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Postnatal effects of incubation length in mallard and pheasant chicks

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Eggs of mallard ducks (*Anas platyrhynchos*) and ring-necked pheasants (*Phasianus colchicus*) were incubated in clutches arranged to stimulate embryos to hatch earlier or later than normal. This manipulation of hatching time was achieved by combining eggs of different age in the same clutch. To ensure hatching synchrony, embryos communicate with each other during the last stage of incubation, resulting in either a delay or an acceleration of hatching. Embryos of both species that accelerated their hatching time suffered a higher mortality rate after hatching. Combining mortality with the proportion of hatchlings that suffered from leg deformities, impeding their movements, resulted in a cost also to pheasant chicks delaying their hatching. Chicks of both species accelerating hatching time had a lower minimum mass and a shorter tarsus length than control chicks, whereas chicks delaying hatching time either grew as well or slightly better than control chicks. Mallard chicks had better balance and mobility immediately after hatching the longer they stayed in the egg. This indicates that the period immediately before hatching, is an important period for muscular and organ maturity. Reducing this period results in costs affecting post-hatching survival. The strategy to assure synchronous hatching in mallards and pheasants probably reflect a trade-off between the negative effects of shifting the age at hatching away from normal and differences in predation risk during different stages of reproduction.

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In precocial bird species, synchronisation of hatching is important for co-ordination of chick departure from the nest (Lack 1968), thereby reducing exposure to nest predation (Clark and Wilson 1981). It is, thus, pivotal that individual embryos manage to hatch simultaneously, as the female abandons the nest soon after hatching even if unhatched eggs remain in the nest (Bjärvall 1968, Cannon et al. 1986, own obs). It is therefore paradoxical that females of precocial species may warm the eggs during laying or continue to lay eggs after the start of incubation and in that way generate a developmental asynchrony within the clutch (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979, Cargill and Cooke 1981, Kennamer et al. 1990, Wilson and Verbeek 1995, Persson and Göransson 1999). To overcome this problem, embryos communicate their developmental stage towards the end of the incubation period (Vince 1969, Brua 2002). Two to three days before actual hatching, the embryo pierces the chorioallantoic membrane (internal pipping), allowing it access to the air in the air cell. Respiratory gas exchange will continue to be performed by the chorioallantoic membrane during the period between internal and external pipping (piercing the egg shell), but pulmonary gas exchange also starts during this period (Vleck and Bucher 1998). This allows the embryo to fill its lungs and some form of breathing can start (Vince 1969, Deeming 2002). When air passes over the syrinx during this initial functioning of the respiratory system, clicking sounds are produced (Driver 1965, McCoshen and Thompson 1968, Forsythe 1971), which have been suggested to serve as the mode of communication between embryos (Vince 1969, Woolf et al. 1976). This form of communication contains information about the developmental stage of individual

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embryos making it possible for individual correction of initial hatch date in relation to the development of the other embryos in the clutch, thereby achieving synchronised hatching. This correction may be accomplished either by shortening or prolonging the incubation period and different strategies may be used by different species (Vince 1964, 1968, Davies and Cooke 1983, Cannon et al. 1986, Holmberg 1991, Persson and Andersson 1999).

Newly hatched chicks of precocial species are dependent on a well developed thermoregulation and muscular maturation, as chicks may have to walk long distances shortly after hatching and may be exposed to stressful environmental conditions. A considerable shortening of the incubation period is therefore likely to affect the chick negatively as both growth and development/maturation may take place during the last days of incubation (Vleck et al. 1979, Ricklefs and Starck 1998a). Besides the negative effects on development, also the effect of smaller size at hatching per se may affect the development and survival of the chick. Even a prolongation of the incubation period may be disadvantageous to newly hatched chicks, because a larger part of the yolk is consumed during the extra days of incubation resulting in smaller energy reserves available to the chick after hatching.

This study examines the possible costs of altering the age at hatching. The aim is to study the effects of an experimental shortening or prolongation of the incubation period in mallards (*Anas platyrhynchos* L.) and pheasants (*Phasianus colchicus* L.), both of which have been shown to be capable of altering the hatching time (Persson and Andersson 1999). We measured size, maturation of neuromuscular systems (measured as balance and mobility) and mortality in newly hatched chicks and related this to age at hatching.

Methods

In natural conditions mallards produce a clutch of 9–15 eggs which is incubated for 27–28 days and pheasants produce a clutch size of 8–15 and incubate it for 23–28 days (Snow and Perrins 1998). In this study, pheasant and mallard eggs were obtained from professional breeders and were incubated in an automatic incubator as described by Persson and Andersson (1999). All the eggs were weighed and individually marked before the start of incubation. In the experiment, we created 50 mallard and 50 pheasant clutches each consisting of 15 eggs. In each clutch, 5 (experimental) eggs were randomly chosen to either be incubated two days shorter or two days longer than the rest of the clutch. We, thus, created three experimental categories: accelerated embryos, which were surrounded by older embryos; control embryos, which were mostly surrounded by embryos of the same age and delayed embryos, surrounded by younger embryos. Mean mass of the mallard eggs used was 61.1 (SD = 5.30) and of pheasant eggs 31.1 g (SD = 2.47). We found no significant mean egg mass differences between experimental categories in either mallards (ANOVA: $F_{2,378} = 0.09$; $P = 0.92$) or pheasants (ANOVA: $F_{2,382} = 1.87$; $P = 0.16$). Each clutch was separated from other clutches by sound-insulating rockwool plates and the eggs were placed on a spongy plastic material to avoid spreading of vibrations between the clutches. In this way, the embryos of experimental eggs could be stimulated by the embryos in the control eggs to either delay or advance their time of hatching. To avoid that too many chicks should be measured on the same day, the incubation was done in two batches, with exactly the same treatment of the eggs.

The end of the incubation period was defined as the time of pipping, i.e. the first breaking of the shell (checked every 12 h). A number of eggs turned out to be unfertilised and in some others the embryo died at an early stage. However, the incubation success did not interact with the experimental treatments as the proportion of eggs which pipped was equal for experimental and control eggs (58% and 63%, respectively for pheasant eggs and 56% for both categories of mallard eggs). At pipping the eggs were put in separate boxes in a brooder, where the chicks stayed until they had hatched and were dry. The chicks were then weighed and individually banded. Thus it was possible to follow each individual from egg to chick.

After hatching, the chicks were kept indoors under an infrared lamp to give them warmth and they had free access to water and food (commercial chicken feed). The pheasants also had a five days older domestic chicken (*Gallus gallus* L.) to let the chicks learn how to feed for themselves. During the hatching day, the balance and mobility of the chicks were estimated using a simple test: the chick was placed on a plane surface (writing-pad) and the balance and ability to walk were assessed using a rank score between 1 and 5. Chicks that had an index of 1 could not stand on their legs, but lay on the floor waving their legs, index 2: could stand up for short periods; index 3: could stand up without trouble but fell when starting to run; index 4: could run but fell often, while chicks with an index of 5 were able to run without difficulty. All balance and mobility tests were conducted by one of us (I.P.) without knowing the origin of the chick. Apart from hatching mass, which was measured as soon as the young was dry, the measurements were taken in the morning. Thus there may be a time lag of 12 h between the measurements of different individuals in relation to time of hatching. This might potentially affect our measure of balance-mobility since it probably is very age-dependent. To control for this, measures made at different times since hatching were analysed separately and we used the category with the largest sample size for the analyses presented here (mallards: measures taken 12 h after hatching, 192 chicks; pheasants: measures taken <5 h after hatching, 216 chicks).

A sub-sample of the chicks from control eggs and all experimental eggs that hatched, were weighed daily until they attained hatching mass after the initial post-hatching mass decrease. These chicks also had their tarsus length measured when 1 day old as well as mass and tarsus when they were 10 days old. The sample sizes in the analyses vary somewhat, mainly due to successive mortality. The minimum mass of a chick is the lowest mass recorded during the post-hatching decline in mass. The time of mass gain is the time taken until the body mass at hatching was regained. All measurements were taken without knowledge of the incubation lengths of different individuals.

All statistical analyses were performed using SYSTAT 9 and all probabilities refer to two-tailed tests. All chi-square tests are presented after the application of Yates' correction.

Results

Hatching spread

The average length of incubation, i.e. time from the start of incubation until external pipping, of the control eggs was 25.4 (SD = 0.81) days in mallards and 24.6 (SD = 0.66) days in pheasants, which is close to earlier measurements (Persson and Göransson 1999). Deviations from normal hatching time were calculated as the difference between observed hatching time and the average hatching time of control eggs. Since pipping was checked each half day, average hatching time was approximated to be 25.5 days in mallards and 24.5 days in pheasants. The time of hatching in mallards ranged from 2 days before normal hatching time to 2.5 days after, with 54.9% of all eggs hatching within ±0.5 days of normal hatching time (Fig. 1). The hatching spread of pheasant eggs ranged from 1.5 days before normal hatching to 2 days after, with 76.1% of the eggs hatching within ±0.5 of normal hatching time (Fig. 1).

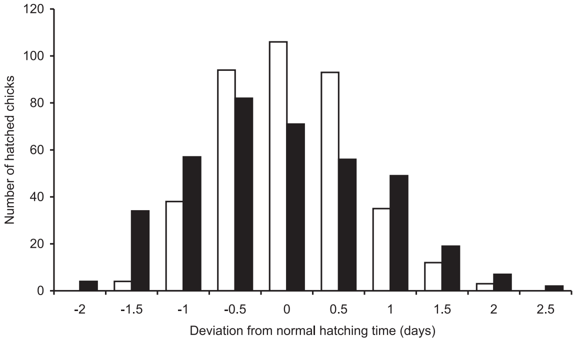

Fig. 1. Number of pheasant (open bars) and mallard (black bars) chicks which hatched after different times spent in the egg, measured as deviation in days from normal time of hatching. Sample sizes are for mallards 381 and for pheasants 385 chicks.

In both species, the maturity of the embryos in the surrounding eggs affected hatching time of experimental eggs (Table 1). Embryos surrounded by older nest mates accelerated their hatching time, whereas embryos surrounded by younger nest mates delayed their hatching. The difference between all three experimental categories was significant (Tukey HSD; $P < 0.001$) for both species. Thus, with our experimental set-up, we were successful in manipulating the length of incubation for individual eggs.

After pipping, the mallard chicks stayed in the egg for on average 1.1 (SD = 0.42) days and pheasant chicks for 1.6 (SD = 1.12) days before emerging completely from the egg. This phase did, however, not differ significantly between the experimental categories (ANOVA: mallard: $F_{2,378} = 2.14$; $P = 0.12$; pheasant: $F_{2,382} = 0.98$; $P = 0.38$).

Survival

Some of the chicks died during the hatching process, i.e. between external pipping and full hatching. In mallards, 7.9% of all ducklings died during this phase. However, this source of mortality did not differ significantly, either between accelerated chicks and their control chicks ($\chi^2 = 0.0$; df = 1; $P = 1$) or between delayed chicks and their controls ($\chi^2 = 2.46$; df = 1; $P = 0.12$). The overall mortality of pheasant chicks during the hatching process was nearly twice as high (14.0%) compared to that of ducklings. The mortality risk for delayed chicks did not differ from the risk of control chicks ($\chi^2 = 0.16$; df = 1; $P = 0.69$), but accelerated chicks had a significantly lower mortality risk (6.3%) than their control (18.7%) chicks ($\chi^2 = 5.56$; df = 1; $P = 0.018$).

Of the chicks that hatched, 6.5% of the mallard ducklings and 7.6% of the pheasant chicks died during the first 10 days. Accelerated chicks in both species suffered a significantly higher risk of dying than control chicks during this early phase of life (Table 2). Also the other manipulated category; delayed chicks, had a somewhat higher mortality risk than control chicks although this difference was not significant (Table 2). Another factor that may affect early survival is the time the chicks spent in the egg between external pipping and actual hatching. We divided this time into fast hatching (up to and including 1 day after pipping) and slow hatching (more than 1 day between pipping and hatching). Speed of hatching did, however, not affect survival in any of the species (mallard: $\chi^2 = 1.43$; df = 1; $P = 0.23$; pheasant: $\chi^2 = 0.63$; df = 1; $P = 0.43$).

Table 1. Mean deviation from normal hatching time and index of balance and mobility for pheasant chicks (A) and mallard ducklings (B) hatching from three different experimental categories; those manipulated to accelerate or delay hatching and control chicks. Differences between experimental categories tested with ANOVAs.

	Accelerated mean ± S.E. (N)	Control mean ± S.E. (N)	Delayed mean ± S.E. (N)	F	P
A					
Pheasant					
Deviation (days)	− 0.32 ± 0.06 (74)	+ 0.06 ± 0.04 (257)	+ 0.41 ± 0.08 (54)	21.99	< 0.001
Balance index	2.40 ± 0.15 (58)	2.48 ± 0.11 (115)	2.58 ± 0.18 (43)	0.33	0.72
B					
Mallard					
Deviation (days)	− 1.04 ± 0.07 (62)	− 0.10 ± 0.05 (250)	+ 0.81 ± 0.07 (69)	105.2	< 0.001
Balance index	2.78 ± 0.13 (41)	3.28 ± 0.10 (111)	3.73 ± 0.17 (40)	8.95	< 0.001

In pheasants, several chicks (overall 14.3% of surviving chicks) hatched with leg deformities (immobile joints), impeding their movements. Also the risk of hatching with such deformities was higher for accelerated chicks (23.8%) and for delayed chicks (20.4%) compared to control chicks although the difference was only significant between accelerated and control chicks ($\chi^2 = 5.25$; df = 1; P = 0.022). Speed of hatching did not affect the risk of being hatched with deformities ($\chi^2 = 0.23$; df = 1; P = 0.63). The deformities are a severe handicap for the newly hatched chicks and most of them will probably succumb under natural circumstances. Combining the chicks that died, with those that carried deformities, with the assumption that they would also die in the wild, resulted in significant disadvantages of both accelerated and delayed hatching (Table 2).

Balance and mobility

The better balance and mobility of mallard chicks compared to pheasant chicks (Table 1) may well be because mallards were measured a little later in relation to hatching than were pheasants (see methods). Hatching time did not affect the ability of pheasant chicks to move after hatching. However, mallard chicks were better at keeping their balance and to move shortly after hatching the longer they stayed in the egg (Table 1). This was significant for all comparisons between the experimental groups (Tukey HSD: ACC vs CON: P = 0.018; ACC vs DEL: P < 0.001; CON vs DEL: P = 0.043).

Size of newly hatched chicks

The length of incubation did not affect hatching mass in either mallard ducklings or in pheasant chicks (Table 3). Neither did the proportion of the egg mass utilised by the chick as evidenced by its hatching mass (mallard: 65.3%, pheasant: 69.1%) differ between the experimental categories (ANOVA; mallards: $F_{2,375} = 2.01$; P = 0.14; pheasants: $F_{2,377} = 0.76$; P = 0.47).

After hatching most chicks lost mass for 1–2 days. On average mallard chicks lost 5.07 g (SD = 3.04), 12.7% of hatching mass and pheasant chicks lost 2.09 g (SD = 1.17), 9.7% of hatching mass, before gaining mass. This led to a minimum mass that differed significantly according to the experimental categories (Table 3). In both species, chicks that accelerated their hatching had a significantly lower minimum mass than the control category (Tukey HSD; pheasant: P < 0.001; mallards: P < 0.001) and a tendency to be lighter than delayed chicks (Tukey HSD; pheasants: P = 0.064; mallards: P = 0.054). The difference between delayed and control chicks, on the other hand, was not significant (P > 0.25 in both cases). It took pheasant

Table 2. Proportion of hatched pheasant (A) and mallard (B) chicks that died during their first 10 days post-hatching. Assumed mortality in pheasant chicks is the observed mortality plus the proportion of chicks that hatched with deformed legs (see text for further information). ACC = chicks manipulated to accelerate hatching; DEL = chicks manipulated to delay hatching; CON = control chicks of respective manipulation. Differences between categories tested with chi-square tests.

	ACC	CON	χ^2	P	DEL	CON	χ^2	P
A								
Pheasant								
Mortality (%)	14.9	5.19	4.53	0.033	10.9	4.65	1.56	0.21
Assumed mortality (%)	35.1	14.8	10.35	0.001	29.1	15.5	3.71	0.05
B								
Mallard								
Mortality (%)	12.7	40.0	4.10	0.043	8.57	4.96	0.47	0.49

Table 3. Mean hatchling mass and tarsus length, mean minimum mass of chicks as well as mean mass and tarsus length at the age of 10 days for pheasant chicks (A) and mallard ducklings (B) hatching from three different experimental categories; those manipulated to accelerate or delay hatching and control chicks. Differences between experimental categories tested with ANOVAs.

	Accelerated mean ± S.E. (N)	Control mean ± S.E. (N)	Delayed mean ± S.E. (N)	F	P
A Pheasant					
Hatchling mass (g)	21.1 ± 0.22 (74)	21.6 ± 0.14 (252)	21.6 ± 0.30 (54)	1.36	0.26
Minimum mass (g)	19.0 ± 0.25 (74)	20.3 ± 0.15 (252)	20.0 ± 0.28 (54)	8.40	< 0.001
Hatchling tarsus (mm)	23.3 ± 0.15 (57)	23.6 ± 0.09 (115)	23.8 ± 0.16 (43)	2.77	0.065
Day 10 mass (g)	50.7 ± 0.94 (50)	50.2 ± 0.84 (99)	53.9 ± 1.42 (38)	2.96	0.055
Day 10 tarsus (mm)	31.4 ± 0.26 (49)	31.2 ± 0.18 (98)	32.1 ± 0.30 (38)	3.16	0.045
B Mallard					
Hatchling mass (g)	39.2 ± 0.50 (62)	40.0 ± 0.23 (247)	40.0 ± 0.45 (69)	1.24	0.29
Minimum mass (g)	34.0 ± 0.58 (62)	37.0 ± 0.30 (247)	36.0 ± 0.60 (69)	9.79	< 0.001
Hatchling tarsus (mm)	23.5 ± 0.16 (56)	24.4 ± 0.10 (151)	24.8 ± 0.16 (59)	17.4	< 0.001
Day 10 mass (g)	149 ± 6.15 (40)	162 ± 3.28 (94)	167 ± 5.29 (37)	3.21	0.043
Day 10 tarsus (mm)	38.0 ± 0.51 (39)	39.2 ± 0.28 (91)	40.1 ± 0.43 (37)	5.49	0.005

chicks on average 3.7 days and mallard chicks 2.8 days to regain their hatching mass. This time to recovery also differed between the experimental categories (ANOVA, pheasants: $F_{2,199} = 3.81$; $P = 0.024$; mallards: $F_{2,177} = 4.38$; $P = 0.014$). This was due to delayed chicks regaining mass faster than accelerated and control chicks (Tukey HSD: $P = 0.04$ and $P = 0.029$, respectively) in pheasants and faster than accelerated chicks (Tukey HSD: $P = 0.009$) in mallards.

In contrast to mass, mean tarsus length of newly hatched chicks differed significantly between the experimental categories (Table 3). In pheasant chicks this was only a tendency and the only significant post-hoc contrast was between accelerated and delayed chicks (Tukey HSD: $P = 0.049$). The differences were greater among mallard ducklings; accelerated ducklings having a significantly shorter tarsus than control and delayed ones (Tukey HSD: $P < 0.001$ in both cases). Furthermore, delayed chicks tended to have a longer tarsus length than control chicks (Tukey HSD: $P = 0.065$).

Size of 10-day old chicks

Even 10 days after hatching, effects emanating from the hatching pattern were still evident among the chicks. In pheasants, accelerated chicks were as large as control ones (Tukey HSD: P = ns in all comparisons) but delayed chicks were both heavier (Tukey HSD: $P = 0.044$) and had longer tarsi (Tukey HSD: $P = 0.032$) than control chicks (Table 3). In mallards on the other hand, delayed chicks did not differ significantly from control chicks (Tukey HSD: P = ns in all comparisons). However, accelerated ducklings lagged behind (Table 3) both in mass (Tukey HSD; ACC vs CON: $P = 0.10$; ACC vs DEL: $P = 0.041$) and in tarsus length (Tukey HSD; ACC vs CON: $P = 0.05$; ACC vs DEL: $P = 0.003$).

Discussion

Accelerating and delaying hatching

This study shows that embryos of two precocial species are to some degree able to choose their time of hatching (Persson and Andersson 1999). The tuning of the hatching time has to be done before external pipping since the time between external pipping and actual hatching did not differ among the experimental categories. The two species differ considerably in the degree to which they choose to either accelerate or delay hatching. Mallard ducklings are prepared to alter their time in the egg, both shortening and prolonging it, to a much greater extent than are pheasant chicks. Still, even the ducklings do not fully compensate for the two days of experimentally induced longer or shorter incubation time compared with their nest mates. This restriction in the flexibility to adjust hatching to that of nest mates, may depend on physiological constraints. This seems, however, not to be the case since some individuals in both species are capable of accelerating or delaying normal hatching time by two days (Fig. 1). Instead, we propose a possible trade-off between the benefits and costs of a flexible length of the incubation period.

Costs of altering incubation length

To be able to understand the nature of potential costs of reducing or prolonging the time in the egg, we need to know what happens in embryonic development towards the end of the incubation period. After about 80% of the total incubation time, embryos of precocial species enter a plateau phase in their oxygen consumption of different length (Vleck et al. 1980, Cannon et al. 1986, Prinzinger and Dietz 1995, Dietz et al. 1998). The plateau phase ends with the external pipping, resulting in more movements and free access to oxygen (Cannon et al. 1986, Vleck and Bucher 1998). During this time, growth rate declines (Dietz et al. 1998) or even stops (Vleck et al. 1979, 1980, Vleck and Bucher 1998). This is in agreement with our results since neither hatching mass nor the proportion of egg mass going into chick biomass differed according to hatching time category. Although, mass seems to have attained hatching values already a couple of days before hatching, structural traits such as tarsus length continues to grow until hatching (Table 3). Thus, the plateau phase in energy utilisation can not be explained solely by a cessation of growth but is probably also due to increased synthesis efficiency late during embryonic development (Dietz et al. 1998).

Precocial chicks possess functional sensory, neuromuscular and thermoregulatory systems already at hatching (Starck 1998). It is suggested that the function of the plateau phase is the maturation of these systems, requiring relatively little energy (Vleck et al. 1979, Ricklefs and Starck 1998a, Vleck and Bucher 1998). The time period when chicks are assumed to be able to communicate with each other is after internal pipping, when the lungs can start to be used (Vince 1969, Woolf et al. 1976, Deeming 2002). Thus, acceleration and delay of hatching will take place during the plateau phase. In line with this, experimentally accelerated Darwin's rhea (*Pterocnemia pennata*) embryos, hatched earlier than normal by reducing the plateau phase (Cannon et al. 1986). Thus, chicks that have shortened this phase of organ maturation, might have to pay a cost in the form of less developed maintenance systems. At least mallard ducklings suffered from a muscular immaturity as accelerated ducklings performed worst in our balance and mobility test (Table 1). It seems as this kind of maturation continues also after normal hatching time since the delayed ducklings had the best balance and mobility.

The result of the immaturity of muscular and other essential systems such as sensory and nervous systems would be most important directly after hatching when the chicks should start to feed for themselves. Hatching earlier than normal, will make it harder for the hatchling to find and handle food items which would probably be very important in nature. Even in an artificial environment with food ad libitum, such costs of a reduced plateau phase were probably responsible for the significantly lower post-hatching mass found in accelerated chicks in both species studied (Table 3).

Although chicks were kept under more or less optimal conditions, experimental hatching category affected post-hatching survival. The lower survival of accelerated chicks of both species can probably be attributed to immaturity of systems important for self-feeding and maybe also to an immature thermoregulating system. Interestingly, if actual mortality was combined with assumed mortality in the wild (those hatched with leg deformities), pheasant chicks suffered from reduced survival also if they delayed hatching (Table 2). Dehydration, which increases after internal pipping, might be a possible mechanism, explaining the reduced survival of those staying longer in the egg than is normal (Vleck and Bucher 1998). Dehydration of the smaller pheasant egg would be more severe compared to the mallard egg, having a smaller surface to volume ratio, potentially explaining the cost difference between the two species.

Cost benefit considerations of altered incubation length

The benefit of an early start of incubation within the laying sequence would be a reduced predation risk of clutches due to increased concealment of the eggs (Persson and Göransson 1999). However, this female behaviour is constrained by its costs in the form of increased hatching asynchrony. For females to stay and wait for the hatching of the entire clutch after normal incubation periods for each egg would probably severely diminish or revert the advantage of an early start of incubation. One of the strong selective pressures, forming the precocial development strategy, is assumed to be a high predation risk of staying in the nest with a partially hatched brood (Bjärvall 1968, Ricklefs and Starck 1998b). This has been reported to result in nest departure before all viable eggs have hatched (Bjärvall 1968, Cannon et al. 1986). This in turn, has led to a selective pressure on the chicks to be able to alter their time of hatching. However, here we show that especially acceleration of hatching are connected to costs for the individual chicks (Table 4). Besides early mortality, accelerated chicks also suffer from hatching in a less developed state, probably rendering them vulnerable to both starvation and predation in the wild. Apart from an increased exposure to nest predators and an increased risk of dehydration during the hatching process, delayed hatching does not seem to be connected to severe costs.

The difference between the species in the degree to which they accelerate hatching, probably depends on differences in nest predation rate (Persson and

Table 4. Summary table of factors being significantly, negatively affected by either an accelerated or a delayed hatching in pheasant and mallard chicks. For tests (Tukey HSD between accelerated and control chicks and between delayed and control chicks, respectively) see text.

	Accelerated	Delayed
Pheasant	Post-hatching survival Minimum mass	Post-hatching survival
Mallard	Survival Balance Minimum mass Hatchling tarsus length Day 10 tarsus length	

Andersson 1999) or in differences in maturity after a normal length of incubation. Chicks of the family Phasianidae are considered to be less developed than chicks of Anatidae since they need a parent to find food items and to point the food items out for them (Starck and Ricklefs 1998). Thus, accelerating the hatching time considerably in a species with already somewhat less developed hatchlings, might greatly increase the costs of a substantially shortened incubation period.

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