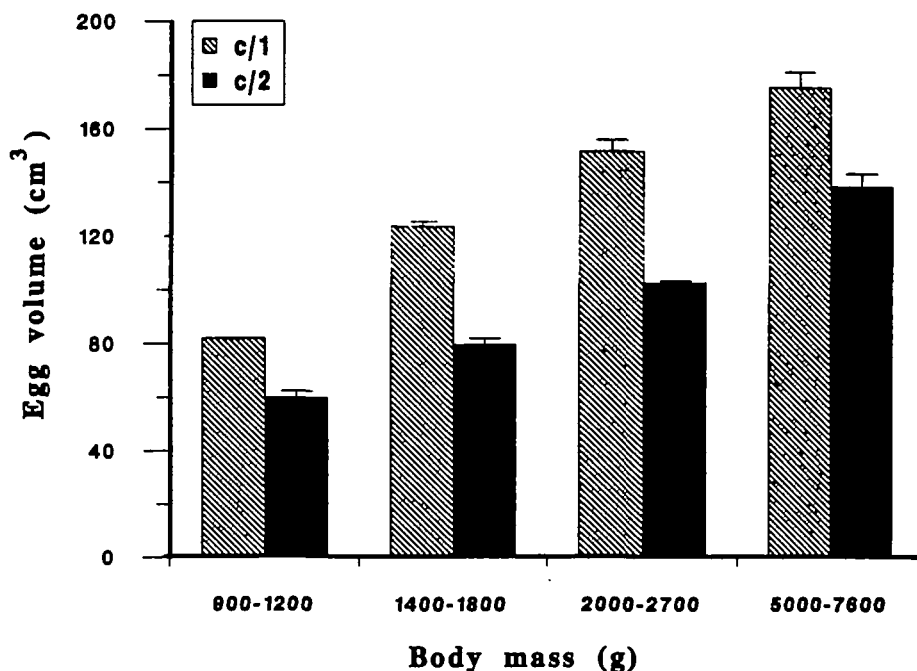


Figure 1

A comparison of egg volumes of c/1 (one-egg) and c/2 (two-egg) eagles (and one vulture) in the same body mass categories. Egg volume for each species was derived from several studies (sources in Simmons, 1989) and the means (± 1 SE) presented here represent between one and five species that fall into each body mass category. C/1 eagles laying single eggs always laid significantly larger eggs than A eggs of c/2 species ($p < .01$). Species include four *Hieraetus* species, five *Aquila* species, three *Circus* species, two *Haliaeetus* species, *Lophastur occipitalis*, *Terrathopius ecaudatus*, *Harpia harpyja*, *Cypsaetus barbatus*, *Polemaetus bellicosus*, and *Pithecochaga jefferyi*.

six *Sula* spp. reported by Anderson (1990). Similar trends are apparent within other siblicidal species: single eggs of Wattled Cranes *Grus carunculata* (Abrey, 1990; Johnson and Barnes, 1991) average 12% larger than the largest (A) eggs in the same population. The A eggs in Wahlberg's populations showed similar trends in one population (Tarboton's study): 16 single eggs were 8% larger than four A eggs in c/2 nests ($\bar{x} = 77.05$ versus 70.6 cm³), but not in my population, where the only two A eggs were larger (89.66 cm³) than the population mean (74.60 cm³, $n = 28$).

Hatchability of larger eggs

I tested whether hatchability was higher for larger eggs by comparing the volumes of hatched and unhatched eggs in the two populations (hatchability and egg size were similar in the two studies). Hatched eggs averaged 77.2 cm³, while unhatched eggs were significantly ($p < .01$) smaller, averaging 69.9 cc (Table 3). A bird laying an egg <70 cm³ had only a 47% probability (7/15) of laying an egg that was likely to hatch. Conversely, all eggs >76 cm³ hatched: this 8% decrease in volume is associated with a decreased probability of hatch from 100% to $<50\%$. Because B eggs of eagles practicing obligate

siblicide are about 12% smaller than their A eggs (Edwards and Collopy, 1983; Slagsvold et al., 1984), this may substantially decrease their chances of hatching. Laying two eggs appears to reduce the size of the A egg (8%) in at least one population of Wahlberg's eagles and 12% in other species.

DISCUSSION

The one-egg clutch of Wahlberg's eagles provides one way to test the insurance egg hypothesis because (1) siblicidal eagles are expected to insure with a second egg, (2) c/1 is an unusual clutch size for a small siblicidal *Aquila* eagle, (3) hatch failure, which should promote the occurrence of insurance eggs, is not trivial at 12%, and (4) the occurrence of c/2 varies with population density. This study showed that when pairs do lay an extra egg, it can act as insurance. However, because most pairs do not insure in this way, either (1) ecological constraints limit their occurrence, (2) insurance may not be the primary selective pressure in the evolution of two-egg clutches, or (3) unforeseen advantages in laying single eggs may occur. I argue that all factors operate in selecting c/1 in some eagles.

Several factors could be ruled out. Allometric relations could not explain the small clutch because the single egg is contrary to typical relationships between small body size and large clutches (Bortolotti, 1986; Klomp, 1970; Newton, 1979; Simmons, 1989). Second, prebreeding food supplements and oologists records indicate that food resources are not limiting. However, the inability of c/1 parents to rear more than one young and the strong density-sensitive influences on clutch size and breeding success (Simmons, 1993b) are both factors influencing the clutch size of these eagles. In particular, the inability of Wahlberg's eagle pairs to rear extra young supports the notion that pairs lay single eggs to match their typical and optimal brood size. This accords with other experimental studies demonstrating that optimal brood size is closely related to clutch size in multi-egg species (Nur, 1984; Pettifor et al., 1988). Moreover, this has been experimentally confirmed in other African species (Mundy and Cook, 1975; Simmons, 1986, 1989). Of more significance is the finding

Table 3
Mean egg sizes (± 1 SD) of all single, A, and B eggs in two populations of Wahlberg's eagles in southern Africa

	Single eggs (n)	A eggs (n)	B eggs (n)
Sabi Sand	74.6 ± 6.9 (49)	89.7 ± 1.9 (2)	76.6 ± 4.0 (2)
Nylsvlei	77.1 ± 9.1 (16)	70.6 ± 5.5 (4)	66.6 ± 4.7 (4)
Hatched eggs	77.2 ± 8.0 (37)	$t = 2.73, p < .01$	
Unhatched eggs	69.9 ± 4.4 (10)		

The mean volume of hatched and unhatched eggs (no c/2 eggs included) differed significantly.

that several c/2 eagles are capable of rearing two young if sibling aggression is bypassed, (Danko, 1987; Gargett, 1970; Meyburg, 1978; Meyburg and Garzon, 1973; Snelling, 1975). This finding has two implications. First, clutch size is not adjusted to the level of siblicide, but to the ability of the parents to rear one or two nestlings (i.e., siblicide has no influence). Second, siblicide can be seen as a proximate fine tuning of brood size (Drummond et al., 1986) for offspring quality (Simmons, 1988) overlaid on the general principle that clutch and brood size are closely matched. Because obligate siblicide is apparent in the longer-lived species, siblicide may be "tolerated" by parents to enhance quality of surviving offspring (Simmons, 1988). Given that the most parsimonious reason for single eggs in Wahlberg's eagles is that their clutch size is adapted to optimal brood size, do we then need to look further for reasons for the single eggs? Clearly, we do: alone these reasons cannot explain why such species do not insure success with a small second egg if insurance is seen as the major determinant of clutch size in siblicidal species (Anderson, 1990; Forbes, 1990; Mock et al., 1990; Stinson, 1979).

Predictions of the egg insurance hypotheses

Assume for the moment that an extra egg was primarily selected as a form of insurance. One would then predict that second eggs should arise when hatching failure is significant and when the costs of producing a B egg are intrinsically low (Anderson, 1990; Forbes, 1990; T.D. Williams, 1994). Yet hatch failure, even at a frequency of 12.5%, should provide selection for an extra egg in Wahlberg's eagles because it terminates breeding for the year. A second egg should also be more likely in dense populations in which reproductive interference may jeopardize hatchability (Koenig, 1982). This too was unsupported; fewer eggs occur per clutch in dense populations (Simmons, 1993b). It is unlikely that second eggs are too expensive to produce because energetic costs are apparently low for large species (Anderson, 1990; Ricklefs, 1974), and Wahlberg's eagles robbed of their clutches quickly relay (Lees, 1968). Second eggs do, however, appear to affect the size of the first egg (the cost-to-benefit ratio is considered below). Thus, despite the potential for insurance and the presumed selection for such eggs in Wahlberg's populations, they do not occur. This suggests that insurance is not a strong selective force in the evolution of two eggs, and other advantages promote single eggs.

The egg quality hypothesis

I propose that the large difference in egg volumes apparent between c/1 and c/2 layers, both within and between species (Figure 1), is the result of selective advantages in laying single, large eggs. Larger eggs occur among c/1 layers in boobies, gannets, and eagles relative to their c/2 counterparts (Anderson, 1990; Nelson, 1980; Simmons, 1989; Figure 1). Larger eggs also occur among nonsiblicidal families (Lack, 1968; Robertson, 1988; T.D. Williams, 1994), and the trend is apparent in the increasing disparity in the size of A and B eggs in *Eudyptes* penguins, where A is rarely hatched and reared (St Clair et al., 1995; T.D. Williams, 1990). Potential benefits to laying a large egg include intrinsically higher hatchability of large eggs and better quality chicks with increased growth rates and chances of survival.

Significantly enhanced hatchability of larger eggs was confirmed for two Wahlberg's eagle populations. The finding parallels reports that lighter eggs often remain unhatched in nests of *Eudyptes* penguins (review in St Clair et al., 1995), subantarctic skuas *Catharacta lonnbergi* (A.J. Williams, 1980b), and several smaller species (O'Connor, 1979; Slagsvold et al.,

1984). This finding raises the probability that c/1 layers are insuring hatch via a different route from c/2 layers—that is, through egg quality not quantity. Single, large eggs may not require second egg insurance because they are intrinsically more likely to hatch. That single large *Sula* eggs in Anderson's (1990) study showed increased hatchability relative to the eggs in c/2 nests, therefore, may have arisen not from substrate temperature differences (as postulated by Anderson) but from egg size differences alone. Controlling for substrate temperature would resolve the two ideas.

A larger body of evidence from within-species studies verifies that chicks hatching from large eggs do enjoy greater chances of nestling survival and enhanced growth characteristics than small chicks and eggs (Davis, 1975; Grant, 1991; Nisbet, 1978; O'Connor, 1975; Parsons, 1970; Skoglund et al., 1952; Thomas, 1983; A.J. Williams, 1980b; T.D. Williams, 1994). Recent experiments have controlled for parental quality and nest environment and shown profound survival effects in other species (Bolton, 1991; Frumkin, 1988; Williams, 1994). Large skeletal size appears to arise from larger energy supplies for the growing embryos in large eggs (Carey, 1985), and some species can allocate different amounts of energy to different eggs (Bolton et al., 1991; Simmons, 1994b). Because large body size at first flight imposes a measurable survival advantage among some species (Bryant, 1989; Garnett, 1981) and is correlated with lifetime success in others (Newton, 1985), large egg size can have a reproductive advantage in later life (T.D. Williams, 1994).

The cost-benefit comparison now focuses on possible costs in not producing a large viable egg. The benefits of producing a high-quality chick (from a large egg) are only likely to outweigh the reduced likelihood of the egg not hatching (and not being insured by a second egg) in the longest-lived species. Such benefits are only likely among long-lived birds because early (i.e., preadult) mortality is very high (review in Simmons, 1988), hence factors promoting survival should be under intense directional selection. The finding that large, single eggs are laid only by the longest-lived eagles (Simmons, 1989) and by sea birds (Warham, 1990) is expected in an offspring quality scenario. Therefore, c/1 laying in long-lived eagles, including Wahlberg's eagles, may have evolved from the enhanced hatchability and survival of chicks from large eggs, which c/2 laying cannot provide.

The egg quality hypothesis may explain the puzzling finding of Brown et al. (1977), who found no greater reproductive success of c/2 laying eagles (relative to c/1 species), which they predicted as a result of increased second egg insurance. They implicitly assumed that each egg, regardless of size, would share the same probability of hatching. If large eggs (of c/1 eagles), however, exhibit increased hatch success, as found for Wahlberg's eagles and other species, one would expect little difference in the productivity of c/1 versus c/2 nests, all else being equal. This is what Brown et al. (1977) found.

Two reproductive strategies are therefore open to long-lived species such as penguins, cranes, boobies, and eagles. Laying two eggs may diminish the chances of complete failure, and the best option is to lay a large first egg followed by a minimum-sized B egg to allow for viability and adequate subsequent growth. However, for some species the smaller egg may be so small as to fall in a size class where hatchability is very low. Indeed, this is found in *Eudyptes* penguins where the A egg is smallest, suffers high hatch failure (52%) under experimental conditions and is generally discarded by the parent shortly before laying the larger second egg (St Clair et al., 1995). Negligible insurance value was apparent for two species in this genus (St Clair et al., 1995, 1996). As important, the trading of single eggs for two eggs appears to decrease the

size of the A egg, which generally gives rise to the surviving chick. This decrease is paradoxical if the B egg is generally seen to be energetically inexpensive. However, even if this is true in absolute terms, the two eggs are being formed virtually simultaneously, and relatively this may be energetically more demanding for the female, resulting in a slight (8–12%) reduction in her main egg. This decrease in egg size/quality may have been due to the constraint imposed by forming eggs at the same time, or it may be due to selection pressures on egg/chick quality being relaxed in *c/2* species (Slagsvold T, personal communication). The latter is unlikely because many *c/2* species are tropical and long lived, and quality selection in these species should be intense (Simmons, 1988, 1989). Without good data on longevity for these species, it is difficult to know at which longevity threshold the trade-off between one good quality egg and a second, slightly smaller (less viable) egg for insurance occurs. All it is possible to state at present is that the species that adopt the single large egg strategy are longer lived than *c/2* species, and some like the Harpy eagle (*Harpyia harpyja*) appear to lie on this threshold, laying a very large first egg for a bird of its longevity (Simmons, 1989), infrequently followed by a small second egg.

In conclusion, I argue that so-called insurance eggs are not laid by the longest lived species because this may compromise their ability to lay large, higher quality eggs. The intrinsically higher hatchability of large eggs offsets the need for second-egg insurance and results in large chicks with enhanced survival prospects. Future studies should simultaneously assess all possible ecological constraints and lifetime benefits in the evolution of two-egg clutches in siblicidal species before concluding that second eggs evolved for purposes of insurance.

Thanks are due to the Sabi Sand landowners who allowed me access to their properties, particularly I. Mackenzie and T. Bignaut. I also thank field assistants K. Beaton, C. Zank, N. Mann, L. Hes, M. Jennions, C. Ferguson, and R. Ellis. I am particularly grateful to W. Tarboton for allowing me to use his Wahlberg's eagles data; clutch size data were provided by the Delaware Museum (D. Loubser), the Zimbabwe National Museum (C. W. Hustler), and the East African Natural History Society nest record scheme (L. Bennun). Financial assistance was provided through M. Markus, the Lealie Brown Award of the Raptor Research Foundation, the Finch-Davies Fund, and the Southern African Ornithological Society Research Fund. The manuscript benefited from critical reviews and discussions with C. Brown, C. C. St Clair, A. Kemp, D. Mock, T. Slagsvold, S. Ulfstrand, A.J. Williams, and an anonymous reviewer.

REFERENCES

- Abrey ANS, 1990. Wattle cranes, destruction of wetlands causes decline in population. *Custos* 19:24–26.
- Anderson DJ, 1990. Evolution of obligate siblicide in boobies: I. A test of the insurance-egg hypothesis. *Am Nat* 135:438–440.
- Baker-Gabb DJ, 1984. The breeding biology of twelve species of diurnal raptor in north-western Victoria. *Aust Wild Res* 11:145–160.
- Bolton M, 1991. Determinants of chick survival in the lesser black backed gull: relative contributions of egg size and parental quality. *J Anim Ecol* 60:949–960.
- Bolton M, Houston D, Monaghan P, 1992. Nutritional constraints on egg formation in the lesser black backed gull: an experimental study. *J Anim Ecol* 61:521–532.
- Bortolotti GR, 1986. Evolution of growth rates in eagles: sibling competition vs. energy considerations. *Ecology* 67:182–194.
- Brown LH, Gargett V, Steyn P, 1977. Breeding success in some African eagles related to theories about sibling aggression and its effects. *Ostrich* 48:65–71.
- Bryant DM, 1989. House Martin. In: *Lifetime reproduction in birds* (Newton I, ed). London: Academic Press; 89–106.
- Carey C, 1985. Structure and function of avian eggs. In: *Current ornithology*, vol. 3 (Johnstone RF, ed). New York: Plenum Press; 69–103.
- Cash K, Evans RM, 1986. Brood reduction in the American white pelican. *Behav Ecol Sociobiol* 18:413–418.
- Copper J, Cupper L, 1981. *Hawks in focus*. Mildura, Australia: Jaclyn Press.
- Cramp S, Simmons KE (eds), 1980. *Birds of the western Palearctic*, vol. 2. *Hawks to bustards*. Oxford: Oxford University Press.
- Danko S, 1987. Report on the activities of the group for research and protection of birds of prey in Czechoslovakia in 1987 [Czech, with English summary]. *Buteo* 2:1–36.
- Davis JWF, 1975. Age egg size and breeding success in the Herring gull *Larus argentatus*. *Ibis* 117:460–473.
- Dorward DF, 1962. Comparative biology of the white booby and the brown booby, *Sula* spp. at Ascension. *Ibis* 109b:174–220.
- Drummond H, Gonzales E, Osorno JL, 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxi*): social roles in infanticidal brood reduction. *Behav Ecol Sociobiol* 19:365–372.
- Edwards TC, Collopy MW, 1985. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* 100:630–635.
- Forbes LS, 1990. Insurance offspring and the evolution of avian clutch size. *J Theor Biol* 147:345–359.
- Forbes LS, 1991. Insurance offspring and brood reduction in a variable environment: the costs and benefits of pessimism. *Oikos* 62:325–332.
- Frumkin R, 1988. Egg quality breeding and dispersal in sparrowhawks (PhD thesis). Oxford: Oxford University.
- Furness B, 1981. A technique for estimating the hatching dates of eggs of unknown laying date. *Ibis* 123:98–102.
- Gargett V, 1968. Two Wahlberg's eagle chicks—a one in forty-eight chance. *Honeyguide* 56:24.
- Gargett V, 1970. Black eagle experiment no. 2. *Bokmakierie* 22:32–35.
- Gargett V, 1990. *The black eagle*. Johannesburg, South Africa: Acorn Books.
- Garnett MC, 1981. Body size its heritability and influence on juvenile survival among great tits *Parus major*. *Ibis* 123:31–41.
- Gould SJ, Vrba E, 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15.
- Grant MC, 1991. Relationships between egg size, chick size at hatching, and chick survival in the whimbrel *Numenius phaeopus*. *Ibis* 133:127–133.
- Graves J, Whiten A, Henzi P, 1984. Why does the ferring gull lay three eggs? *Anim Behav* 32:798–805.
- Hustler CW, Howells WW, 1986. A population study of tawny eagles in the Hwange National Park. *Ostrich* 57:101–106.
- Johnson DN, Barnes PR, 1991. The breeding biology of the wattled crane in Natal. In: *Proceedings of the 1987 International Crane Workshop* (Harris J, ed). International Crane Foundation; 377–385.
- Klomp H, 1970. The determination of clutch-size in birds. A review. *Ardea* 58:1–96.
- Koenig W, 1982. Ecological and social factors affecting hatchability of eggs. *Auk* 99:526–536.
- Lack D, 1954. *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Lack D, 1968. *Ecological adaptations for breeding in birds*. London: Methuen.
- Lees SC, 1968. Notes on the nesting of Wahlberg's eagle *Aquila wahlbergi*. *Ostrich* 39:192–193.
- Meyburg B-U, 1974. Sibling aggression and mortality among nestling eagles. *Ibis* 116:224–228.
- Meyburg B-U, 1978. Productivity manipulation in wild eagles. In: *Birds of prey management techniques* (Geer TG, ed). Br Falconers Club; 81–93.
- Meyburg B-U, 1987. Clutch size, nestling aggression and breeding success of Spanish Imperial eagles. *Br Birds* 80:308–320.
- Meyburg B-U, Garzon J, 1973. Sobre la proteccion del Aguila Imperial (*Aquila heliaca adalberti*) aminorando artificialmente la mortalidad juvenil. *Ardeola* 19:105–128.
- Mock DW, Drummond H, Stinson CH, 1990. Avian siblicide. *Am Sci* 78:438–449.
- Mundy PJ, Cook AW, 1975. Hatching and rearing of two chicks by the hooded vulture. *Ostrich* 46:45–50.
- Nelson JB, 1980. *Seabirds: the biology and ecology*. London: Hamlyn.
- Newton I, 1977. Breeding strategies in birds of prey. *Living Bird* 16:51–82.

- Newton I, 1979. Population ecology of raptors. Berkhamsted, UK: Poyser.
- Newton I, 1985. Lifetime reproductive output of female sparrowhawks. *J Anim Ecol* 54:241–253.
- Nisbet ICT, 1978. The dependence of fledging success on egg-size parental performance and egg composition in common and roseate terns, *Sterna hirundo* and *S. dougallii*. *Ibis* 120:207–215.
- Nur N, 1984. The consequences of brood size for breeding blue tits II. Nestling weight offspring survival and optimal brood size. *J Anim Ecol* 53:497–517.
- O'Connor RJ, 1975. Initial size and subsequent growth in passerine nestlings. *Bird-banding* 46:329–340.
- O'Connor RJ, 1979. Egg weights and brood reduction in the European Swift (*Apus apus*). *Condor* 81:133–145.
- Parsons J, 1970. Relationship between egg size and post-hatching mortality in the herring gull *Larus argentatus*. *Nature* 228:122.
- Petlfors RA, Perrins CM, McCleery RH, 1988. Individual optimization of clutch size in great tits. *Nature* 336:160–162.
- Ricklefs RE, 1974. Energetics of reproduction in birds. In: Avian energetics (Paynter RA, ed). Cambridge, Massachusetts: Nuttall Ornithological Club; 152–297.
- Robertson HA, 1988. Relationship between body weight, egg weight, and clutch size in pigeons and doves (Aves: Columbiformes). *J Zool* 215: 217–229.
- Siegfried WR, 1968. Breeding season, clutch size and brood sizes of Verreaux's eagle. *Ostrich* 39:139–145.
- Simmons RE, 1986. Food provisioning, nestling growth and experimental manipulation of brood size in the African redbreasted sparrowhawk *Accipiter rufiventris*. *Ornis Scand* 17:31–40.
- Simmons RE, 1988. Offspring quality and the evolution of Cainism. *Ibis* 150:339–357.
- Simmons RE, 1989. Adaptation and constraint in the breeding of subtropical harriers and eagles (PhD thesis). Johannesburg, South Africa: University of the Witwatersrand.
- Simmons RE, 1991a. Offspring quality and sibling aggression in the Black Eagle. *Ostrich* 62:89–92.
- Simmons RE, 1991b. A sex and colour guide to Africa's commonest eagle. *Birding* 43:11–14.
- Simmons R, 1993a. Chance, choice and habitat-related breeding success in a dense population of Wahlberg's eagles *Aquila wahlbergi*. *Proc Pan-Afr Ornithol Congr* 8:133–139.
- Simmons RE, 1993b. Effects of supplementary food on density-reduced breeding in an African eagle: adaptive restraint or ecological constraint? *Ibis* 135:394–402.
- Simmons RE, 1994a. Conservation lessons from one of Africa's richest raptor reserves. *Gabari* 9:2–13.
- Simmons RE, 1994b. Supplemental food alters egg size hierarchies in harrier clutches. *Oikos* 71:341–348.
- Skoglund WC, Seegar KC, Ringrose AT, 1952. Growth of broiler chicks hatched from various sized eggs when reared in competition with each other. *Poultry Sci* 31:796–799.
- Slagvold T, Sandvik J, Rofstad G, Lorensten Husby M, 1984. On the adaptive value of intrachlutch egg-size variation in birds. *Auk* 101: 685–697.
- Snelling J, 1975. Endangered birds of prey: ideas on the management of some African species. *J South Afr Wildl Manag Assoc* 5:27–31.
- St Clair CC, Waas JR, St Clair RC, Boag PT, 1995. Unfit mothers? Maternal infanticide in royal penguins. *Anim Behav* 50:1177–1185.
- St Clair CC, St Clair RC, 1996. Causes and consequences of egg loss in rockhopper penguins *Eudyptes chrysocome*. *Oikos* (in press).
- Steyn P, 1982. Birds of prey of southern Africa. Beckenham, UK: Croom Helm.
- Stinson CH, 1979. On the selective advantage of fratricide in raptors. *Evolution* 33:1219–1225.
- Tarboton W, Allan D, 1984. The status and conservation of birds of prey in the Transvaal. Transvaal Museum monograph no. 3. Pretoria, South Africa.
- Temme DH, Charnov EL, 1987. Brood size adjustment in birds: economic tracking in a temporally varying environment. *J Theor Biol* 126:137–147.
- Thomas CS, 1983. The relationship between breeding experience egg volume and reproductive success of the kittiwake *Rissa tridactyla*. *Ibis* 125:567–574.
- Warham J, 1990. The petrels, their ecology and breeding systems. London: Academic Press.
- Western D, Semakula J, 1982. Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia* 54:281–290.
- Williams AJ, 1980a. Offspring reduction in macaroni and rockhopper penguins. *Auk* 97:754–759.
- Williams AJ, 1980b. Variation in weight of eggs and its effect on the breeding biology of the great skua. *Emu* 80:198–202.
- Williams TD, 1989. Aggression, incubation behavior and egg loss in macaroni penguins, *Eudyptes chrysolophus*, at South Georgia. *Oikos* 55:19–22.
- Williams GC, 1966. Natural selection the costs of reproduction and a refinement of Lack's principle. *Am Nat* 100:687–690.
- Williams TD, 1990. Growth and survival in macaroni penguins *Eudyptes chrysolophus* A- and B-chicks: do females maximise investment in the large B-egg? *Oikos* 59:349–354.
- Williams TD, 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol Rev* 68: 35–39.
- Zammuto RM, 1986. Life histories of birds: clutch size, longevity, and body mass among North American game birds. *Can J Zool* 64:2739–2749.