

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

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27	Running title: Food availability and maternal antibodies

#### 28 Abstract

It is now widely acknowledged that mothers can transfer their own immune experience to 29 their progeny through the allocation of specific maternal antibodies (hereafter referred as 30 MatAb) that can shape offspring phenotype and affect their fitness. However, the importance 31 of environmental variability in modulating the effects of MatAb on offspring traits is still 32 elusive. Using an experimental approach, we investigated how food availability interacted 33 with MatAb to solve the trade-off between humoral immunity and growth in young feral 34 pigeons (Columba livia). Results show that the inhibitory effect of MatAb on the humoral 35 response of chicks was detected regardless of the food treatment. In addition, body mass 36 growth was higher in chicks receiving lower amounts of maternal antibodies but only in 37 chicks of the ad libitum food treatment. This contradicts previous studies and suggests that the 38 transfer of MatAb could entail some costs for chicks and reduces their growth. Taken together 39 40 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 41 42 context in which they take place.

Keywords: humoral response, immuno-ecology, maternal effects, transgenerational effects,
trade-off.

#### 45 Introduction

The transfer of antibodies from mothers to their offspring has now been well documented in 46 domesticated (Smith et al. 1994) and wild animals (Gasparini et al. 2001, 2002, Boulinier and 47 Staszewski 2008, Garnier et al. 2012, 2013, Jacquin et al. 2013) and researchers have started 48 to investigate the adaptive significance of such transfer and their consequences for host-49 parasite interactions (Grindstaff et al. 2003, Siegrist 2003, Gasparini et al. 2006). MatAb are 50 transferred across the follicular epithelium into the yolk during oogenesis by an active process 51 (Loeken & Roth 1983; Kowalczyk 1985; Apanius 1998) and a positive correlation between 52 antigen specific antibodies level in mother's plasma and the level in egg yolk has been 53 reported in several studies (Apanius 1998; Blount et al. 2002; Gasparini et al. 2002; Saino et 54 55 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 56 destruction of antigens encountered by the young (Wang et al. 2004; Hamal et al. 2006; 57 58 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 59 protection against pathogens with beneficial effects on fitness (Heeb et al. 1998; Buechler et 60 al. 2002; Kristan 2002; Grindstaff 2008). The persistence of MatAb in chick's circulation may 61 be variable among individuals and species (Garnier et al. 2013), but even after they are 62 catabolized their effects on immunity may affect offspring phenotype by influencing growth 63 and developmental rate through potential trade-offs (Robison et al., 1988; Gustafsson et al., 64 1994). 65

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, 75 MatAb may also reduce the energy allocated to the immune system (Grindstaff 2008; 76 Rutkowska et al. 2012), and therefore, may positively impact the growth of offspring 77 (Buechler et al. 2002; Pihlaja et al. 2006; Grindstaff 2008), constituting an indirect beneficial 78 79 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 80 available for the chick, so that the effect of MatAb on offspring phenotype is likely to strongly 81 82 vary with environmental conditions and food availability. However, the effect of environmental heterogeneity on the effects of MatAb is still elusive. 83

Food availability encountered during early life has important effects on the 84 development of the immune system (Gasparini et al. 2006) and offspring growth (Hoi-Leitner 85 et al. 2001), and may affect the trade-offs between these two life-history traits. In particular, 86 when food availability is low, energy is limited and trade-offs between growth and immunity 87 might be more detectable (Soler et al. 2003; Brommer 2004; Pihlaja et al. 2006; Arriero et al. 88 2013). Under food limitation, we therefore expect that juveniles might reduce their investment 89 in their humoral immune response (e.g. Bonneaud et al. 2003). Furthermore, we can also 90 91 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 92 availability conditions. 93

To test these predictions we experimentally manipulated post-hatching food 94 availability and MatAb received by chicks in feral pigeons (Columba livia) kept in captivity 95 and examined their immune responses and growth parameters across time after antigen 96 injections. In a previous study, we showed that limited food availability reduced the transfer 97 of MatAb in mothers (Ismail et al. 2013). Here, we focused on the effects of these MatAb and 98 food availability on their chicks. We investigated how food availability could modulate the 99 inhibitory effects of MatAb on the humoral immune response of chicks and associated costs 100 101 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 102 period (food availability of foster parents) and the level of MatAb transmitted. 103

104

#### 105 Materials and methods

#### 106 Study populations and general design

60 females and 60 males adult feral pigeons were captured in 2010 near Paris by the SACPA 107 108 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 109 (CEREEP-Ecotron Ile-de-France, UMS 3194, Ecole Normale Supérieure, St-Pierre-les-110 Nemours, France). Adults were submitted to a food and an immune treatment in a cross 111 design. Then, eggs of similar laying date  $(\pm 1 \text{ day})$  were swapped between nests (within or 112 between aviaries) to obtain experimental groups of chicks differing in prenatal and postnatal 113 female injection and food availability experienced by biological and foster parents (see Ismail 114 et al. 2013). Using this design, we were able to investigate the interacting role of food 115 availability and MatAb transferred on immune responses and growth parameters of chicks. 116

117

118 *Food treatment* 

Young feral pigeons can fledge between 30 and 40 days of age but they are still fed by parents 119 until the age of 50-60 days (Johnston and Janiga 1995). Food treatment of chicks was thus 120 determined by the amount of food provided by foster parents. Food treatments of parents was 121 initiated two weeks before the immune treatment (i.e. the 8 of March 2010) and lasted 6 122 months. Adult females and males (N = 120) were randomly assigned to one of two groups: 123 one "food-limited" group and other "ad libitum food" group. In the "food-limited" group 60 124 pigeons (in five aviaries) were fed with 30g of wheat per day per bird (low protein and lipid 125 126 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 127 was added during their first week of life. During their second week of life, 15 g per chick per 128 day were added. From the third week onwards, 30 g per chick per day were added. Therefore, 129 the food treatment of chicks was same as that of the foster parents because they were sharing 130 131 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 132 and vitamin-enriched and water. 133

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#### 135 Parental and chicks immunization treatment

The immunization treatment of parents started two weeks after the beginning of the food 136 treatment (i.e. the 22 of March 2010). 60 birds (three breeding pairs chosen randomly in each 137 aviary) received a subcutaneous injection of a 100- $\mu$ L solution containing 0.5 mg.mL<sup>-1</sup> 138 Keyhole Limpet Hemocyanin (KLH) (antigen-injected group). The 60 remaining birds were 139 injected with phosphate-buffered saline (PBS) (sham-injected group). A second injection was 140 performed two weeks later to ensure that blood anti-KLH Ab levels differed between antigen-141 and sham-injected treatment groups. Nests were monitored daily to record laying and hatching 142 dates. We used immune treatment of females to create two groups of chicks that had or not 143

received anti-KLH MatAb. We collected blood samples from 3-days-old chicks to measure 144 their anti-KLH Ab level. This anti-KLH Ab level at 3-days-old was significantly higher in 145 chicks from KLH-injected females (mean  $\pm$  se: 1.88  $\pm$  0.21) than in chicks from sham-146 injected females (0.59  $\pm$  0.07; F<sub>1.102</sub> = 41.13, P < 0.0001) ensuring that we were able to create 147 two groups of chicks differing by their levels of anti-KLH MatAb (MatAb+ group: chicks 148 from KLH injected females and MatAb- group: chicks from sham-injected females). Note that 149 female injection did not impact body mass ( $F_{1,102} = 0.39$ , P = 0.53), tarsus size ( $F_{1,102} = 0.27$ , P 150 = 0.60) or wing size ( $F_{1,102}$  = 0.43, P= 0.51) of hatchlings. We also used these blood samples 151 to determine sex of chicks using a molecular method following Griffiths et al. (1998). 152

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#### 154 Immunity and growth of chicks

To examine the primary and secondary humoral immune response, all 21- and 35days-old chicks were injected subcutaneously with 100-μL solution containing 0.5 mg.mL<sup>-1</sup> of KLH (the same antigen as their mother). We collected blood samples from chicks across time, i.e. 21, 28, 35, 42, 49 and 56 days post-hatching to follow the dynamics of anti-KLH Ab production following the injections.

To examine growth during this time period, we measured body mass at each blood collection to the nearest g, and wing size and tarsus size to the nearest mm. We analysed the three growth variables separately because body mass, wing size and tarsus length are believed to reflect different aspects of chick quality in birds (Nilsson and Gårdmark 2001; O'Brien and Dawson 2008). Indeed, body mass depends on fat storage and is linked to fledging success, while tarsus length reflects skeletal growth patterns, and wing size depends on both skeletal 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).

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#### 177 Statistical analyses

178 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. 179 2006) with anti-KLH Ab level, body mass, wing and tarsus size of chicks as response 180 181 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, 49 182 and 56 days) as a covariate. We also added the sex of chicks as a cofactor. The foster nest and 183 nestlings identities were included as random factors to take into account pseudoreplication 184 issues. We compared all models possible involving second- and third-order interactions and 185 186 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 187 degrees of freedom which is recommended whenever the Proc Mixed is used for repeated 188 measures (Littell et al. 2006). Exact P values are reported, and Bonferroni corrections were 189 not applied (Moran 2003; Garcia 2004; Nakagawa 2004). 190

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#### 192 **Results**

Food treatment during rearing period did not affect the dynamics of anti-KLH Ab production 193 in nestlings (Table 1), but anti-KLH MatAb had an inhibitory effect on the primary and 194 secondary immune response of chicks (significant female injection x age interaction: Table 1) 195 (Fig. 1). Indeed, statistical analyses performed at different ages show significant lower 196 anti-KLH Ab level at 35 days (primary immune response, P =0.009) and at 42 and 49 197 days of age (secondary immune response, P = 0.007 and P = 0.03, respectively) for 198 MatAb+ chicks as compared to MatAb- chicks. Note that at 21 days of age, MatAb+ 199 chick had still higher maternal anti-KLH Ab level than MatAb- chicks (P=0.03). 200

Chicks from the *ad libitum* food treatment had a significant higher body mass, wing 201 202 and tarsus size than chicks from the restricted food treatment (Table 1). Furthermore, body mass was differently affected by the amount of maternal anti-KLH Ab transferred depending 203 on food availability as shown by the significant interaction between female injection and food 204 205 treatment. Indeed, in the ad libitum treatment group, chicks having received lower amounts of MatAb (MatAb- chicks from sham-injected females), were heavier than chicks having 206 207 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 treatment ( $F_{1,254} = 1.45$ , P = 0.23). In addition, female injection did not affect tarsus and wing 209 210 size growth of chicks (Table 1).

211

#### 212 **Discussion**

This study aimed at investigating the role of food variability in modulating the effects of MatAb on life-history traits of young vertebrates. The first goal was to identify the respective effect of food availability and MatAb on the humoral immune response of chicks against an injected antigen. Results show first that MatAb had an inhibitory effect on the primary and 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 218 food availability. Contrary to previous studies reporting an energetic cost of the humoral 219 immune response in adults (e.g. Bonneaud et al. 2003), we did not find any negative effect of 220 221 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 222 potential explanation is that when food availability is low, chicks might favor immunity at the 223 expense of body mass and size growth (Stearns 1992). This interpretation is consistent with 224 225 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 226 227 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 228 229 factor on adult fitness and life-history strategies.

230 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 231 232 growth of chicks having received a higher amount of MatAb, because MatAb are supposed to 233 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 234 receiving lower amounts of MatAb in the ad libitum food treatment (Fig. 2). This contrasts 235 with previous studies that either failed to detect an effect of MatAb on growth (Grindstaff et 236 al. 2006, Staszewski et al. 2007) or found positive effects of MatAb on growth parameters 237 (Heeb et al. 1998, Grindstaff 2008). Our results rather suggest that receiving MatAb entails 238 some costs for chicks in terms of growth and does not enable them to save energy from a 239 costly immune response. This is consistent with a previous study on pigeons in which we 240 found, on a smaller sample size, that postnatal non-specific MatAb could impair growth 241

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

As we performed a cross-fostering experiment and swapped eggs between nests, this 244 negative effect of MatAb on growth cannot be explained by differences in postnatal parental 245 care (for instance, differences in feeding rates). Although further studies will be necessary to 246 decipher the underlying mechanisms, this negative effect of MatAb on body mass might be 247 explained by differences in nutrients or hormones packed into the eggs. Indeed, in 2008, 248 Boulinier and Staszewski suggested that MatAb transfer might represent a significant energy 249 drain for females since high amounts of antibodies are diverted from blood circulation into the 250 eggs (10 to 20%). This could impact the ability of mothers to transfer other substances, such 251 as nutrients or hormones, into the eggs, which could potentially impact offspring growth 252 (Gasparini et al. 2007). For instance, it is possible that injected mothers could transfer higher 253 254 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 255 256 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. 257

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			<b>Body mass</b>			Wing size			Tarsus Size		
	DF	F	Р	DF	F	Р	DF	F	Р	DF	F	Р
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.



Fig. 2

