NOTE / NOTE

Dynamics of anti-*Borrelia* antibodies in Black-legged Kittiwake (*Rissa tridactyla*) chicks suggest a maternal educational effect

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Abstract: In the presence of parasites, mothers can transfer specific immunoglobulins to their offspring. These antibodies are typically thought to provide protection until the juvenile produces its own immune response, but they may also act to educate the developing immune system so as to prepare the individual for future parasite challenge. We examined this hypothesis in a natural host–parasite system involving the Black-legged Kittiwake (*Rissa tridactyla* (L., 1758)), the seabird tick (*Ixodes* (*Ceratixodes*) *uriae* White, 1852), and the Lyme disease bacterium (*Borrelia burgdorferi* s.l. (Johnston, 1984)). We compared the dynamics of anti-*Borrelia* antibodies in chicks between ages 5 and 20 days that received a large amount of maternal anti-*Borrelia* antibodies to those that did not. The results suggest that the presence of maternal antibodies against *Borrelia* increases the overall production of anti-*Borrelia* immunoglobulins by chicks and support the existence of an adaptive maternal effect. Experimental approaches are now called for to better appraise the ecological and evolutionary consequences of the maternal transfer of antibodies in host–parasite interactions.

Résumé : En présence de parasites, les mères peuvent transmettre des anticorps spécifiques à leurs juvéniles. Ces anticorps sont susceptibles de conférer une protection temporaire contre le parasite jusqu'à ce que le juvénile soit capable de produire sa propre résistance immunologique. Cependant, ils pourraient aussi servir à éduquer le système immunitaire en développement, préparant ainsi le juvénile contre une future exposition à un parasite spécifique. Nous avons testé cette hypothèse dans un système hôte–parasite naturel impliquant la mouette tridactyle (*Rissa tridactyla* (L., 1758)), la tique des oiseaux de mer (*Ixodes* (*Ceratixodes*) *uriae* White, 1852) et l'agent bactérien de la maladie de Lyme (*Borrelia burgdorferi* s.l. (Johnston, 1984)). Nous avons comparé la dynamique des anticorps anti-*Borrelia* de l'âge de 5 et à l'âge de 20 jours chez des poussins qui avaient reçu une grande quantité d'anticorps anti-*Borrelia* d'origine maternelle à celle de poussins qui n'en n'ayant pas reçu une telle quantité. La présence de ces anticorps maternels chez les poussins est associée à une plus forte augmentation de leur production d'anticorps anti-*Borrelia*, suggérant ainsi l'existence d'un effet maternel éducateur et adaptatif. Des approches expérimentales sont maintenant nécessaires afin de valider cette hypothèse et de mieux comprendre les conséquences écologiques et évolutives d'un tel transfert d'anticorps maternels dans les systèmes hôte–parasite.

Introduction

In the presence of parasites in the environment, a transfer of specific immunity from mother to offspring has been shown to occur in several vertebrate species (Pastoret et al. 1998; Gasparini et al. 2001). In natural avian systems, specific immunoglobulin Y (IgY, which is equivalent to mammalian IgG; Leslie and Clem 1969) can be transferred to the egg yolk in response to parasite infection (Gasparini et al. 2001; Buechler et al. 2002) and may then be proportionally transferred to the young chick (Gasparini et al. 2002). In domestic and captive-reared birds, maternal IgY has been

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shown to provide effective protection to the young until they develop their own immune system (e.g., Smith et al. 1994; Lung et al. 1996). However, the relationship between maternally derived immunoglobulins and offspring protection may not always be simple.

Maternally transferred immunoglobulins may not only confer passive protection, but may also modulate the young's immune response (for a review see Grindstaff et al. 2003). For example, maternal antibodies may enhance the offspring's life-long resistance to disease (Hassan and Curtiss 1996; Lemke and Lange 1999; Lundin et al. 1999). Studies in domestic rodents have suggested that maternal immunoglobulins can specifically educate the developing immune system. That is, young that have received maternal immunoglobulins are able to mount a stronger immune response against the specific antigen when it is encountered later in life (Anderson 1995; Lemke and Lange 1999; Lundin et al. 1999). Although, some research has suggested a protective role of maternal immunoglobulins in chicks of natural bird populations (Heeb et al. 1998; Brinkhof et al. 1999; Gasparini et al. 2001, 2002; Buechler et al. 2002; Grindstaff et al. 2003), no study as of yet has examined how maternal IgY may modulate the immune defence of juveniles, especially in relation to parasite exposure early in life (Heeb et al. 1998).

In this study, we investigate how maternal antibodies against a microparasite, *Borrelia burgdorferi* s.l. (Johnston, 1984), affect the immune response of the young chick in a spatially structured host–ectoparasite system consisting of the tick *Ixodes* (*Ceratixodes*) *uriae* White, 1852 and a colonial seabird, the Black-legged Kittiwake (*Rissa tridactyla* (L., 1758); henceforth simply referred to as Kittiwake). The spirochaete *B. burgdorferi* is the causative agent of human Lyme disease (Barbour and Fish 1993; Kurtenbach et al. 1998) and is transmitted between individual seabirds via the tick. At least one of the strains responsible for this disease (*Borrelia garinii* Baranton, 1992) is frequently found in seabird colonies where the vector is present (Olsen et al. 1993, 1995; Gylfe et al. 1999). We have previously shown the presence of specific antibodies against the Lyme disease agent in Kittiwake eggs (Gasparini et al. 2001) and that these maternal antibodies were transferred from the egg to the young chick (Gasparini et al. 2002). In infested areas, ticks start to feed on chicks when they are approximately 5 days old and parasitism may continue until fledging (Boulinier and Danchin 1996). If the transfer of maternal antibodies is adaptive, it should confer an immediate and (or) long-term advantage to the chick (Mousseau and Fox 1998). More specifically, if maternal IgY educates the immune system of the young Kittiwake, chicks that have received specific maternal IgY should mount a stronger immune response later in development than chicks that have not received these maternal antibodies. We investigate this prediction by examining how the presence of maternally derived IgY against *Borrelia* modulates the dynamics of specific IgY against *Borrelia* during development in Kittiwake chicks.

Materials and methods

Sampling

Fieldwork was conducted in the summers of 2000, 2001, and 2002 on Hornøya, an island in northern Norway (70°22′N, 31°10′E), where approximately 21 000 pairs of Kittiwake breed (Lorentsen 1998). Several isolated breeding cliffs with different levels of tick infestation were used to conduct this study (see Gasparini et al. 2001, 2002).

During the incubation period, we checked Kittiwake nests every 2 days to estimate the hatching dates. The hatching date was defined as the first day we saw a chick in a nest. We then sampled chicks at ages 5, 10, and 20 days, estimating tick infestation and collecting a small amount of blood. The seabird tick typically starts to exploit Kittiwake chicks when they are approximately 5 days old. This ectoparasite has three active stages (larva, nymph, and adult) that feed on the bird for a continuous period of 3–10 days (McCoy et al. 2002). To estimate infestation levels, we counted the number of ticks of each life stage over the entire body of the chick a single time (McCoy et al. 2002). For each chick, we collected approximately 0.1 mL of blood with a sterile syringe rinsed with heparin. Blood samples were centrifuged soon after sampling. The blood plasma was isolated and kept frozen until immunological analyses. Initial sample sizes were large, with 65 chicks in 2000 (from 55 nests), 93 chicks in 2001 (from 73 nests), and 52 chicks in 2002 (from 31 nests). However, natural variation in food availability and predation affected the survival of chicks. To study the dynamics of IgY concentration with age, blood samples at all three ages were required. Overall, we obtained the three blood samples for 13 chicks (from 11 nests) in 2000, 4 chicks (from 4 nests) in 2001, and 29 chicks (from 24 nests) in 2002.

Immunological analyses

Plasma samples were used directly for the immunological assay tests. *Borrelia*-specific enzyme-linked immunosorbent assay (ELISA) tests were performed on all samples using an ELILYME-G/M kit (Diagast, Loos, France). Because this kit was manufactured for human use and was designed to recognise mammalian antibodies, we replaced the anti-IgG antibody of the kit by an anti-chicken IgG antibody (Gasparini et al. 2001). Tests were performed as outlined in Gasparini et al. (2002), except that a new rabbit – anti-chicken IgG antibody (Sigma A-9046) was used. Preliminary analyses showed that this anti-chicken antibody was more powerful in detecting small concentrations of specific antibodies with the ELISA. The optic density (OD) of the resulting solution was read at a wavelength of 492 nm in a spectrophotometer (Microplate Reader 550; Bio-rad Laboratories, Marnes-la-Coquette, France). The OD provided us with a relative measure of specific immunoglobulin concentration in the plasma samples. We measured the OD values of several samples multiple times, both within and across kits to ensure that measures from different kits were comparable. All measurements were highly repeatable (within kit: $r = 0.96$, $F_{[14,15]} = 45.02$, $P < 0.0001$; between kits: $r = 0.96$, $F_{[5,16]} = 246.46$, $P < 0.0001$). Because OD values were not normally distributed, they were log-transformed for statistical analyses.

Presence of maternal IgY in chicks

As chicks are not exposed to ticks, and therefore to *Borrelia*, before they are 5–6 days old, any specific anti-*Borrelia* IgY detected in their plasma at this age should be

of maternal origin. To determine if chicks received maternal IgY against *Borrelia*, we quantified the IgY concentration of 36 six-day-old chicks from tick-free areas of the Kittiwake colony on Middleton island, Alaska. As the transfer of specific maternal anti-*Borrelia* IgY is strongly related to tick infestation (Gasparini et al. 2001), we assumed these chicks received no maternal anti-*Borrelia* IgY. Therefore, the OD values of such samples correspond to a concentration of anti-*Borrelia* that is close to zero. We used the 95% confidence interval of the OD values of this sample as the threshold for a positive test. In particular, 5-day-old chicks from Hornøya with OD values above the upper limit of the 95% confidence interval were considered to have received maternal anti-*Borrelia* IgY (MIg^+). Below this limit, chicks were considered not to have received maternal IgY ($MIg^–$). The mean and variance of the distribution of OD values of Alaskan Kittiwake chicks were not different from those of 7 five-day-old chicks from uninfested nests on Hornøya (mean: $t_{[41]} = –1.27$, $P = 0.21$; variance: $F_{[35,6]} = 1.43$, $P = 0.69$).

Tick exposure

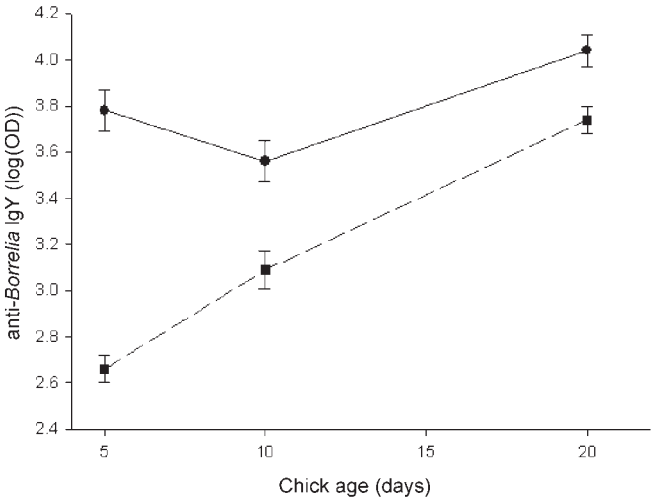
The intensity of the immune response depends, in part, on the dose of the antigen to which individuals are exposed (Goldsby et al. 2000). To control for this factor, we considered the effect of different levels of tick infestation. Based on the distribution of tick infestation on 20-day-old chicks found in a previous study (McCoy et al. 2002), infestation levels were divided into two groups: low infestation (<5 ticks) and high infestation (≥5 ticks). However, these categories were not equally represented in the 3 years of this study (Fisher's exact test, $P = 0.0002$). For this reason, and because tick infestation is likely a more important factor than year, we pooled samples from all years to test for an effect of tick exposure on the immune response.

Statistical analyses and predictions

A chick's immune response against the bacterium *B. burgdorferi* should not be detectable in the first days after hatching, but should be detectable by the time the Kittiwake chick is 20 days old (Apanius 1998). In MIg^+ chicks, we therefore predicted a decrease of these specific IgY between ages 5 and 10 days, reflecting the natural disappearance of maternally derived IgY. Inversely, in $MIg^–$ chicks, we predicted an increase or no change of these specific IgY between ages 5 and 10 days, depending on tick exposure and whether local ticks carried *Borrelia*. The fact that we used the OD values at age 5 days to assign chicks to the MIg^+ and $MIg^–$ groups may also contribute partially to this pattern (non-independence between the values at 5 days old and chick category). After age 10 days, maternal IgY should no longer be detectable (Apanius 1998). Therefore, if the hypothesis of an educational role of maternal IgY is true, we expected to observe an increase of specific IgY concentrations between ages 10 and 20 days for both groups, but a higher overall IgY concentration in MIg^+ chicks compared with $MIg^–$ chicks. This should be particularly the case in areas of high tick infestation where exposure to *Borrelia* is likely to be more homogeneous.

We used an analysis of variance for repeated measures between ages 10 and 20 days to investigate the change in IgY concentration with chick age, the level of tick infestation, and the chick category ($MIg^+/MIg^–$) as class variables (Proc Mixed; SAS Institute, Inc. 1996). We included two repeated factors in the model, chick and nest, because there were repeated measures on the same chick and because sibling chicks were not statistically independent (see McCoy et al. 2002). OD values of 5-day-old chicks were not included in this analysis because these data were used to assign chicks to a chick category ($MIg^+/MIg^–$). For all statistical tests, the significance level was set at $P < 0.05$. Values are reported as means ± SE.

Fig. 1. Variation in the relative concentration of anti-*Borrelia* IgY (log(OD), where OD is optical density; mean ± SE) with chick age (days) in Black-legged Kittiwakes (*Rissa tridactyla*). The solid line represents MIg^+ chicks (with maternal IgY) and the broken line represents $MIg^–$ chicks (without maternal IgY).



Results

As expected, the change in relative antibody concentration between ages 5 and 10 days was different for the two categories of chicks (Student's t test, $t_{[44]} = 5.03$, $P < 0.0001$). There was a decrease over time from a high IgY concentration in MIg^+ chicks (paired t test, difference of log(OD) = –0.021 ± 0.07, $t_{[15]} = –2.99$, $P = 0.009$; Fig. 1), whereas there was an increase in these antibodies in $MIg^–$ chicks (paired t test, difference of log(OD) = 0.44 ± 0.09, $t_{[29]} = 5.09$, $P < 0.0001$; Fig. 1). The dynamics of anti-*Borrelia* IgY concentrations between ages 10 and 20 days were similar for MIg^+ and $MIg^–$ chicks (Fig. 1, Table 1); both groups showed an increase in their specific IgY concentrations. However, MIg+ chicks had significantly higher concentrations of anti-*Borrelia* IgY than did $MIg^–$ chicks (Table 1, Fig. 1), especially at age 20 days when maternal antibodies are absent (Student's t test, $t_{[44]} = 2.95$, $P = 0.005$). There was no effect of the level of tick infestation on the change of anti-*Borrelia* IgY concentrations between the two ages (Table 1).

Discussion

The overall effect of maternally derived immunoglobulins in offspring may be greater than just the direct effect of these IgY in terms of the initial protection afforded to young

Table 1. Results of mixed-model ANOVA for repeated measures for 10- and 20-day-old Black-legged Kittiwake (*Rissa tridactyla*) chicks with anti-*Borrelia* concentrations as the dependent variable, and age, chick category (MIg^-/MIg^+), and tick infestation as categorical variables.

(*a*) Fixed effects.			
	F	df	*P*
Age	83.33	1,45	<0.0001
Tick infestation	0.66	1,45	0.42
Chick category	44.89	1,45	<0.001
(*b*) Repeated effects.			
	Z	*P*	
Chick (Nest)	0.74	0.23	
Nest	0.47	0.32	

Note: Nonsignificant interactions were removed in a stepwise fashion from the model (all $P > 0.13$). Chick and nest were included in the models as repeated effects (Wald's *Z*, Proc Mixed, SAS Institute, Inc. 1996), but did not significantly affect general results ($P > 0.23$).

against pathogens. It may also stimulate the young's immune response to prepare it for future parasite challenge. In this study, we examined a possible adaptive effect of the presence of maternal immunoglobulins against the tick-borne bacterium *B. burgdorferi* in Kittiwake chicks. In particular, we investigated the hypothesis of an educational role of these specific IgY on the development of the immune system. We report observations supporting this hypothesis in the natural host–parasite system considered; at age 20 days and controlling for the level of tick exposure, chicks that received anti-*Borrelia* antibodies via a maternal transfer (MIg^+) had higher concentrations of anti-*Borrelia* IgY than chicks that did not (MIg^-). Maternal IgY could thus be a significant way by which individuals inherit their future abilities to mount specific immune responses (Lemke et al. 2003).

As this study is correlational, these results could also be explained by a relationship between the prevalence of *Borrelia* in the ticks infesting Kittiwake chicks and mothers from the same nests. Mothers exposed to ticks with a high prevalence of *Borrelia* might transmit more anti-*Borrelia* IgY to their chicks and these chicks might also be more exposed to *Borrelia* once tick infestation begins. This could result in MIg^+ chicks with higher concentrations of specific IgY simply because of parasite exposure. However, in a previous study, no relationship was found between anti-*Borrelia* antibody concentrations of fathers and their eggs (Gasparini et al. 2002). As attendance on the nest is shared between males and females in this species, a purely environmental effect should be equally reflected in both parents. Likewise, we expected tick infestation to be a significant factor affecting dynamics, as it is directly linked to the probability of *Borrelia* exposure. The fact that both chick categories increased between ages 10 and 20 days, regardless of tick exposure, could be due to a high prevalence of *B. burgdorferi* in ticks, resulting in apparent homogeneous exposure or to the development of natural antibodies and a cross-reaction with the ELISA kit. However, these possibilities do not invalidate our test, as the MIg^+ group still shows greater values than the MIg^- group. These observations suggest that the increased antibody levels in 20-day-old chicks are more likely linked to maternally derived antibodies than to other features, lending support to the educational effect hypothesis. However, additional factors that may increase the transfer of maternal antibodies in young such as food availability and egg hormones may also covary with the immune response of the chick (e.g., Blount et al. 2002). Experimental evidence is now required to validate this hypothesis.

More generally, the potential role of maternal IgY may depend on the timing of infection in the young. A direct effect of maternal IgY occurs when maternal IgY bind to the antigen, but do not stimulate the chick's immune system. When exposure to an antigen occurs very early (e.g., at 1 day old), the presence of maternally derived antibodies may even inhibit the young's immune reaction (Mondal and Naqi 2001; Siegrist 2003). However, if exposure occurs later or is chronic, maternal IgY may not be directly useful in protecting the chick because they will have already disappeared. An educational role of maternal IgY could thus have evolved in response to such chronic infections, as is the case in the tick–Kittiwake system. Experimental studies, involving the vaccination of offspring at different ages that have received specific maternal IgY against the same antigen, should allow us to better understand the immunomodulatory role of maternal IgY in relation to the timing of infection. If the role of specific maternal IgY depends on the timing of parasite exposure, the transfer of specific IgY may have evolved differently in relation to the type of parasite involved.

In conclusion, this study has shown that the transfer of specific maternal IgY against *B. burgdorferi* may not only confer passive protection, but may also influence the development of the Kittiwake chick's immune system. Recent studies have stressed the potential importance of a maternal transfer of specific immunity in the ecology and evolution of host–parasite interactions (Boulinier et al. 1997; Heeb et al. 1998; Brinkhof et al. 1999; Gasparini et al. 2001; Lozano and Ydenberg 2002; Grindstaff et al. 2003; Müller et al. 2004). However, until now, little consideration has been given to the potential effect of such a transfer on juvenile immunity. Controlled experimental approaches will now be required to validate this hypothesis.

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