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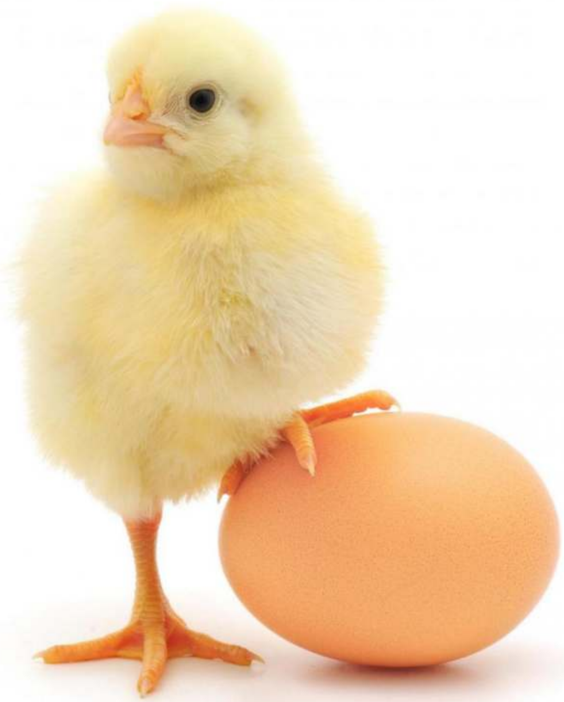

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Egg Weight Declines to Baseline Levels over the Laying Season in Domestic Geese (*Anser anser domesticus*)

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Abstract: Egg weight increased with age (one to four years) in domestic geese and was followed by a senescent decline. However a more striking finding in adult geese was a within season decline in egg weight over the first eight weeks of lay, until baseline weight levels were achieved and were then maintained until the end of the laying season. The egg weight decline (wks 1-8) was significantly different from the baseline egg weight (wks 9-19) in adult flocks. The within season decline in egg weight is attributed to constraints on the ability of birds to acquire the necessary nutrients exogenously during the laying season, requiring the geese to utilise their limited endogenous reserves. The seasonal decline in egg weight is consistent with that in other waterfowl. However, a baseline egg weight level was found here that may be difficult to identify in wild geese, as in nature clutch completion is followed by incubation. The baseline level reflect the minimum egg weight necessary for viable gosling production. In one year old geese egg weight was lower from the genesis of egg laying through the first eight weeks and weight then steadily increased between weeks 9-19 tending towards the adult baseline levels. This is consistent with the maturation of one year old birds and shows that young geese are working towards the production of eggs with a viable egg weight.

Key words: Domestic geese, egg weight, female age, maternal investment, seasonality

INTRODUCTION

Reproductive performance in birds and mammals improves with age and experience (Clutton-Brock, 1988; Forslund and Pärt, 1995). In birds-especially long-lived species-four distinct life history phases in reproductive performance have been identified: (1) Delayed breeding in young birds, when no reproduction is attempted; then (2) Improving breeding performance, (3) The experienced adulthood with constant reproductive performance and (4) A senescent decline (Fowler, 1995). Clutch size and egg size increased with age in a variety of wild geese (Lesser snow geese, *Anser caerulescens caerulescens* Rockwell *et al.*, 1983, 1993; Cooke and Rockwell, 1988; Robertson *et al.*, 1994; Barnacle geese, *Branta leucopsis* Forslund and Larsson, 1992; Hawaiian geese, *Branta sandvicensis* Woog, 2002).

In domestic geese, egg production and hatchability increased from one to two years (Merritt *et al.*, 1960) and laying synchrony improved with age (Kent and Murphy, 2003). In Lesser snow geese only 50% of two year old females attempt to breed, while nearly all four year olds reproduce (Cooke and Rockwell, 1988). The attainment of maximum reproductive output is a gradual process over several years for the long-lived geese (Lesser snow goose, Rockwell *et al.*, 1983; Conover, 2012) and the gradual process, i.e., increase in egg weight and clutch size from two to five years, is associated with physiological maturation (Lesser snow goose, Hamann and Cooke, 1987; Robertson *et al.*, 1994). Non-breeding yearlings of Lesser snow geese and White-fronted geese (*Anser albifrons*) tend to stay with the parents (Cooke and Rockwell, 1988; Fox *et al.*, 1995) and during this period yearlings associated with the parents fed more, gained more weight and spent less time being vigilant than did lone yearlings (Barnacle goose, Black and Owen, 1989; White-fronted goose, Fox *et al.*, 1995; Black, 2005), showing the importance of social maturation.

Waterfowl rely on endogenous reserves for egg production, especially if they start laying shortly after arrival on the breeding grounds, as in Ross' geese (*Anser rossii*, Ryder, 1970) and Dark-bellied brent geese (*Branta bernicla bernicla*, Spaans *et al.*, 1993). According to the nutrient reallocation hypothesis, from their limited endogenous reserves, geese can trade investment in another egg for investment in the remaining reproductive effort (Ryder, 1970; Flint *et al.*, 1996). However, the clutch size is less than the maximum possible as reserves are retained for incubation (Ryder, 1970; Flint *et al.*, 1996). For example, additional laying can be stimulated by egg removal from the clutch in Lesser black-backed gulls (*Larus fuscus*), however the egg size declines over the laying sequence

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as evidence of resource depletion (Nager *et al*., 1999). Other larger goose species feed on arrival at the breeding grounds (White-fronted goose, Budeau *et al*., 1991; Dusky Canada goose, *Branta canadensis occidentalis*, Bromley and Jarvis, 1993; Greater snow goose, *Anser caerulescens atlantica*, Choiniére and Gautier, 1995; Lesser snow goose, Ganter and Cooke, 1996) and the nutrients acquired contribute to rapid yolk deposition on arrival (Bromley and Jarvis, 1993; Gauthier *et al*., 2003). However, endogenous reserves accounted for 7% of the daily energy requirement during laying in Dusky Canada geese (Bromley and Jarvis, 1993). Using stable-carbon and stable-nitrogen isotope techniques to determine the contribution of endogenous and exogenous reserves, Gauthier *et al*. (2003) found in Greater snow geese that endogenous reserves accounted for up to 33% of protein and 25% of lipids of egg nutrients. In Greater snow geese, the peak rate of protein and lipid deposition in a two day period is not sufficient to produce one egg (Choiniére and Gauthier, 1995; Lepage *et al*., 2000) and one must also consider the nutrient requirements of other developing follicles. Thus in this context endogenous reserves are necessary for egg production. If Greater snow geese lay an egg every second day, as domestic geese do (Romanov, 1999; Kent and Murphy, 2003), then endogenous resource depletion would occur rapidly over the laying season. Put another way, foraging alone is not sufficient to cover the energy requirement for egg laying in these geese (Bromley and Jarvis, 1993; Choiniére and Gauthier, 1995; Gauthier *et al*., 2003). In contrast, in altricial species like the Tree swallow (*Tachycineta bicolor*), endogenous reserves are not relied upon for egg production, which is based on current foraging intake of abundant insect prey (Winkler and Allen, 1996) in the days preceding egg laying when the follicles are developing rapidly (Ardia *et al*., 2006).

Egg volume or weight declined over the breeding season in Thick-billed murres (*Uria lomvia*, Hipfner *et al*., 1997), domestic geese (Mroz and Lepek, 2003) and Upland geese (*Chloephaga picta leucoptera*, Gladbach *et al*., 2010). Seasonal decline in egg size was found in several studies (reviewed in Christians, 2002), which can be explained by females in better condition laying larger eggs earlier in the season (Williams, 2012). Further, larger bodied Wood ducks (*Aix sponsa*) and Upland geese tended to lay larger clutches of larger eggs (Hepp *et al*., 1987; Gladbach *et al*., 2010). Egg size correlates positively with hatchling weight (Shanawany, 1987; Williams, 1994) and larger hatchlings have higher growth potential (Bogenfürst, 2004) and survival (Ankney, 1980; Hipfner and Gaston, 1999; reviewed by Krist, 2011). In hatcheries small domestic goose eggs (<140 g in one year old, <150 g in two years or older geese) are regarded unsuitable for artificial incubation, due to their low hatchability (Bogenfürst, 2004). Thus the combined evidence suggests that a certain baseline egg weight level is necessary for the productions of viable goslings.

Here, we are concerned (1) With changes over the laying season in egg weight in domestic geese where eggs are removed daily inducing laying and (2) With the effects of age on maternal investment in egg weight.

MATERIALS AND METHODS

406 female and 97 male domestic geese (Legarth strain) were maintained in nine flocks, ranging in size from 15 to 108 individuals and in age from one to eight years with each flock containing birds of the same age at Ballyrichard, 72 km south of Dublin, Ireland (52.83°N, 6.13°W) during 2009 (February-June). Flock ages are described in Table 1.

Housing and management were as described by Kent and Murphy (2003) with each flock housed separately at night, released at 9:30 h to adjacent grass field with water supply. The geese had access to their houses during the day where meal was provided. They were maintained on a natural daylight schedule, but an additional half hour of electric light was provided in the evenings from mid-January until natural day length extended to 19:00 h (GMT) in order to stimulate the start of egg laying.

For the 19 weeks of this study, eggs laid in houses at night (18:00 and 9:00 h) were collected on goose release in the morning. Domestic geese lay every second day (Romanov, 1999; Kent and Murphy, 2003) and thus eggs from two consecutive days each week, were used for recording egg weight. When eggs were collected they were taken to a central room, counted and weighed to the nearest 0.1 g using an electric balance (Ohaus Corporation, USA). Double yolked eggs were identified at weighing by candling and excluded from the analysis. Total egg production (day and night) of all flocks combined was used to study changes in rate of lay over the season (Kent and Murphy, 2003).

Using Minitab 16, GLM analysis was employed to examine the role of day of year, female age and flock on changes in egg weight. The interactions day of year*female age and day of year*flock were also included in the model and day of year, female age and flock were used as covariates due to the skewed pattern of seasonal laying. The residuals obtained from the GLM were tested for normal distribution. Equations were calculated to describe the change in egg weight in relation to day of year and female age for the total population (See Results). For each calculated equation, two of the factors were kept constant by substituting their mean values into the equation obtained from the GLM.

The effect of day of year was examined on egg weight using forward stepwise regression analysis (the variable was added to the model if the Alpha value was 0.15 or less) for each flock. The first and second order variables of day of year were used, as a linear or a quadratic egg weight change was expected over the season. In flocks 2, 4 and 5 only one egg was produced on day 41 and data from that day was therefore excluded from the analysis. Two sample t-tests were used to compare egg weights of two flocks of the same age (2 years old: flocks 3 and 9; 3 years old: flocks 1 and 6; 6 years old: flocks 2 and 7).

For the total population and for individual flocks, regression lines were fitted on the two periods of egg production and were then compared following Bailey (1995). The following formula was used for comparing regression lines: $d = b_1 - b_2/\text{sqrt}\ (SE_1^2+SE_2^2)$, where b_1 and b_2 are the slope values for each regression line and SE_1 and SE_2 are the standard errors for each regression slope value respectively. Two regression lines differed significantly ($p<0.05$), if the value obtained from the formula was larger than 1.96 (Bailey, 1995).

RESULTS

Data collection began on day 41 (10/Feb) with 125 eggs (day and night production) from a total population of 406 females (all flocks combined) over two days (i.e., 125 eggs/406 female/2 days = rate of lay of 0.15 egg/goose/day). The rate of lay increased until day 62 (03/Mar; i.e., 0.41 egg/goose/day = 336 eggs/406 female/2 days) and reached a plateau of = 0.4 egg/goose/day that was maintained for ten of the 19 weeks of production until day 125 (12/May; i.e., 0.4 egg/goose/day = 322 eggs/406 female/2 days). This plateau is close to the maximal production of 0.5 egg/goose/day (Kent and Murphy, 2003). Then, egg production decreased until day 167 (16/Jun; i.e., 0.07 egg/goose/day = 56 eggs/406 female/2 days), when the study ended (Fig. 1). Thus the laying season can be divided into three phases based on the rate of lay: rapid increase, a plateau (days 62-125 with rate of lay = 0.4 egg/goose/day) and rapid decrease phases. Housed egg production correlated with the total egg production ($r = 0.98$, $p<0.001$) with 66% of the eggs laid in houses between 18:00 and 9:00 h (62.5% of total day).

When studying egg weight changes, using night egg production, neither interaction terms (day of year*female age, day of year*flock) in the GLM model were significant ($p>0.05$), suggesting that egg weight changed over the laying season in a similar pattern in all flocks. Data was then reanalysed to produce an equation without the interaction terms. Day of year, female age and flock all had significant effects on egg weight, but a model with a quadratic term for both day of year and female age provided a better fit ($Y = 175.63 - 0.7x+0.003x^2+20.82y-1.97y^2+0.58z$; where x = day of year, y = female age, z = flock; adj. R^2 = 40.05%; n = 3443 eggs). Significance levels for all terms in the GLM were $p<0.001$ and the residuals were normally distributed.

Over the season for the total population (night egg production), egg weight decreased steadily from day 41 (10/Feb; 193.93 g±17.33 [sd]) to day 90 (31/Mar; 172.47 g±17.21 [sd]). Then from day 90 (31/Mar) to day 160

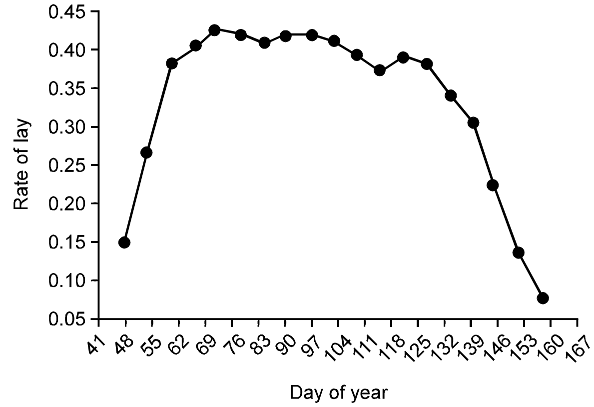

Fig. 1: Change in the rate of lay in the total population (flocks combined) over the laying season; i.e., total egg production (night and day) over two consecutive days/each week/no. female/2. Day of year = 1st of the two consecutive days of egg collection

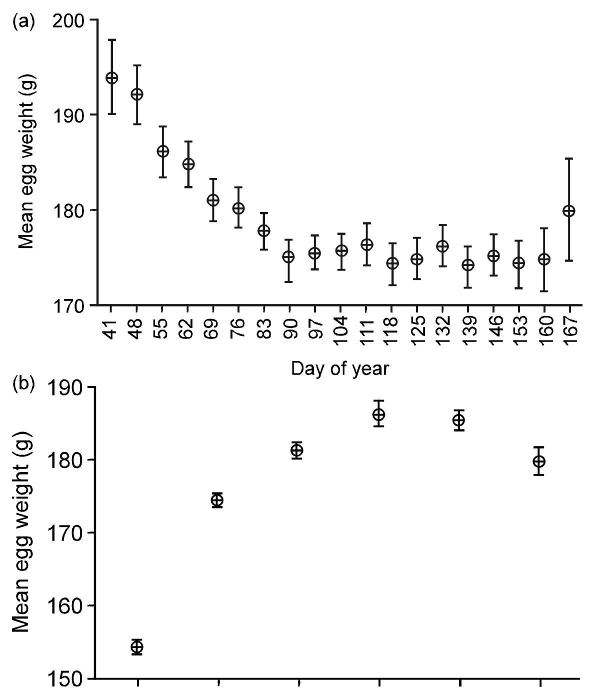

Fig. 2(a-b): Changes in mean egg weight (a) Over the laying season and (b) In relation to female age using all flocks combined (night egg production)

(09/Jun) egg weight change reflect a constant trend with a weight range from 171 g to 174 g with a slight increase at the end of the laying season to 177.93 g±17.98 [sd] on day 167 (16/Jun) with only 36 eggs produced (Fig. 2a). Egg weight change over the entire season reflect a

Table1: Egg weight changes over the laying season in nine flocks of domestic geese

Age (years)	Flock No.	No. of females	Equation	Flock	P	Adjusted R^2 (%)
1	5	73	$Y = 170-0.36x+0.002x^2$	4.96	0.007	1.4
2	3	46	$Y = 218.2-0.75x+0.003x^2$	72.17	<0.001	21.4
2	9	84	$Y = 224.9-0.8x+0.003x^2$	118.58	<0.001	22.4
3	6	32	$Y = 218.7-0.59x+0.002x^2$	9.5	<0.001	6.5
3	1	73	$Y = 220-0.67x+0.003x^2$	40.47	<0.001	12.8
4	8	45	$Y = 225.5-0.62x+0.002x^2$	20.75	<0.001	12.5
6	7	11	$Y = 235.9-0.93x+0.004x^2$	5.72	0.005	8.8
6	2	27	$Y = 202.7-0.14x$	21.01	<0.001	8.5
8	4	15	$Y = 218.6-0.62x+0.002x^2$	9.74	<0.001	10.3

Table 2: Regression equations for egg weight change for the two periods of the laying season (day 41-90) and (day 97-167) and the comparisons of their slopes for each of nine flocks (Total No. of eggs for each flock = No. of eggs*3.5/0.66)

		Day 41-90			Day 97-167			Comparison	
Age (years)	Flock No.	Equation	P	No. of Eggs	Equation	P	No. of Eggs	D	P
1	5	Y = 159.1-0.07x	0.333	272	Y = 138.3+0.12x	<0.001	299	-2.49	<0.02
2	3	Y = 212-0.47x	<0.001	258	Y = 179.4-0.09x	0.046	265	-5.27	<0.001
2	9	Y = 216.3-0.47x	<0.001	397	Y = 178.9-0.06x	0.052	419	-7.03	<0.001
3	6	Y = 211.6-0.33x	0.006	99	Y = 183.8-0.02x	0.811	145	-2.31	<0.05
3	1	Y = 214.2-0.41x	<0.001	272	Y = 185.1-0.06x	0.249	267	-4.48	<0.001
4	8	Y = 221.1-0.4x	<0.001	133	Y = 194-0.07x	0.172	144	-2.95	<0.01
6	7	Y = 229.7-0.56x	0.003	46	Y = 179.9+0.04x	0.615	53	-3.05	<0.01
6	2	Y = 209.4-0.21x	0.143	88	Y = 189.9-0.04x	0.445	130	-1.12	ns
8	4	Y = 208.3-0.33x	0.004	53	Y = 187.7-0.07x	0.357	100	-1.99	<0.05

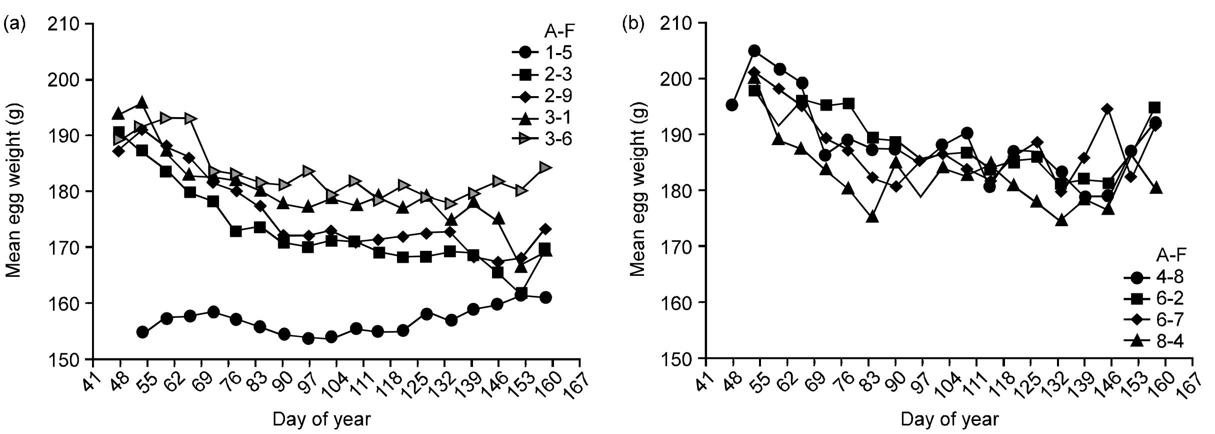

Fig. 3(a-b): Egg weight changes in (a) Five flocks of 1-3 year old geese and (b) Four flocks of 4-8 year old geese (A female age, F: flock no.). See description in Table 1

quadratic trend, decreasing steadily with a slight increase at the end when egg production was declining (calculated $Y = 222.05-0.7x+0.003x^2$). Two periods were identified based on changes in the egg weight pattern: the first period between days 41-90 and the second period between days 97-167. When these two periods were analysed separately for the total population, a significant decline in egg weight was found in the first period ($Y = 209.1-0.41x$; $F = 147.54$; $p<0.001$), while egg weight change over the second period did not differ significantly from the constant ($Y = 173.5-0.01x$; $p = 0.733$). The slopes of the two periods differed significantly ($p<0.001$).

When individual flocks were examined over the laying season, egg weight decreased in a linear manner in flock 2 (6 years old) and in a quadratic manner in the remaining eight flocks that is it decreased to a point and then the trend changed (Table 1; Fig. 3a,b). When the two periods, i.e., pre and post day 90 were analysed separately for each flock, egg weight declined linearly in all flocks until day 90, although the decline was not significant in flocks 2 (6 years old; $p = 0.143$) and 5 (1 year old; $p = 0.333$). After day 90, egg weight increased in flock 5 (1 year old; $p<0.001$). In six flocks egg weight did not change significantly over the second period, i.e., egg weight was constant, though in one flock egg weight declined further (flock 3, 2 years old; p = 0.046). Comparisons of the regression slopes between the two periods revealed significant differences in eight of the nine flocks (Table 2). Thus, in adult geese egg weight trends showed a significant weight decline during the first period and then a general baseline trend was maintained until the end of lay. However, in one year old geese (flock 5) the pattern was different; egg weight was low and relatively constant in the first period with a steady and significant increase in the second period toward adult baseline levels (Table 2).

As the geese aged egg weight increased from one year old (153.86 g±12.67 [sd]) to four years old (188.72 g± 15.43 [sd]) and then declined in six (187.65 g±14.82 [sd]) and eight years old geese (181.66 g±13.93 [sd]) (calculated $Y = 138.79+20.82x-1.97x^2$; Fig. 2b).

DISCUSSION

The general decrease in egg weight up to a certain point over the laying season in adult geese (2 years or older) and the subsequent stabilization in egg weight to what we call baseline levels is the most striking finding of this study. More specifically, egg weight declined during the first eight weeks (day 41-90) in all adult flocks (Fig. 3a,b) until it reached the baseline levels, which we regard as the minimum egg weight required to produce viable offspring. In the second period (day 97-167) egg weight remained constant showing the baseline weight pattern in seven adult flocks, where no significant changes in weight were detected. The egg weight decline (day 41-90) and the baseline egg weight (day 97-167) differed significantly in seven of the eight adult goose flocks (Table 2). Mroz and Lepek (2003) with two year old Polish domestic geese, measured egg weight at three points over the laying season (early, mid and late) and found a significant decrease in egg weight between the early and a middle point with no change to the later point, consistent with our finding in adult geese. Further, in hatcheries small domestic goose eggs (<140 g in one year old, <150 g in two years or older geese) are regarded as unsuitable for artificial incubation, due to their low hatchability (Bogenfürst, 2004). This is consistent with the view that a baseline egg weight level is necessary for the production of viable goslings below which eggs are not laid. A baseline egg weight may be difficult to identify in wild geese, due to ecological constraint on the laying pattern, as when a clutch is laid incubation commences. Further, a trade-off between producing another egg and retaining reserves for incubation was proposed (nutrient reallocation hypothesis, Ryder, 1970; Flint *et al.*, 1996). However, domestic geese can lay between 20-60 eggs in a laying season where eggs are collected daily (Horn, 2000; Mazanowski *et al.*, 2005; Shi *et al.*, 2008). In contrast, in the relatively non-seasonal breeder laying hens an increasing egg weight pattern over the season was shown in light controlled environment (Álvarez and Hocking, 2012). The difference in the egg weight pattern over the laying season is attributed to the difference in the means of energy supply for egg production, as the utilization of endogenous reserves is of known importance for egg production in geese (Ross' goose, Ryder, 1970; Dark-bellied brent goose, Spaans *et al.*, 1993; Dusky Canada goose, Bromley and Jarvis, 1993; Greater snow goose, Gauthier *et al.*, 2003). Interestingly, decline in egg weight over the laying sequence was found both in supplement fed and non-supplemented control female Lesser black-backed gulls when their eggs were continuously removed to stimulate additional laying (Nager *et al.*, 1999). Further, it is known that supplemental feeding improves maternal condition in Lesser black-backed gulls (Bolton *et al.*, 1993) and supplement fed females laid heavier eggs than non-supplemented females, still egg weight declined in both groups over the laying sequence showing evidence of reserve depletion (Nager *et al.*, 1999).

Here, egg weight decline reflects the depletion of endogenous reserves especially early in the laying season. Egg production is costly and in Greater snow geese the peak rate of protein and fat deposition in eggs was 9.5 and 6.3 g/day, respectively when laying (Choiniére and Gauthier, 1995) and an egg contains about 17.5 g of protein and 14.5 g of fat (Lepage *et al.*, 2000). If Greater snow geese lay an egg every second day, as domestic geese do (Romanov, 1999; Kent and Murphy, 2003), then the time to acquire the nutrients for one egg would be 1.8 days for protein and 2.3 days for fat with peak deposition rates, not considering the nutrient requirements of other developing follicles and depletion of endogenous reserves would occur early in the season. This could explain the decrease in egg weight or volume early in the season in this and earlier studies (Thick-billed murres, Hipfner *et al.*, 1997; domestic geese, Mroz and Lepek, 2003; Upland geese, Gladbach *et al.*, 2010). Further, Dusky Canada goose and Greater snow goose females were significantly lighter after laying a clutch of eggs, than before laying (Bromley and Jarvis, 1993; Choiniére and Gauthier, 1995) demonstrating the cost of their maternal investment. One year old Polish regional geese lost 12.7-17.4% of body weight during the reproductive season (Mazanowski *et al.*, 2005), demonstrating evidence of resource depletion.

Here, in one year old geese (flock 5), there was no significant change in egg weight in the first period (day 41-90). However, egg weight increased significantly towards adult baseline weight levels over the second period (day 97-167) and is consistent with the increasing egg weight found in one year old domestic White Rhine Dutch geese (Dodu, 2010). This is attributed to physiological maturation of the young geese, where early light eggs are attributed to physiological constraints of a developing bird.

The seasonal decrease in egg weight found here corresponds to the seasonal increase in testosterone in domestic goose egg yolks over the laying season (Kent *et al.*, 2013) suggesting a trade-off with increasing testosterone compensating for decreasing investment in egg weight, as found in Black-headed gulls (*Larus ridibundus*, Groothuis and Schwabl, 2002). It is known that in smaller, later laid eggs the high testosterone accelerates embryonic development (Black-headed gull, Eising *et al.*, 2001; Müller *et al.*, 2004) and enhances postnatal growth (Canary, *Serinus canaria*, Schwabl, 1996) and this may have similar effects in wild or domestic geese.

Age is a significant factor in the level of maternal investment in each egg. One year old geese laid smaller eggs (Fig. 2b) and egg weight increased from first and second year in Polish regional geese (Mazanowski *et al.*, 2005). An increase in egg weight with age up to four years was found in wild goose studies (Giant Canada goose, *Branta canadensis maxima*, Cooper, 1978; Lesser snow goose, Robertson *et al.*, 1994). Here, egg weight decreased in geese from four to eight years old (Fig. 2b), reflecting a senescent decline under intensive production systems i.e., consequence of domestication and is consistent with the now general practice of culling geese at five to six years of age on commercial breeding farms (Horn, 2000; Bogenfürst, 2004). In contrast in long-lived species, such as Giant Canada geese that can live for 24 years (Clapp *et al.*, 1982; Wasser and Sherman, 2010), a senescent decline in egg weight was found after 18 years (Cooper, 1978), but hatchability and brood survival decreased after six years in Lesser snow geese (Rockwell *et al.*, 1993), while the number of hatched eggs declined after eight years in Hawaiian geese (Woog, 2002).

It is concluded that the seasonal changes in egg weight found here reflect changes in the availability of resources, such as body condition and the constraint of a necessary baseline egg weight to produce viable goslings later in the season.

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