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Food availability modulates the effects of maternal antibodies on growth and immunity in young feral pigeons

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Running title: Food availability and maternal antibodies

Abstract

It is now widely acknowledged that mothers can transfer their own immune experience to their progeny through the allocation of specific maternal antibodies (hereafter referred as MatAb) that can shape offspring phenotype and affect their fitness. However, the importance of environmental variability in modulating the effects of MatAb on offspring traits is still elusive. Using an experimental approach, we investigated how food availability interacted with MatAb to solve the trade-off between humoral immunity and growth in young feral pigeons (*Columba livia*). Results show that the inhibitory effect of MatAb on the humoral response of chicks was detected regardless of the food treatment. In addition, body mass growth was higher in chicks receiving lower amounts of maternal antibodies but only in chicks of the *ad libitum* food treatment. This contradicts previous studies and suggests that the transfer of MatAb could entail some costs for chicks and reduces their growth. Taken together these results reinforce the idea that the transfer of MatAb play a central role in shaping host life-history traits but that their adaptive value is highly dependent on the environmental context in which they take place.

Keywords: humoral response, immun**o**-ecology, maternal effects, transgenerational effects, trade-off.

Introduction

The transfer of antibodies from mothers to their offspring has now been well documented in domesticated (Smith et al. 1994) and wild animals (Gasparini et al. 2001, 2002, Boulinier and Staszewski 2008, Garnier et al. 2012, 2013, Jacquin et al. 2013) and researchers have started to investigate the adaptive significance of such transfer and their consequences for host-parasite interactions (Grindstaff et al. 2003, Siegrist 2003, Gasparini et al. 2006). MatAb are transferred across the follicular epithelium into the yolk during oogenesis by an active process (Loeken & Roth 1983; Kowalczyk 1985; Apanius 1998) and a positive correlation between antigen specific antibodies level in mother's plasma and the level in egg yolk has been reported in several studies (Apanius 1998; Blount et al. 2002; Gasparini et al. 2002; Saino et al. 2002; Morales et al. 2006). MatAb are absorbed into embryonic circulation (Kowalczyk 1985) and confer passive protection to offspring by binding and participating to the destruction of antigens encountered by the young (Wang et al. 2004; Hamal et al. 2006; Gasparini et al. 2006; Castinel et al. 2008). Since neonatal vertebrates have a limited ability to mount an immune response during the first days of their life, MatAb can provide an important protection against pathogens with beneficial effects on fitness (Heeb et al. 1998; Buechler et al. 2002; Kristan 2002; Grindstaff 2008). The persistence of MatAb in chick's circulation may be variable among individuals and species (Garnier et al. 2013), but even after they are catabolized their effects on immunity may affect offspring phenotype by influencing growth and developmental rate through potential trade-offs (Robison et al., 1988; Gustafsson et al., 1994).

A direct effect of this maternal protection is a reduction in the level of specific antigens circulating in offspring blood, which in turn should inhibit the own synthesis of antibodies by the offspring towards the same antigens (inhibitory effect). Therefore, it is possible to indirectly measure the protective role of MatAb by examining the inhibitory effect

on the production of specific antibodies in offspring (Anderson, 1995; Carlier and Truyens 1995; Siegrist 2003; Boulinier and Staszewski 2008; Gasparini et al. 2009; Merrill and Grindstaff 2014). Using this approach, several studies confirm this adaptive effect of MatAb in different species (Gasparini et al. 2009; Staszewski et al. 2007; Staszewski and Siitari 2010; Jacquin et al. 2012; Garnier et al. 2012, 2013).

By reducing the intensity of the humoral and innate immune response of the chick, MatAb may also reduce the energy allocated to the immune system (Grindstaff 2008; Rutkowska et al. 2012), and therefore, may positively impact the growth of offspring (Buechler et al. 2002; Pihlaja et al. 2006; Grindstaff 2008), constituting an indirect beneficial effect of the inhibitory effect of MatAb (Boulinier and Stazsewski 2008). However, the intensity and adaptive value of such reallocation is likely to depend on the amount of resource available for the chick, so that the effect of MatAb on offspring phenotype is likely to strongly vary with environmental conditions and food availability. However, the effect of environmental heterogeneity on the effects of MatAb is still elusive.

Food availability encountered during early life has important effects on the development of the immune system (Gasparini et al. 2006) and offspring growth (Hoi-Leitner et al. 2001), and may affect the trade-offs between these two life-history traits. In particular, when food availability is low, energy is limited and trade-offs between growth and immunity might be more detectable (Soler et al. 2003; Brommer 2004; Pihlaja et al. 2006; Arriero et al. 2013). Under food limitation, we therefore expect that juveniles might reduce their investment in their humoral immune response (e.g. Bonneaud et al. 2003). Furthermore, we can also expect that the positive consequences of the inhibitory effect of MatAb on growth parameters might be more pronounced under low food availability conditions compared to high food availability conditions.

To test these predictions we experimentally manipulated post-hatching food availability and MatAb received by chicks in feral pigeons (*Columba livia*) kept in captivity and examined their immune responses and growth parameters across time after antigen injections. In a previous study, we showed that limited food availability reduced the transfer of MatAb in mothers (Ismail et al. 2013). Here, we focused on the effects of these MatAb and food availability on their chicks. We investigated how food availability could modulate the inhibitory effects of MatAb on the humoral immune response of chicks and associated costs on growth. To this end, we measured the immune response and growth of chicks injected with KLH antigen (Keyhole Limpet Hemocyanin) in relation to food availability during rearing period (food availability of foster parents) and the level of MatAb transmitted.

Materials and methods

Study populations and general design

60 females and 60 males adult feral pigeons were captured in 2010 near Paris by the SACPA Company (France) under the authorization of local authorities. 10 groups of 6 females and 6 males were placed in 10 outdoor aviaries (2.20 m x 2.20 m) at the CEREEP field station (CEREEP-Ecotron Ile-de-France, UMS 3194, Ecole Normale Supérieure, St-Pierre-les-Nemours, France). Adults were submitted to a food and an immune treatment in a cross design. Then, eggs of similar laying date (± 1 day) were swapped between nests (within or between aviaries) to obtain experimental groups of chicks differing in prenatal and postnatal female injection and food availability experienced by biological and foster parents (see Ismail et al. 2013). Using this design, we were able to investigate the interacting role of food availability and MatAb transferred on immune responses and growth parameters of chicks.

Food treatment

Young feral pigeons can fledge between 30 and 40 days of age but they are still fed by parents until the age of 50-60 days (Johnston and Janiga 1995). Food treatment of chicks was thus determined by the amount of food provided by foster parents. Food treatments of parents was initiated two weeks before the immune treatment (i.e. the 8 of March 2010) and lasted 6 months. Adult females and males (N = 120) were randomly assigned to one of two groups: one ‘‘food-limited’’group and other "*ad libitum* food" group. In the‘‘food-limited’’group 60 pigeons (in five aviaries) were fed with 30g of wheat per day per bird (low protein and lipid diet), corresponding to a basal diet necessary to maintain non-breeding captive pigeons (Hawkins et al. 2001). When the chicks in this group hatched, no additional food in the aviary was added during their first week of life. During their second week of life, 15 g per chick per day were added. From the third week onwards, 30 g per chick per day were added. Therefore, the food treatment of chicks was same as that of the foster parents because they were sharing the same aviary. In the "*ad libitum* food" group, 60 pigeons from 5 aviaries were fed *ad libitum* with a mix of corn, wheat, and peas. All pigeons were supplemented with minerals and vitamin-enriched and water.

Parental and chicks immunization treatment

The immunization treatment of parents started two weeks after the beginning of the food treatment **(**i.e. the 22 of March 2010**)**. 60 birds (three breeding pairs chosen randomly in each aviary) received a subcutaneous injection of a 100-µL solution containing 0.5 $mg.mL^{-1}$ Keyhole Limpet Hemocyanin (KLH) (antigen-injected group). The 60 remaining birds were injected with phosphate-buffered saline (PBS) (sham-injected group). A second injection was performed two weeks later to ensure that blood anti-KLH Ab levels differed between antigen- and sham-injected treatment groups. Nests were monitored daily to record laying and hatching dates. We used immune treatment of females to create two groups of chicks that had or not

144 received anti-KLH MatAb. We collected blood samples from 3-days-old chicks to measure
145 their anti-KLH Ab level. This anti-KLH Ab level at 3-days-old was significantly higher in
146 chicks from KLH-injected females (mean ± se: 1.88 ± 0.21) than in chicks from sham-
147 injected females (0.59 ± 0.07; $F_{1,102} = 41.13$, $P < 0.0001$) ensuring that we were able to create
148 two groups of chicks differing by their levels of anti-KLH MatAb (MatAb+ group: chicks
149 from KLH injected females and MatAb- group: chicks from sham-injected females). Note that
150 female injection did not impact body mass ($F_{1,102} = 0.39$, $P = 0.53$), tarsus size ($F_{1,102} = 0.27$, P
151 = 0.60) or wing size ($F_{1,102} = 0.43$, P= 0.51) of hatchlings. We also used these blood samples
152 to determine sex of chicks using a molecular method following Griffiths et al. (1998).
153
154 *Immunity and growth of chicks*
155 To examine the primary and secondary humoral immune response, all 21- and 35-
156 days-old chicks were injected subcutaneously with 100-µL solution containing 0.5 $mg.mL^{-1}$ of
157 KLH (the same antigen as their mother). We collected blood samples from chicks across time,
158 i.e. 21, 28, 35, 42, 49 and 56 days post-hatching to follow the dynamics of anti-KLH Ab
159 production following the injections.
160 To examine growth during this time period, we measured body mass at each blood
161 collection to the nearest g, and wing size and tarsus size to the nearest mm. We analysed the
162 three growth variables separately because body mass, wing size and tarsus length are believed
163 to reflect different aspects of chick quality in birds (Nilsson and Gårdmark 2001; O'Brien and
164 Dawson 2008). Indeed, body mass depends on fat storage and is linked to fledging success,
165 while tarsus length reflects skeletal growth patterns, and wing size depends on both skeletal
166 and feather growth (Johnston and Janiga 1995).
167 Blood samples were centrifuged, and the plasma was stored at -20°C for
168 immunological assays. Anti-KLH IgY Ab levels in the plasma samples were assayed using an

ELISA method described in Jacquin et al. (2012). Overall, 122 chicks **hatched** and 104 survived until 56 days. This mortality was not associated with maternal injections and food treatments (GLM for binomial distribution, Maternal injection Ab: $\chi^2_1 = 0.72$, P = 0.40; Food treatment of chicks: $\chi^2_1 = 0.80$, P = 0.37 and their interaction: $\chi^2_1 = 1.97$, P = 0.16). Finally, we successfully sampled 104 chicks (18 MatAb+ chicks of the restricted food treatment, 26 MatAb+ chicks of the *ad libitum* food treatment, 34 MatAb- chicks of the restricted food treatment and 26 MatAb-chicks of the *ad libitum* food treatment).

Statistical analyses

To test the effects of food treatment and MatAb on humoral immune response and growth of chicks, we performed four mixed models for repeated measures (Proc Mixed, see Littell et al. 2006) with anti-KLH Ab level, body mass, wing and tarsus size of chicks as response variables. We included the food treatment during rearing period and female injection group (reflecting the amount of antibodies transferred) as cofactors and chick age (21, 28, 35, 42, 49 and 56 days) as a covariate. We also added the sex of chicks as a cofactor. The foster nest and nestlings identities were included as random factors to take into account pseudoreplication issues. We compared all models possible involving second- and third-order interactions and the best-fitting models were chosen following the AICc criterion. All statistical analyses were performed using SAS (version 9.2). We used the Kenward-Roger correction to compute degrees of freedom which is recommended whenever the Proc Mixed is used for repeated measures (Littell et al. 2006). Exact P values are reported, and Bonferroni corrections were not applied (Moran 2003; Garcia 2004; Nakagawa 2004).

Results

193 Food treatment during rearing period did not affect the dynamics of anti-KLH Ab production
194 in nestlings (Table 1), but anti-KLH MatAb had an inhibitory effect on the primary and
195 secondary immune response of chicks (significant female injection x age interaction: Table 1)
196 (Fig. 1). **Indeed, statistical analyses performed at different ages show significant lower**
197 **anti-KLH Ab level at 35 days (primary immune response, P =0.009) and at 42 and 49**
198 **days of age (secondary immune response, P = 0.007 and P =0.03, respectively) for**
199 **MatAb+ chicks as compared to MatAb- chicks. Note that at 21 days of age, MatAb+**
200 **chick had still higher maternal anti-KLH Ab level than MatAb- chicks (P=0.03).**
201 Chicks from the *ad libitum* food treatment had a significant higher body mass, wing
202 and tarsus size than chicks from the restricted food treatment (Table 1). Furthermore, body
203 mass was differently affected by the amount of maternal anti-KLH Ab transferred depending
204 on food availability as shown by the significant interaction between female injection and food
205 treatment. Indeed, in the *ad libitum* treatment group, chicks having received lower amounts of
206 MatAb (MatAb- chicks from sham-injected females), were heavier than chicks having
207 received higher amounts of MatAb (MatAb+ chicks from KLH injected females) (Fig. 2,
208 Mixed Model, $F_{1,255} = 4.40$, $P = 0.04$). This difference was not found in the food restricted
209 treatment ($F_{1,254} = 1.45$, $P = 0.23$). In addition, female injection did not affect tarsus and wing
210 size growth of chicks (Table 1).
211
212 **Discussion**
213 This study aimed at investigating the role of food variability in modulating the effects of
214 MatAb on life-history traits of young vertebrates. The first goal was to identify the respective
215 effect of food availability and MatAb on the humoral immune response of chicks against an
216 injected antigen. Results show first that MatAb had an inhibitory effect on the primary and
217 secondary humoral responses of young pigeons, as previously reported in other species (Fig.

1; e.g. Staszewski et al. 2010). But interestingly, this inhibitory effect did not interact with food availability. Contrary to previous studies reporting an energetic cost of the humoral immune response in adults (*e.g.* Bonneaud et al. 2003), we did not find any negative effect of food restriction on the humoral immune response of young chicks, and chicks mounted similar immune responses against the injected antigen whatever their food treatment. One potential explanation is that when food availability is low, chicks might favor immunity at the expense of body mass and size growth (Stearns 1992). This interpretation is consistent with the negative effect of food restriction on body mass, wing and tarsus size of growing chicks (but not on immunity) found in this study. Overall, these results reinforce the idea that MatAb play a central role in neonates by modulating the immune response (Boulinier & Staszewski 2008), and call for long term studies to elucidate the consequences of this early environmental factor on adult fitness and life-history strategies.

The second aim of our study was to investigate the interacting effects of MatAb and food availability on the trade-off between immunity and growth. We expected a higher growth of chicks having received a higher amount of MatAb, because MatAb are supposed to allow chicks to save energy for growth by reducing the cost of mounting a humoral immune response. Contrary to our expectations, we found that body mass growth was higher in chicks receiving lower amounts of MatAb in the *ad libitum* food treatment (Fig. 2). This contrasts with previous studies that either failed to detect an effect of MatAb on growth (Grindstaff et al. 2006, Staszewski et al. 2007) or found positive effects of MatAb on growth parameters (Heeb et al. 1998, Grindstaff 2008). Our results rather suggest that receiving MatAb entails some costs for chicks in terms of growth and does not enable them to save energy from a costly immune response. This is consistent with a previous study on pigeons in which we found, on a smaller sample size, that postnatal non-specific MatAb could impair growth

(Jacquin et al. 2012). This study provides the first experimental evidence of a cost associated with MatAb.

As we performed a cross-fostering experiment and swapped eggs between nests, this negative effect of MatAb on growth cannot be explained by differences in postnatal parental care (for instance, differences in feeding rates). Although further studies will be necessary to decipher the underlying mechanisms, this negative effect of MatAb on body mass might be explained by differences in nutrients or hormones packed into the eggs. Indeed, in 2008, Boulinier and Staszewski suggested that MatAb transfer might represent a significant energy drain for females since high amounts of antibodies are diverted from blood circulation into the eggs (10 to 20%). This could impact the ability of mothers to transfer other substances, such as nutrients or hormones, into the eggs, which could potentially impact offspring growth (Gasparini et al. 2007). For instance, it is possible that injected mothers could transfer higher amounts of MatAb at the expense of other proteins and molecules in their eggs (for instance lysozymes, vitamins, corticosterone, carotenoids). Further experimental works will help investigating potential trade-offs between MatAb and other active substances in eggs and elucidate the underlying mechanisms of this negative effect of MatAb on offspring growth.

In conclusion, this study reinforces the idea that variations in resource availability can strongly impact the effects of MatAb on the ontogeny of life-history traits. Since wild animal populations will likely be submitted to increased resource fluctuations due to global changes, we advocate to explicitly take into account such interacting effects of resource availability and MatAb since they could determine the outcome of host-parasite interactions across generations and affect pathogen epidemiology in wild populations

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409 **Table 1**. Output of the best-fit generalized mixed models explaining variations in anti-KLH
410 Ab levels, body mass, wing and tarsus size in chicks as they age in interaction with the food
411 treatment during rearing period and the female injection. Sex was added as a cofactor. All
412 interactions removed from the final model were non-significant.

	Anti-KLH Ab level			Body mass			Wing size			Tarsus Size		
Effects	DF	F	P	DF	F	P	DF	F	P	DF	F	P
Age	5, 502	97.72	< **0.001**	5,499	135.9	< **0.001**	5,500	2048.42	< **0.001**	5,500	28.29	<**0.001**
Food treatment	1,40.9	1.91	0.17	1,34.6	16.4	< **0.001**	1,43.6	3.48	0.07	1,36.4	11.59	**0.002**
Female injection	1,92.6	5.15	**0.03**	1,86.5	0.09	0.77	1,98	0.01	0.93	1,89.8	0.04	0.83
Sex	1,93.7	2.01	0.16	1,94.1	11.57	**0.001**	1,86.5	9.66	**0.003**	1,92.8	24.58	<**0.001**
Age x Female injection	5,502	3.77	**0.002**	5,499	0.52	0.76	5,500	0.58	0.72	_	_	_
Female injection x Food treatment	_	_	_	1,85.2	4.32	**0.04**	1,97.9	0.54	0.46	1,88.8	0.91	0.34
Age x Food treatment	_	_	_	5,499	0.96	0.44	5,500	1.00	0.42	_	_	_
Female injection x Food treatment x age	–	_	_	5,499	0.83	0.53	5,500	0.47	0.80	_	_	_

Fig. 1. Humoral immune response of chicks over time, measured by anti-KLH Ab level in relation to maternal level of anti-KLH Ab. Chicks were split into two categories on whether they received (MatAb+: KLH injected mother) or not (MatAb-: sham-injected mother) anti-KLH from their mothers. MatAb+ chicks are represented by black squares and MatAb- chicks are represented by white dots. The arrows signal the timing of KLH injections.

Fig. 2. Chicks body mass as they age in relation to maternal injection (MatAb+ vs. MatAb-) and the food treatment. MatAb+ Chicks of the restricted food treatment are represented by white squares, MatAb+ chicks of the *ad libitum* food treatment are represented by black squares, MatAb- chicks of the restricted food treatment are represented by white dots and MatAb- chicks of the *ad libitum* food treatment are represented by black dots.

Fig. 1.

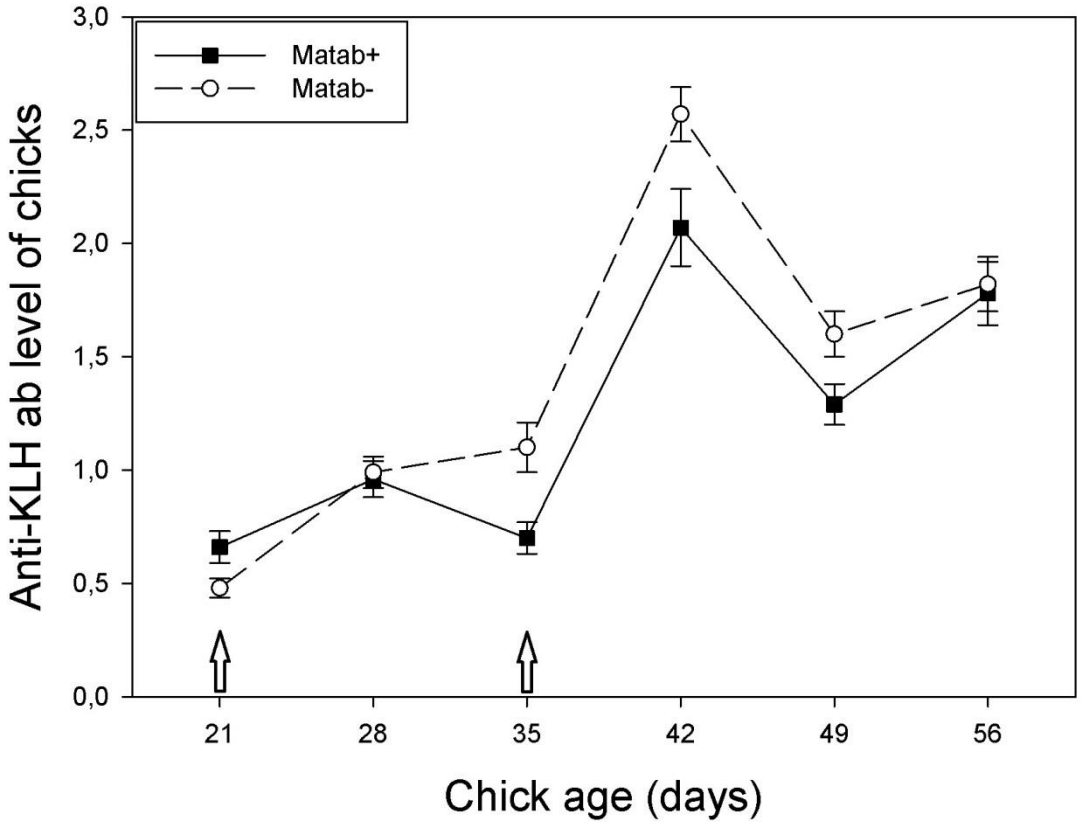
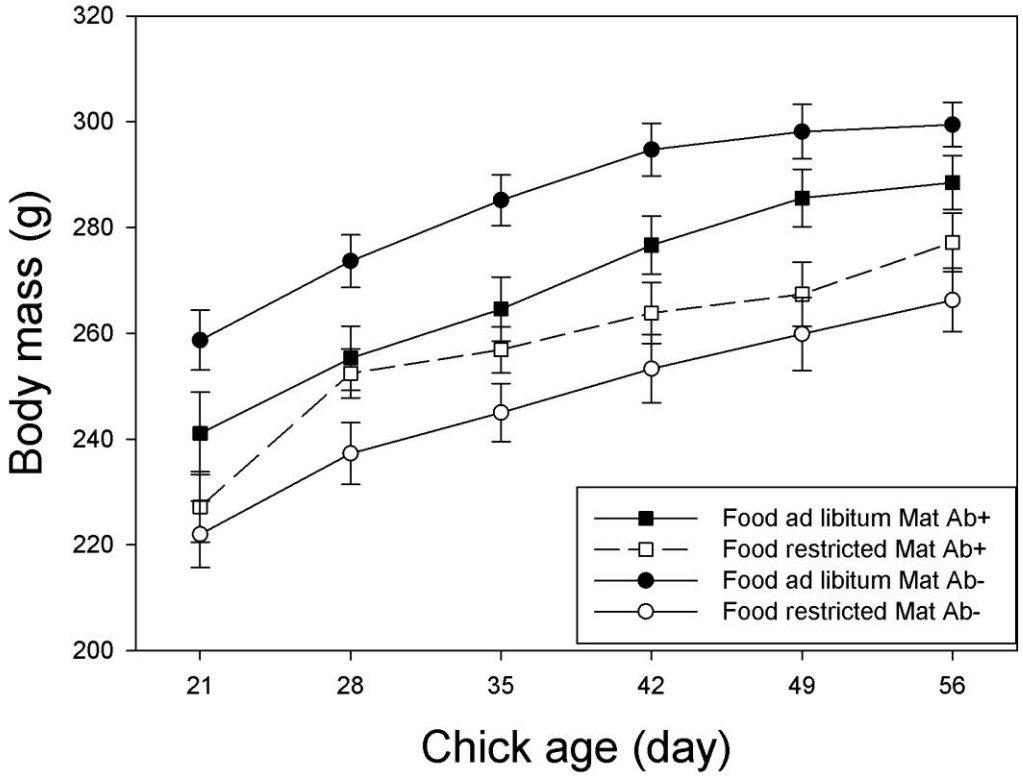

Matab+
Matab-
Anti-KLH ab level of chicks
3,0
2,5
2,0
1,5
1,0
0,5
0,0
21
28
35
42
49
56
Chick age (days)

Fig. 2


320
300
280
260
240
220
200
Body mass (g)
21
28
35
42
49
56
Chick age (day)
Food ad libitum Mat Ab+
Food restricted Mat Ab+
Food ad libitum Mat Ab-
Food restricted Mat Ab-