Spring fattening in non-migratory female Greylag Geese *Anser anser* regardless of social status

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Abstract

Geese vary their body mass throughout the annual cycle. Before energy-demanding processes such as migration, breeding and moult, they accumulate fat reserves, mainly in their abdomen. Females in particular may face a nutritional bottleneck during spring, when they produce and incubate eggs. Clutch size and thus reproductive success is positively linked to female body condition and ultimately evolutionary fitness. Using a marked flock of resident Greylag Geese *Anser anser* in southwest Germany, where only *c.* 12% of the local birds breed (according to 2016 data), we showed that female geese put on weight regardless of their breeding or social status, but males did not. Even unpaired females with no breeding opportunity in the coming season gained weight, taking advantage of the ample feeding opportunities. This strongly suggests an underlying endogenous process of spring fattening in female Greylag Geese.

Key words: abdominal profile index, annual cycle, body mass, breeding status.

Geese vary their body mass throughout the annual cycle (Ankney 1982). Before energy-demanding processes such as migration, breeding and moult they accumulate fat reserves, mainly in their abdomen. The majority of studies have concentrated on migratory geese and cover spring staging (Owen 1981; Black *et al.* 1991; Boyd *et al.* 1998; Féret *et al.* 2005; Madsen 2001; Alisauskas 2002; Prop *et al.* 2003; Bêty *et al.* 2003; Mini & Black 2009), pre-laying (Ganter & Cooke 1996), breeding (Bêty *et al.* 2003), wintering (Owen 1981; Wang *et al.* 2013) and the moulting periods (Fox *et al.* 1999; Fox & Kahlert 2005). Few studies exist on resident goose flocks in Europe that do not migrate (though see Johnson & Sibly 1993; Käßmann & Woog 2007; Fox 2019).

Towards the end of winter, the northern geese – the *Anser* or *Branta* species – accumulate body reserves to prepare for migration and breeding (Owen 1981; Black *et al.* 1991; Madsen 2001). Females face a nutritional bottleneck when producing and incubating eggs. Clutch size is correlated with the female's body condition (*e.g.* Ankney & MacInnes 1978); thus, the ability to put on fat is positively linked to the number of young produced (Owen & Black 1989; Ganter & Cooke 1996; Prop *et al.*

2003), and ultimately the fitness of a bird in an evolutionary sense (Davies *et al.* 1988; Inger *et al.* 2008). Individuals are not equally effective in their ability to obtain access to high-quality food for building fat reserves (Black & Owen 1989; Bowler 1994; Boyd *et al.* 1998; Van Eerden *et al.* 1991) and geese in poor condition lay eggs at relatively later dates (Bêty 2003). Habitats used by the birds for spring fattening can have a major effect on their ability to accumulate body reserves (*e.g.* Prop & Black 1998; Mini & Black 2009) and their subsequent reproductive success (Black *et al.* 1991).

Our own studies of a resident Greylag Goose *Anser anser* population in Stuttgart, southwest Germany, have shown that especially paired female geese accumulate fat reserves in late winter, even when there is still snow and ice cover, and food resources are limited (Käßmann & Woog 2007). In this paper, we aim to investigate whether geese vary their fat acquisition over time in relation to their social and actual breeding status. This could clarify if fattening in geese is controlled by endogenous mechanisms irrespective of food availability or feeding opportunity, as in waders (*e.g.* Pienowski *et al.* 1979; Araújo *et al.* 2019) or songbirds (Bairlein 2002). The resident flock is well suited for such a study, because food resources are similar for all individuals and the lack of migratory behaviour minimises ecological and individual variation caused by migration constraints.

Methods

Study population

In the late 1980s, a feral Greylag Goose population started to establish itself in Stuttgart, southwest Germany (48°46'N, 9°10'E; Woog *et al.* 2008; Fig. 1). In contrast to autochthonous populations, locally introduced birds are non-migratory, and results of the local colour-ringing programme showed that movements are usually small-scale (Woog *et al.* 2008). They do not mix with migratory geese. After a first brood fledged successfully in 1995, Greylag Goose numbers in Stuttgart started to increase steadily to a flock of *c.* 260 birds in 2019. From 2002–2016 inclusive, 736 Greylag Geese caught whilst moulting in Stuttgart were fitted with unique blue leg-rings, each engraved with a white three-letter code, so that observers could identify individual birds. As the geese were often tame, the codes could be read easily with the naked

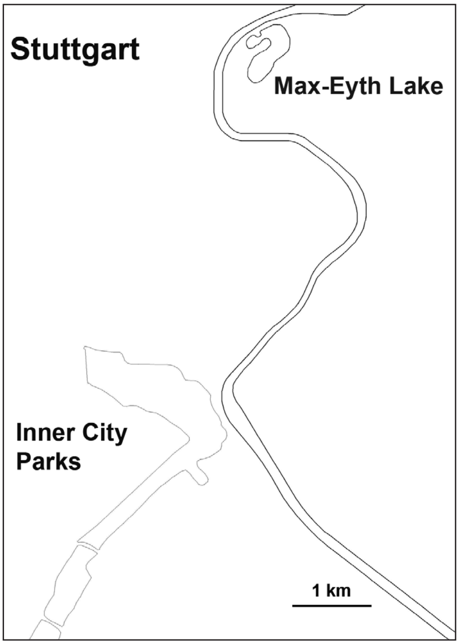

Figure 1. Study sites in Stuttgart, including the parks of the inner city and the Max-Eyth Lake.

eye or by using binoculars. First clutches are laid at the beginning of March and the first young hatch in early April, with late broods hatching at the end of May. Goslings were usually ringed a few weeks before fledging, in the first two weeks of June.

Study area

Stuttgart's Greylag Geese frequent regularly mown pastures around parkland lakes, which offer year-round high-quality grazing (Woog *et al.* 2012), and all of the geese use these habitats. Within the city, the geese occur at several sites, as outlined by Käßmann & Woog (2007, 2008; Fig. 1). The number of breeding pairs is limited by the number of islands that the birds can use for nesting. In 2016, the year of this study, only 12% of the birds present had nests (Ehret 2016).

Abdominal profiles

The relative increase or loss of weight in wild geese was determined using the "Abdominal Profile Index", API (Owen 1981; Black *et al.* 2007). Since abdominal fat is a good indicator of overall body fat, the API also gives a useful estimate of changes in overall body mass (Bowler 1994; Wiersma & Piersma 1995; Zillich & Black 2002; Madsen & Klaassen 2006; Black *et al.* 2007). The API measure is widely used because it allows repeated assessment of body condition for individually marked birds without capturing and stressing them. We used the method described by Zillich & Black (2002), where Owen's API scores (0 = concave, 1 = straight, 2 = convex, 3 = rounded, thick, 4 = intensely rounded, very fat) are made more detailed, by subdividing into intermediate (0.5 step) scores. To determine the API of a goose it was observed for at least 15 s when it had its head down grazing, ensuring a body held parallel to the ground. Abdominal profiles of all ringed geese present in the study area were determined once a week between 7 February and 30 June 2016. Changes in abdominal profiles recorded for individually marked geese of different social status were then compared throughout the study.

Social status

We collected API data for single males (*n* = 46) and females (*n* = 54), and for male (*n* = 50) and female (*n* = 49) paired birds without young (non-breeders), as well as for parental males and females with young (*n* = 15). Sexes were identified in the field by using behavioural clues and size differences (males are on average larger than females). In addition, we sexed the birds using molecular methods (Hedges *et al.* 1990; Clinton *et al.* 2001; Huang *et al.* 2003). Birds that we were unable to sex were not included in the analyses. In 2016, more than half of the population was paired, but among them only 12% were breeders (*n* = 15 pairs). Of the 45% of the population found to be unpaired, 9% had hatched in the previous year.

Statistical analyses

The effects of calendar week and social status on the APIs recorded for individual birds was tested in a linear mixed-effects model (LMM) in RStudio (R Core Team 2019; RStudio Team 2020). All LMMs were fitted using the lme4 package (Bates *et al.* 2015), with *P* values calculated using the lmerTest package (Kuznetsova *et al.* 2017).

The LMMs were fitted with the APIs as the response variable, calendar week (continuous) and social class (factor) as the explanatory fixed effects, whilst accounting for individuals as a random effect. As API data were normally distributed, single effects of either week or social status were tested using ANOVAs for all data points, not accounting for pseudo-replication (*i.e.* individuals and weeks were included several times). Mean APIs are given with s.e. values throughout.

Results

Between 7 February and 28 June 2016, a total of 2,140 abdominal profile indices were recorded by the first author. The APIs of females (mean API = 1.75 ± 0.021, n = 1,100 samples on 118 individuals) and males (mean API = 1.55 ± 0.017, n = 1,040 samples on 111 individuals) differed significantly (t-test: $t_{2058.4} = -7.41$, $P < 0.0001$). Regardless of week, females had a larger API score than males in each class (t-test: $t_{989.28} = 5.48$, $P < 0.0001$ for non-breeding pairs; $t_{260.06} = 2.09$, $P < 0.04$ for parental pairs; $t_{757.87} = 5.12$, $P < 0.0001$ for single birds).

APIs of birds varied with social class (ANOVA: $F_{5,2134} = 14.37$, $P < 0.0001$) and calendar week (ANOVA: $F_{1,149} = 33.81$, $P < 0.0001$ for parental females; $F_{1,134} = 5.78$, $P < 0.02$ for parental males; $F_{1,422} = 82.74$, $P < 0.0001$ for single females; $F_{1,334} = 21.45$, $P < 0.0001$ for single males; $F_{1,523} = 140.7$, $P < 0.0001$ for paired females; and $F_{1,566} = 23.57$, $P < 0.0001$ for paired males).

On fitting a LMM over the entire study period for each sex separately, the API measurements showed very small variations between weeks (calendar week (CW): estimate = 0.05 ± 0.003, $t_{1086.46} = -15.97$, $P < 0.0001$ for females; estimate = 0.02 ± 0.002, $t_{1023.87} = -7.33$, $P < 0.0001$ for males) but did not show any trend for the social classes (estimates < 0.1, $P \leq 0.6$, n.s. across all groups). Therefore, a series of LMMs was fitted by time period for each sex separately (pre-breeding: CW = 6–11; breeding: CW = 12–15; rearing: CW = 16–20; and post-breeding: CW = 21–26).

In the pre-breeding period, parental females showed the most marked increase in their API scores (estimate = 0.35 ± 0.06, $t_{17.68} = 5.85$, $P < 0.0001$) (Fig. 2), but this increase was also visible in paired females that did not breed (estimate = 0.17 ± 0.03, $t_{82.65} = 4.88$, $P < 0.0001$) and even in single females (estimate = 0.15 ± 0.04, $t_{38.68} = 3.7$, $P < 0.001$). For paired and parental females, the APIs then decreased by the same amount in the breeding period, continued to decrease in the rearing period and flattened after the breeding period (Table 1). Parental females were fatter in the pre-breeding and breeding period but leaner in the rearing period. Single females had the lowest APIs during the pre-breeding and breeding period but showed a marked increase and therefore higher APIs in the middle of the rearing period (estimate = 0.15 ± 0.08, $t_{87.29} = 1.85$, $P < 0.07$, n.s.; Fig. 2). From week 17, the APIs of all social classes decreased in both sexes, especially strongly in single birds. Finally, the APIs were very similar between social classes and both males and females in the post-breeding period (estimates ≤ 0.07, $P \leq 0.9$, n.s. across all groups). Finally, the APIs were very similar between males and females in each social class in the post-breeding period.

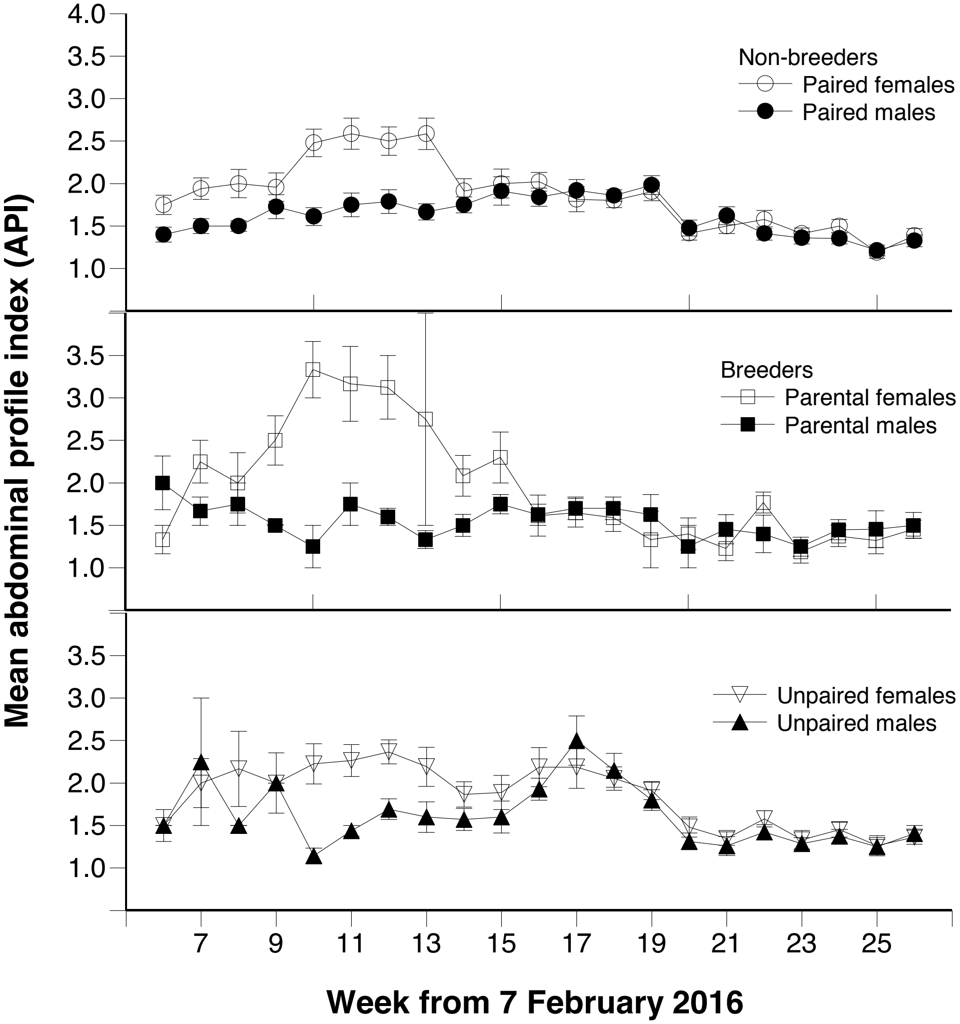

Figure 2. Changes in the mean (± s.e.) abdominal profile indices recorded for Greylag Geese of different social and breeding status during spring and early summer (7 February–30 June 2016). Sample sizes (*n*) for each week in consecutive order (weeks 6–26): paired females (15, 12, 12, 11, 31, 22, 26, 27, 28, 17, 25, 25, 32, 30, 44, 33, 33, 40, 38, 35, 32), paired males (14, 17, 10, 12, 25, 23, 27, 23, 21, 13, 24, 19, 33, 32, 35, 34, 26, 40, 36, 32, 27), parental females (6, 4, 4, 3, 3, 3, 4, 2, 6, 5, 13, 10, 11, 3, 5, 11, 13, 8, 12, 14, 11), parental males (6, 3, 2, 1, 2, 2, 5, 6, 6, 6, 12, 10, 10, 9, 2, 11, 10, 6, 10, 11, 11), single females (5, 2, 3, 1, 7, 8, 13, 10, 7, 9, 7, 3, 10, 18, 24, 21, 18, 26, 32, 26, 26) and single males (7, 6, 3, 4, 11, 17, 15, 13, 15, 9, 8, 8, 19, 23, 28, 23, 19, 27, 31, 21, 22). Nesting occurred from 4 March–18 April 2016, and hatching from 04 April–18 May 2016, respectively. Non-breeders may start to moult as early as mid-May; parental birds moult when the young fledge, from mid-June onwards.

Table 1. Linear mixed-effects model of the effect of calendar week and social class (paired, parental, unpaired) on the abdominal profiles (APIs) of female Greylag Geese for each time period. P values: *** < 0.001; ** < 0.01; * < 0.05; **.** < 0.1 (n.s.); n.s. > 0.1.

Time period	**Pre-breeding**					**Breeding**				
No. observations	177					169				
No. individuals	81					79				
Random effects:	Var.	s.d.				Var.	s.d.			
ID	0.18	0.42				0.18	0.42			
Residual	0.28	0.53				0.40	0.63			
Fixed effects:	Est.	s.e.	d.f.	*t*	*P*	Est.	s.e.	d.f.	*t*	*P*
(Intercept)	0.59	0.24	165.91	2.45	*	4.56	0.65	136.34	7.06	***
Calendar week	0.18	0.02	142.96	7.34	***	–0.17	0.05	133.54	–3.61	***
Parental female	0.10	0.20	83.37	0.51	n.s.	0.21	0.24	79.34	0.90	n.s.
Unpaired female	–0.41	0.14	88.00	–2.83	**	–0.20	0.15	70.87	–1.31	n.s.
Time period	**Rearing**					**Post-breeding**				
No. observations	302					452				
No. individuals	110					114				
Random effects:	Var.	s.d.				Var.	s.d.			
ID	0.05	0.22				0.04	0.20			
Residual	0.29	0.54				0.17	0.41			
Fixed effects:	Est.	s.e.	d.f.	*t*	*P*	Est.	s.e.	d.f.	*t*	*P*
(Intercept)	4.03	0.43	254.90	9.41	***	2.05	0.29	393.32	7.16	***
Calendar week	–0.12	0.02	246.71	–5.35	***	–0.03	0.01	381.49	–2.20	*
Parental female	–0.28	0.12	86.29	–2.37	*	–0.02	0.08	95.98	–0.18	n.s.
Unpaired female	0.15	0.08	87.29	1.85	.	–0.05	0.06	107.28	–0.77	n.s.

Males of all social classes did not fluctuate as much over the weeks (estimates ≤ 0.2, $P \leq 0.8$, n.s. across each of the four time periods). Their APIs were also more similar between social classes as compared to the females.

Discussion

In spring, the increase in body weight in female geese has been attributed to an increased food quality due to spring flush of the vegetation (Owen 1981). At that time ovaries of females become enlarged and female geese accumulate fat reserves for egg production (Owen 1981) and incubation. It has been suggested that such endogenous cycles control body mass irrespective of food availability or feeding opportunity (Pienowski *et al.* 1979). Owen *et al.* (1992) could not entirely exclude this hypothesis but argued that, for Barnacle Geese *Branta leucopsis* wintering in southwest Scotland, declining food resources caused a loss in body weight towards spring. In contrast, female Greylag Geese in Stuttgart put on body weight in February although food resources were scarce (Käßmann & Woog 2007). This could indicate that environmental variation could override circannual endogenous patterns of body weight variation. Therkilsden & Madsen (2000) suggested that pink footed geese adjusted their winter weights to an optimum based on a trade-off between the need for accumulation of body reserves to meet periods with high energy demands such as egg production and incubation and the increased metabolic cost of maintenance and activities. In Greater White-fronted Geese *Anser albifrons*, females spent more time feeding during spring than males (Budeau *et al.* 1991) indicating a difference in demand between the sexes (*i.e.* Moriguchi *et al.* 2010). In a flock of feral Canada Geese in England, females with higher APIs nested earlier. Early nesting correlated positively with both hatching and fledging success. Thus, breeding success appeared to be strongly influenced by the reserves acquired by the female and her timing (Johnson & Sibly 1993).

In our study, the relative body weight (API) of females increased before the breeding season regardless of the social status of a female – even single females and non-breeding females put on body mass during this time. This supports the hypothesis of Pienowski *et al.* (1979) of an underlying endogenous cycle that does not distinguish between the different probabilities of a female to produce offspring that year. Whilst feeding conditions are favourable in the public parks, nesting opportunities in Stuttgart are scarce and restricted to a few islands. In 2016, only 12% of the population bred (Ehret 2016). Non-breeding paired and single females nevertheless put on body weight whilst males did not. When paired, it may be a good strategy for a female to put on weight in case one of the rare nesting sites becomes vacant. She would then be instantly ready to produce eggs within a few days. On the other hand, the probability of becoming a breeder is very low when a female is not paired by the end of winter, thus supporting the existence of an endogenous mechanism. Males in our study did not put on body weight during that time, indicating that the increase in weight is linked to the female sex only. In spring, males may be limited in their ability to accumulate body reserves, as they defend their female partner and feeding areas around her and show higher vigilance rates (Owen 1981; Zillich & Black 2002).

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Photograph: Greylag Goose, by Richard Taylor Jones.