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Mothers provide similar care to related and 1 unrelated chicks in quail

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Highlights:

- Mothers show similar warming and rejection levels and mother-chicks distances toward unrelated and related chicks.
- Related and unrelated chicks show similar behaviours toward the mother and similar distances between themselves.
- Related and unrelated chicks show no difference of emotional and social development after mothering.

Abstract:

Adoption is a usual procedure to experiment non-genomic influences on young development. However relatedness may be a variation factor of maternal behaviour who can recognize and/or discriminate her own young that non-related ones. Here we investigate the influence of relatedness on maternal and chicks' behaviour during breeding period in a precocial bird, the Japanese quail. We placed 2 non-related chicks and 2 related chicks with a mother (N=24). We recorded their behaviour and their distance during the 11 days of mothering. Then we tested the emotivity and social development of chicks with 4 behavioural tests: openfield/novel object, emergence with sudden test for emotivity; separation and runway for social. We analysed the data with PCA, one for mothers' behaviour, one for chicks' behaviour and one for behavioural development. We compared by GLMM the distances and the PCA factorial scores of the individuals. We had not noticed any difference of maternal behaviour (Factor 1: $p=0.71$; Factor 2: $p=0.64$), chicks' behaviour (Factor 1: $p=0.71$; Factor 2: $p=0.64$) and distances between individuals ($P=0.38$) according to the relatedness of the chicks. Their emotivity (Factor 1: $p=0.39$) and social (Factors 2 & 3: $p=0.80$ & $p=0.90$) profiles were not significantly different whether they were related or not. Our results had shown that relatedness was not a crucial factor of maternal behavioural

variation in quail and raised the question about recognition and discrimination of the chicks by the mother in precocial solitary birds.

Keywords: adoption, recognition, kinship, maternal influence

1 INTRODUCTION

Adoption is a process often used in breeding, for reintroduction but also in laboratories (Darnaudéry et al., 2004; Sánchez-García et al., 2011). Indeed, adoption enables the scientists to be free of the genetic constraints (Pittet et al., 2014a; Richard-Yris, 1994). In addition, adoption and alloparenting behaviours are naturally present in many taxa such as social insects (Emlen et al., 1991), some fish (McKaye and McKaye, 1977; Schaedelin et al., 2013), more than 120 species of mammals and 150 species of birds with varied ecology and sociality (Riedman, 1982; Wysocki et al., 2018). Adoption can be defined as a process by which an individual, the alloparent, other than a direct genetic parent, accept to give offspring vital care for its survival (Riedman, 1982). If adoption is possible and relatively common, few studies have investigated the possible effects on parental care. Nevertheless, such effects could bias results obtained with experiments produced by adoption.

Indeed, if offspring adoption means accepting by the adoptive parent to give them vital care for its survival, it can still cause a change in parenting behaviour and/or in other offspring. Many mammals, such as lions, prefer to nurse their own offspring over another (Pusey and Packer, 1994). Spotted hyenas, in a communal den, are particularly sensitive to suckling attempts of unrelated offspring, and refuse to care for young other than their own (Pusey and Packer, 1994). In some birds living in colonies, the presence of adopted chicks tends to increase the negative parental behaviours particularly concerning adopted chicks. For example, eider parents were more aggressive when adopted ducklings were present (Öst and Bäck, 2003). The unrelated young were also at a greater distance from their adoptive parents than related ducklings, and therefore more exposed to predators. Similarly, for the stork and geese, adoption leads to a peak of aggressiveness towards adopted chicks from parents especially if the adoption is late (Kalmbach, 2006; Redondo et al., 1995) with a greater distance between mother and adopted chicks (Nastase and Sherry, 1997).

Moreover, introducing unrelated chicks in the nest increases the competition within the offspring already present. For instance, when there is a mix of adopted and biological chicks, barn swallow young's solicitations, both postures and vocalizations, are more numerous (Boncoraglio et al., 2009) and the intensity of the vocal begging is higher (Boncoraglio and Saino, 2008). In the same way, young storks are very aggressive towards a new foreign chick (Redondo et al., 1995). In another study, chicks of Bengalese finches make more allopreening between biological siblings than adopted ones, showing that they can recognize biological siblings and produce affiliative behaviour according relatedness (Ju and Lee, 2016).

Contrary to these cases, where parents gave less care to unrelated young, some studies have reported evidences of more attention to adopted offspring. Indeed, rats and mice lick more adopted pups during an early adoption (Barbazanges et al., 1996; Darnaudéry et al., 2004). In the same way, adopted rat pups are returned more quickly to the nest (Misanin et al., 1977). Here, a particular attention is paid to these offspring. In rodents living in colonies, mothers are able to discriminate their own pup from alien ones on the basis of olfactory and gustatory cues and therefore spend more time inspecting these alien pups (Ostermeyer and Elwood, 1983).

While adoption concerned mostly colonial/group living species, it has also been observed in some solitary birds species where egg parasitism or extrapair copulations can sometimes occur (Tengmalm's Owl: Kouba et al., 2017; Eagle Owl: Penteriani and Del Mar Delgado, 2008; Peregrine falcons: Ancil and Francke, 2013). However, the influence of the adopted chicks on parental behaviour and on chicks' behaviour has been very few studied, even if it is known that some features of the chick (such as sex) or of the brood (e.g. size) can affect parental cares (Aigueperse et al., 2019, 2018, 2017). In mammals, mothers usually recognize first the nest before the pup themselves (Gubernick, 1981). In solitary bird species, the risk of mothering non-related chicks being extremely limited, the cost to recognize and discriminate would exceed its benefits (Beecher 1988). That idea was supported by experimental comparisons made between colonial and non-colonial swallows that had shown that parent-offspring recognition is well developed in first ones but not existent or weak in the second (Beecher, 1988; Medvin et al., 1993). According to these studies, we hypothesised that in quail, a non-colonial solitary bird

species, the mother is not able to discriminate related and unrelated chicks, and therefore will take care to them in the same way.

Moreover, we know that early social partners influence the social and emotional development of young. Maternal behaviours particularly are well known to change behavioural development of young (e.g.: Desmedt et al., 2020; Galuret et al., 2020; Laviola and Alleva, 1995; Pittet et al., 2014b, 2012; Schino et al., 2001). Therefore we also hypothesised that if maternal behaviour would not change according to relatedness, related and unrelated chicks would not show any significant difference in behavioural development.

Then, in this study, we propose to investigate these questions in Japanese quail (*Coturnix coturnix japonica*) which is a species of precocial birds whose mother raises its chicks alone. It is also a common model to study the influences of early life conditions as pre- and post-natal care (Guibert et al., 2013, 2011; Pittet et al., 2014b; Zimmer et al., 2017) . By performing artificial adoption, we hypothesise that mother gives similar care to unrelated or related chicks.

2. MATERIALS AND METHODS

2.1. GENERAL PROCEDURE

2.1.1. Ethic statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the departmental direction of veterinary services (Ille-et-Vilaine, France, permit number 005283) and were realised in accordance with the European Communities Council Directive 2010/63/EU. The breeding procedure and tests were approved by the regional ethics committee (agreement number: R-2011-SLU-02).

2.1.2. Animals and housing conditions

All quails came from a broiler line of a commercial farm (*Les cailles de Chanteloup*, France). Food was high protein cereal in granulates for adult, in mix pellet for chicks and provided ad libitum, like water. All rooms were maintained at $20\pm 1^{\circ}\text{C}$ and in LD (Light:Dark) 12:12.

Parents: In order to have as little relatedness as possible between our chicks (we cannot know the relatedness of commercial individuals), we have paid particular attention to the lineage of our reproductive adults as much as chicks. We realised a first generation with thirty five males and females as breeders with only one male by female. Therefore, each chick of a female was not related to the descendants of other females. We obtained twenty-eight males and twenty-eight females used as second breeders (between non-related), with always only one male by female. From born chicks, we obtained, twenty-four females non-related and twenty-four males, unrelated, which we mated. Therefore each experimental chick of a female used as a mother was not related to the descendants of other females over 2 generations minimum. Females were lodged in individually wire mesh cages (51×40×30cm) with a feeder and drinker in a breeding room. Males were placed individually in batteries (35×25×21cm) in another room. Then one male was paired to a particular female and we placed then in a circular cage until we noted successful copulation. Meetings took place once every two days during a period of three weeks to collect 15 eggs per couple, artificially incubated in the laboratory (37.7°C , 55% of humidity and 2rotations $45^{\circ}/\text{day}$) for 17 days.

Chicks: From hatching, chicks were weighed and identified by a numbered coloured leg ring. They were immediately placed by family in plastic cages (98×35×42cm) with heater ($37\pm 1^{\circ}\text{C}$), drinker and feeder. In the evenings, we had placed 4 chicks with each mother. Females had their 2 related chicks and 2 unrelated chicks. Females are matched two by two, one receiving chicks of the second one, and conversely. Chicks were weighed on post-hatching day 11 (PHD11), and, then, once a week during a period of 3 weeks. As sexual dimorphism appears only after 3 weeks (Mills et al., 1997), chicks were chosen randomly but the general sex ratio was 0.81.

2.1.3. Maternal induction procedure

We used the fostering procedure previously described by Richard-Yris (1994). We added one plastic square nestbox (18cm×18cm×18cm) to each cage for habituation, three days before hatching, and we closed in females for the night a first time the day before induction. The evening of hatching in the dark, the 4 chicks were gently placed underneath each female which were closed in nestboxes one hour before. Maternal behaviour was inducted by tactile and auditory stimuli of chicks. The next morning, we opened and removed the nestboxes and checked if the induction was successful; i.e. if females warmed chicks and did not have inadapted behaviours (attacking, pecking, over-warming posture). Only one mother failed the induction, and we removed 3 mothers because they were too aggressive, 1 on PHD3 and 2 on PHD4. Chicks showing significant high signs of malaise (trembling, hypothermia) were immediately removed to plastic cage under a heater and replaced by others throughout the mothering. One chick had to be replaced beyond the third day of mothering and was removed from the analysis. So, in total we conserved 20 mothers with 35 unrelated chicks and 34 related chicks.

On PHD11, mothers were removed and placed together in boxes (4m²) while the 4 chicks stayed together during a period of 3 weeks for behavioural tests. The distribution of related and unrelated chicks according sex was homogeneous (Related: F=18 & M=16; Unrelated: F=24 & M=11; Fisher test: p=0.22).

2.2. MOTHERING STUDY

All the observations and tests described below were performed by a unique human observer.

2.2.1. Observations of mothers and chicks' behaviour in their home cage

Both mother and chicks' behaviour were sampled hidden by one-way-mirror. The method used was instantaneous scan sampling (SCAN) for the time budget on PHD2, 4, 6, 8 & 10 and focal sampling (FOCUS) to spot the punctual behaviours, very short in duration and with a low frequency, so not representative in scan, and interactions on PHD3, 5, 7 & 9.

SCAN mothers and chicks: We recorded 30 scans every 6 min in the morning and 30 scans every 6 min in the afternoon for a total occurrences of 60. All general behaviours of all individuals were listed: rest, locomotion, exploration, observation (stay without move, eyes opened) and maintenance. For each chick, the type of rest strategy was noted: alone, huddling or warmed. Then the type of warming posture used by the mother was recorded: covering (i.e. chicks are fully hidden by feathers of the mother) or non-covering (i.e. the mother is high posture or lying on the side not allowing chicks to be warmed well). The distance between each chick and the mother and with other chicks was also noted: 0 (in warming with mother or in huddling with chicks), contact (chick touching the individual), near (distance is less than one chick length), proximity (distance of one chick to 2 chicks' length), distant (distance between two chicks length and half of the cage) and opposite (distance longer than half of the cage). From these surveys, an index of interindividual distance (ID) was calculated according to the formula:

$$ID = \frac{(N^{opposite} + (N^{distant} \times 0.8) + (N^{proximity} \times 0.6) + (N^{near} \times 0.4) + (N^{contact} \times 0.2))}{Total\ Nscan}$$

This index was calculated by cage between mother and related/unrelated chicks, and between related/unrelated chicks themselves.

FOCUS: The frequency of interactive behaviours between a mother and each chick was recorded as well as the initiator and the receptor when it was possible, continuously for two 5 min. sessions. For the mother, maternal vocalizations, trampling, contact breaks and agonistic behaviours were noted; pecks (mother pecked chick by a rapid movement of the bust), attacks (mother runs after chick which escapes, and tends to peck it. For chick, calls, successful and unsuccessful solicitations (chicks gently pecking the feathers of the mother and/or pushing them to slip below followed by a phase of warming or avoidance of mother) were recorded.

2.2.2. Reaction to separation

On PHD11, to see if the link between mother and chicks may be different according to relatedness, chicks from the cage were removed and placed in a similar cage in another room and the chicks' reaction

for 3 min was noted. Latencies to call and to walk, number of calls and steps and latency of comfort behaviour (feeding, rest, maintenance) were also recorded.

2.3. BEHAVIOURAL TRAITS ASSESSMENT OF CHICKS

Several complementary tests were performed to get a comprehensive idea of sociality and fearfulness. Tests were listed by chronological order.

2.3.1. Separation from siblings. With this test, the reactivity of the chicks to the isolation was assessed. So, on PHD16, one chick was removed and placed it in a similar cage to its home cage in another room and for 3 minutes, and latencies of distress call and of first steps and their frequencies were noted. Then, chick was replaced and, after a 1/4 hour, a second chick was removed. Unrelated and related chicks were tested alternately.

2.3.2. Emergence test and response to a sudden predator call. This test assesses the shyness/boldness of an individual and its sociality confronted to a novel open environment, in social isolation. Individuals were enclosed individually, for 1mn, in a dark wooden box (18×18×18cm) placed at the input of a wooden lighted test cage (62×60×30cm). The floor was covered with wood shavings and one wall is an observation window where light passed through, hiding the experimenter. After opening, chick had 3min to exit and latencies to pass head and whole body out of box was recorded. If the chick did not come out, we put a maximal score of 180s. Then if there was output, the latency of first distress call, their number and all fear (low and high postures, pacing, freezing) and comfort behaviours (dustbathing) in a cage for 3 min were noticed. Then, a sudden noise, cries of buzzard (natural predator) of 60 dBs was diffused for 10 seconds and the immediate reaction of the individual was recorded, especially time of freezing and number of steps during a period of 30 seconds. This test was carried out on PHD17.

2.3.2. Runway test. This test assesses the motivation of the quail to reach a social stimulus (Mills and Faure, 1991). The apparatus was a long corridor (150×20×20cm) with a cage (20×35×20cm) at one end containing two unfamiliar chicks of the same age as the test chick. As chicks are motivated to join familiar or non-familiar conspecifics (Formanek et al., 2008), we used unfamiliar conspecifics to limit the unknown effect of affinity between familiar individuals. The test chick was placed in a small wooden

box (18×18×18cm) at the other end. The box was kept closed for 1 minute and then it was opened in order to record latency to leave the small box and once out, the box was delicately closed again. The tunnel was divided into 4 virtual segments, with, starting from the test chick's end: zones A, B, C (32cm for each part) and P (14cm, the part nearest to the social stimulus). During a period of 3 minutes, we recorded the time to reach zone P, the time spent in each zone, latency to emit first call, and the number of attempts to reach conspecifics and to peck the cage. It was performed on PHD18.

2.3.3. Open Field test & novel object. The individual was deposited in a centre of a brightly lit unfamiliar arena (ø 120cm, H60cm) and were noted for 5 min, behind a one-way mirror, latencies of the first distress call and of the first step, their number and the frequencies of fear behaviours (freezing, pacing, high and low observation postures). Then, the light was switched off and we set a new object (a brown cylinder ø 7cm, H15cm) in the arena at the opposite side from the chick. After switching on the light, the latency to approach, to reach the object part, to touch it, and all occurrences of fear behaviours were noted during 3min. This test was carried out on PHD24&25.

2.4. STATISTICAL ANALYSES

For analysing mother and chicks' behaviour during mothering period, we have performed two principal component analyses (PCA) with, for the first, the main variables of maternal behaviour, and for the second, the main variables of chicks (interactions with mother and general activities), from each observation day. We employed a varimax rotation to maximise the independency between components (Abdi, 2003). We chose a criterion of PC loading of |0.5| or higher to consider a variable relevant to a specific component. Factorial scores from each PCA component were examined with a general linear mixed models on repeated measures (GLMMr) to study the influence of time, relatedness (fixed factors) and their interaction on mothers' and chicks' behaviour. We considered mothers identity as a random factor. The distributions used were Gaussian after logit transformation if there was no-normality of residuals. We used LSD tests for post-hoc comparisons.

Distances between chicks according their relatedness were analysed using GLMMr with the mother and the interaction between the relatedness of the 2 individuals of the distance as random factors. The reaction of chicks to the mother's separation were analysed with general linear mixed models (GLMM), relatedness was fixed factor and mother was random factor. The distributions used were Gaussian after logit transformation if there was no-normality of residuals for continuous variables and Poisson for occurrences.

To analyse data on behavioural development of chicks, we made a third PCA analysis by varimax rotation with the data of behavioural tests to describe the emotivity and sociality profile of chicks according to relatedness. Factorial scored obtained were analysed by GLMM with relatedness as fixed factor and mothers as random factor.

The threshold of significance was 0.05 and the tendencies between 0.1 and 0.05 were mentioned. PCA were realised with XLStat (www.xlstat.com) and scores were analysed with SPSS Statistics 20. (IBM).

3. RESULTS

3.1. Mothering study

3.1.1. Maternal behaviour

Maternal behaviour PCA highlighted two components with eigenvalues greater than one and which together explained 60.79% of the variance. The first component (34.79%) was mainly represented by two opposite variables, the mother-chicks' distance and the percentage of warming time, so we named "Distance/Warming" (Fig1). The second component (25.99%) was mainly represented by three variables of avoidance and neglected behaviours, and was termed "Rejection" (Fig 1).

GLMMr comparisons revealed a time effect on both components (Distance/Warming: $F_{3,272}=136.0$, $P<0.001$; Rejection: $F_{3,272}=17.43$, $P<0.001$) (Fig 2). There were neither significant relatedness effect (Distance/Warming: $F_{1,274}=0.139$, $P=0.709$; Rejection: $F_{1,274}=0.221$, $P=0.638$) nor time×relatedness effect (Distance/Warming: $F_{7,268}=1.360$, $P=0.255$; Rejection: $F_{7,268}=0.553$, $P=0.646$)

3.1.2. Chicks' behaviour

Chicks' behaviour PCA highlighted two components with eigenvalues greater than one and which together explained 47.40% of the variance. The first component (24.50%) was mainly represented by two variables, the percentage of active behaviour (exploration, locomotion, feeding) and maintenance (grooming, defecation, bathing) and so was named "Activity" (Fig 3). The second component (22.90%) was mainly represented by three variables of interaction with mother, neutral or positive (contact break and warming attempts) opposite to negative ones (escape) and called "Interaction with mother" (Fig 3).

GLMMr comparisons revealed a time effect on "Activity" component ($F_{3,272}=20.24$, $P<0.001$) but not on "Interaction with mother" component ($F_{3,272}=1.737$, $P=0.160$) (Fig 4). There was no significant relatedness effect on "Activity" ($F_{1,274}=1.097$, $P=0.296$) and a tendency for unrelated chicks to make more neutral and positive interaction with mother ($F_{1,274}=2.767$, $P=0.097$) (Fig 4). There were not significant time×relatedness effects (Activity: $F_{7,268}=0.578$, $P=0.630$; Interaction with mother: $F_{7,268}=0.572$, $P=0.634$).

3.1.3. Distances

GLMMr showed a significant time effect on the distance between chicks ($F_{4,595}=63.74$, $P<0.001$) (Fig 5), no significant difference according to their relatedness ($F_{2,597}=0.981$, $P=0.376$) and no significant interaction time×relatedness ($F_{14,585}=0.648$, $P=0.738$).

3.1.4. Reaction to mother's separation

There were no significant differences between chicks according their relatedness in call latency ($A=90.78\pm 15.12$; $B=117.36\pm 14.23$; GLMM: $F_{1,67}=7.143$; $P=0.103$) and number of calls ($A=7.66\pm 3.13$; $B=9.88\pm 2.95$; GLMM: $F_{1,67}=0.450$; $P=0.505$).

3.2. Behavioural development assessment of chicks

Behavioural tests PCA highlighted three components with eigenvalues greater than one and which together explained 54.22% of the variance (Fig 6). The first component (variance: 26.99% and 22.16% after varimax rotation) represented the emotivity profile of our chicks. The high loadings could assimilate with the passive strategy while negative loadings were illustrated the active strategy. The second component (variance: 15.06% and 14.66% after varimax rotation) was defined by social motivation in presence of conspecifics represented by high loadings. The third component (variance: 12.16% and 17.55% after varimax rotation) was the reaction to isolation with high loading for strong response, labelled “social motivation without conspecifics”.

There were neither significant effect of relatedness neither on emotivity profile (GLMM, $F_{1,67}=0.740$, $P=0.393$) nor on social motivation with conspecifics ($F_{1,67}=0.062$, $P=0.803$) or on social motivation without conspecifics ($F_{1,67}=0.015$, $P=0.903$).

4. DISCUSSION

Our results suggest that i) maternal behaviour is not of significant difference towards unrelated or related chicks present in the same brood, ii) the behaviour of chicks towards other chicks is not significantly according to their relatedness, iii) we found no difference in the mother-chicks or chick-chicks distances according to their relatedness. Thus unrelated and related chicks having experienced a substantially similar mothering, have not developed significantly different emotivity profile or social behaviour. So adoption procedure seems not to be biased by mother or chicks. Earlier studies in precocial birds had shown that the adoption of chicks were accompanied by an increased aggressiveness of parents (Öst and Bäck, 2003) and adopted chicks were generally found at a greater distance than related chicks (Nastase and Sherry, 1997; Öst and Bäck, 2003). However these species of birds live in colonies and we can observe both nest parasitism, i.e. a foreign female lays eggs in the nest of another; or adoption of chicks during breeding (Andersson and Ahlund, 2000; Choudhury et al., 1993). Parents recognize the presence of a stranger chick but accept it. In this case, the increase of parental aggression may be related to the recognition of the presence of a stranger and then remains

temporary, as is the case with the stork on the first day of the adoption (Redondo et al., 1995). It may also be related to maintaining in periphery of adopted chicks by parents, and is then coupled with a greater distance between parents and adopted chicks; to reduce the chances of predation on their related chicks (Eadie et al., 1988). However, here the quail is a precocial bird of which the female raises its young alone (Orcutt and Orcutt, 1976). Thus, the risk of breeding chicks that are not her own, especially at hatching, is greatly limited. This is why quail has no strong ecological constraint imposing her to develop important behavioural methods of unrelated discrimination. However, the quail is perfectly able to recognize a familiar individual from an unfamiliar one (Jones et al., 1996; Schweitzer et al., 2010). In our study the adoption of unrelated chicks was realized on the first day of mothering at the same time as related chicks. It takes a few days to set up mutual recognition by association between mothers and chicks (Collias and Jahn, 1959; Ramsay, 1951). This recognition could even happen before hatching since chicks already emit different kind of cries in their egg to which the female usually responds with cooing. This mother's response is not immediate and requires prolonged exposure to chicks' cries (Guyomarc'h, 1971). So we can well imagine that during a late adoption, the behaviour of the mother would have been different and that she could show aggressive behaviour towards those unfamiliar chicks, as it was the case for storks (Redondo et al., 1995), chicken and ducks (Ramsay, 1951).

The process that underlies a difference of the mother's behaviour towards unrelated or related young involves two mechanisms: first the cognitive ability to recognize young related or unrelated, then the distinctive behaviour expressed by the female towards each of both of the young, i.e. discrimination (Hayes et al., 2004). These two mechanisms, are independent of each other (Mateo, 2002). Thus, the fact that quail do not behave differently towards the unrelated or related chicks from the first day means either (1) she does not recognize her chicks according their relatedness, or (2) the cost of rejecting these unrelated chicks is higher than that to breed them. Indeed, when mothers raise their chicks alone, where there is not any other individual and brood parasitism do no occur, they invest by default only on their own chicks. So Mateo (2004) concludes that mothers can recognize their nest or their raising area indirectly but not their chicks directly. As kin recognition is still important for reproduction, maybe individuals can recognize relatedness but mother would not discriminate the chicks. In the chili degu for

example, the female is able to recognize its related youth or the unrelated ones but does not act differently towards them in terms of interactions or retrieval (Ebensperger et al., 2006).

In both of these cases, the cost of recognition/discrimination between related and unrelated seems not to make any profits or even be more expensive than to take care of them (Mateo, 2002). The quail chicks are precocial, walk and actively follow the mother shortly after hatching. Even if they are able to eat alone, they need to be warmed up and regularly seek the mother even when she rejects them. The female would have to expend considerable energy to get to reject them. Especially as compared to altricial species, which must feed their nestlings, and so practice "shared" care, i.e. whose the direct benefit concerns only one chick (Lazarus and Inglis, 1986), quail as a precocial species have less to invest in post-hatching maternal care. The warming up and protection against predators she provides can be considered here as an "unshared" parental care, which means it is beneficial to all individuals of the brood (Lazarus and Inglis, 1986) and is therefore less expensive. Indeed, chicks are highly synchronized during the breeding period (Lumineau et al., 2001), and maternal behaviour increases this synchronization (Galuret et al., 2020; Wauters et al., 2002). They warm up together under the mother and are relatively close to each other which optimizes the care received. So, within the brood itself, unrelated and related chicks would have no advantage in discriminating amongst themselves. In this sense our results did not actually shown a behaviour or a distance between chicks whether they are related or not. On the contrary, they remain closer to each other irrespective of their relatedness. In this way, the mother has a clear role of synchroniser because when chicks are raised without a mother they are closer and interact more with related siblings (Waldman and Bateson, 1989). They are also more synchronized between related than non-related when they are not brooded by a mother (Pincemy and Guyomarc'h, 2004). Rhythmicity has a genetic basis that can facilitate the synchronisation between related individuals (Favreau et al., 2009; Formanek et al., 2011; Guyomarc'h et al., 1998), but the presence of a mother can regulate this rhythm (Formanek et al., 2009). However, this influence would dependent on the flexibility of the intrinsic behavioural characteristics of the chicks (Houdelier et al., 2011).

Many experiments were based on adoptions to show a non-genetic transmission of some behaviours (reviewed in (Houdelier et al., 2013)). It appears as the standard line of chicks adopted by mothers selected for high or low sociality have similar social characteristics to the adoptive mother (Formanek et al., 2008) . Similarly when chicks were adopted by mothers of high emotivity, they have stronger emotivity than those adopted by mothers of low emotivity, even after weaning(Richard-Yris et al., 2005). However if these experiences have clearly shown the influence of the adoptive mother on the behavioural development of chicks, a legitimate question arises, namely would the adoption of an unrelated chick in itself not have changed the development of these chicks by a different maternal behavioural expression in particular? For instance, in mice, the mother is more maternal towards an adopted pup, licking them more, which then leads to a decrease of pup responsiveness in a stressful situation of separation (Darnaudéry et al., 2004). Indeed young are not only sensitive to the fact of having a mother or not but also to her behaviour (Ten Cate, 1989). For example, social motivation expressed by chicks is positively correlated with rejection rates expressed by adoptive mothers (Lumineau et al., 2019; Pittet et al., 2014a). Our experience shows here that the mother's behaviour is not changed towards related or unrelated chicks. So it was not surprising that it also shows that emotivity profile and social motivation with or without conspecifics have not been affected differently between unrelated and related chicks.

5. CONCLUSION

In conclusion, the relatedness is not a major factor in the variation of maternal behaviour in quail. The ecological characteristics of this species, precocial with a solitary breeding, does not imply that females develop sharp discriminatory mechanisms towards unrelated and related chicks. The familiarity that is set up with its young during the first days after hatching would be a more suitable mechanism to fight against an investment towards alien chicks than may appear. Therefore we can conclude that experiments produced with adoption seem not to be biased by a change in maternal behaviour due to adoption procedure itself. It remains to determine whether the adoptive mother is just indiscriminate

between its young but able to recognize a related/unrelated chick or if it does not have this ability to distinguish between them, our experience cannot answer this question.

AUTHOR DECLARATION TEMPLATE

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

We further confirm that any aspect of the work covered in this manuscript that has involved either experimental animals or human patients has been conducted with the ethical approval of all relevant bodies and that such approvals are acknowledged within the manuscript.

We understand that the Corresponding Author is the sole contact for the Editorial process (including Editorial Manager and direct communications with the office). He/she is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs. We confirm that we have provided a current, correct email address which is accessible by the Corresponding Author and which has been configured to accept email from sophie.lumineau@univ-rennes1.fr

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Figure 1: Maternal behaviour during the mothering period described by the 6 main behavioural variables on the first two axes of PCA with varimax rotation. The first axis represents mother-chicks' distance and warming. The second is the level of chicks' rejection by mother.

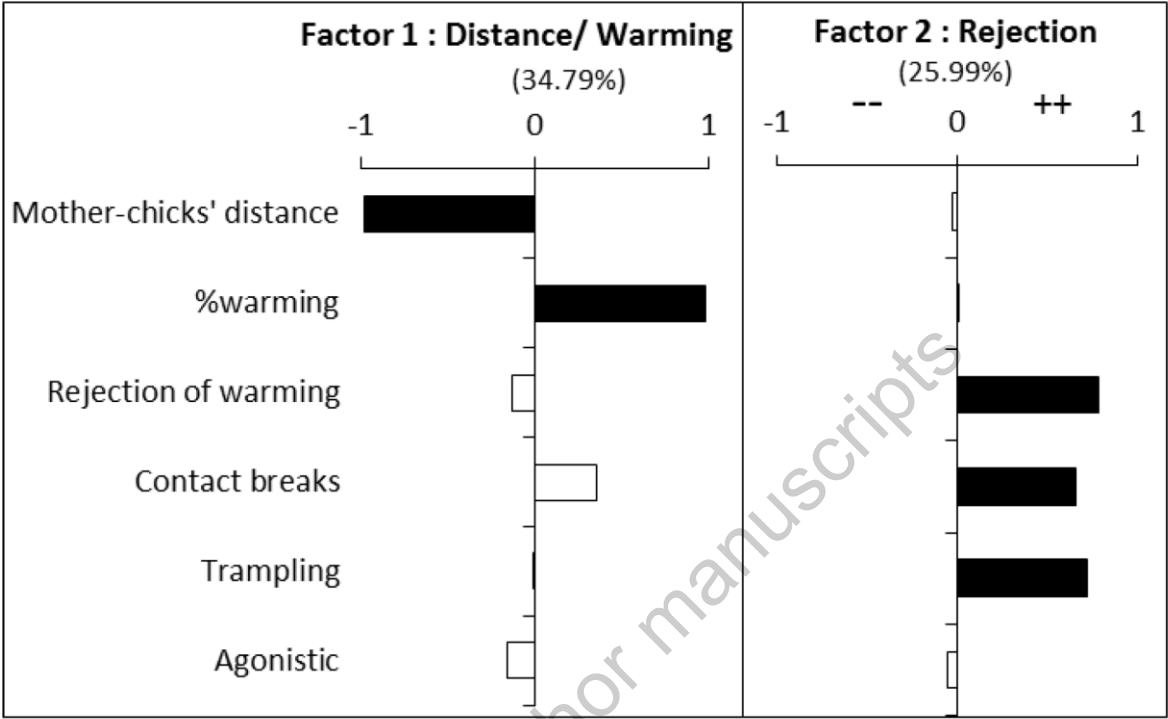


Figure 2: Scores (means \pm SE) of maternal behaviour PCA on the two axis “Distance/warming” & “Rejection”, in relation to day, according relatedness: unrelated (black bars) and related chicks (white bars). The boxes give the general result of the LMr Test (there are no significant interactions effects), and the result of Post-hoc LSD are on the graph: #: $P < 0.10$ & ***: $P < 0.001$.

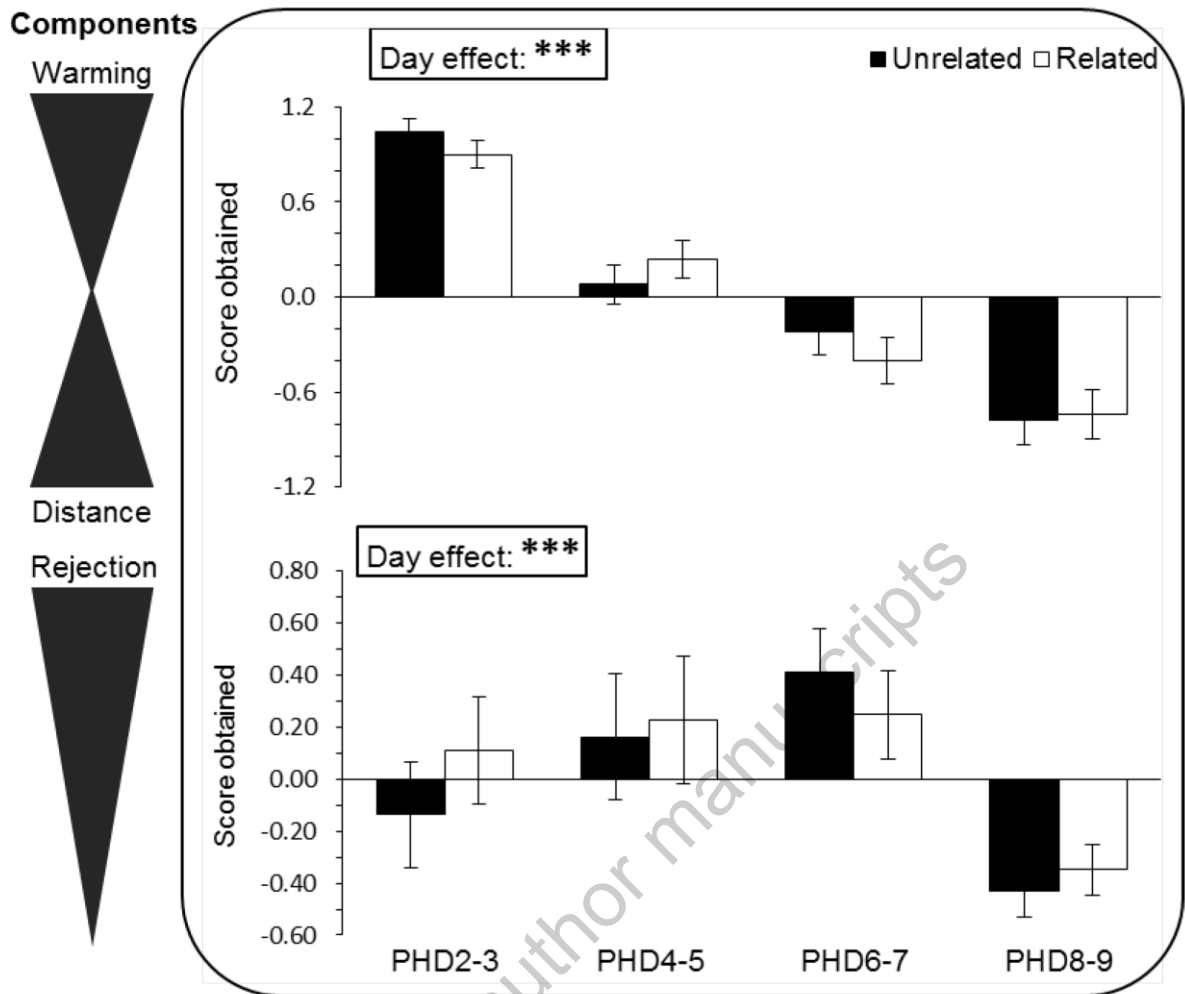


Figure 3: Chicks' behaviour during the mothering period described by the 5 main behavioural variables on the first two axes of PCA with varimax rotation. The first axis represents chicks' activity and maintenance. The second is the interactions with mother.

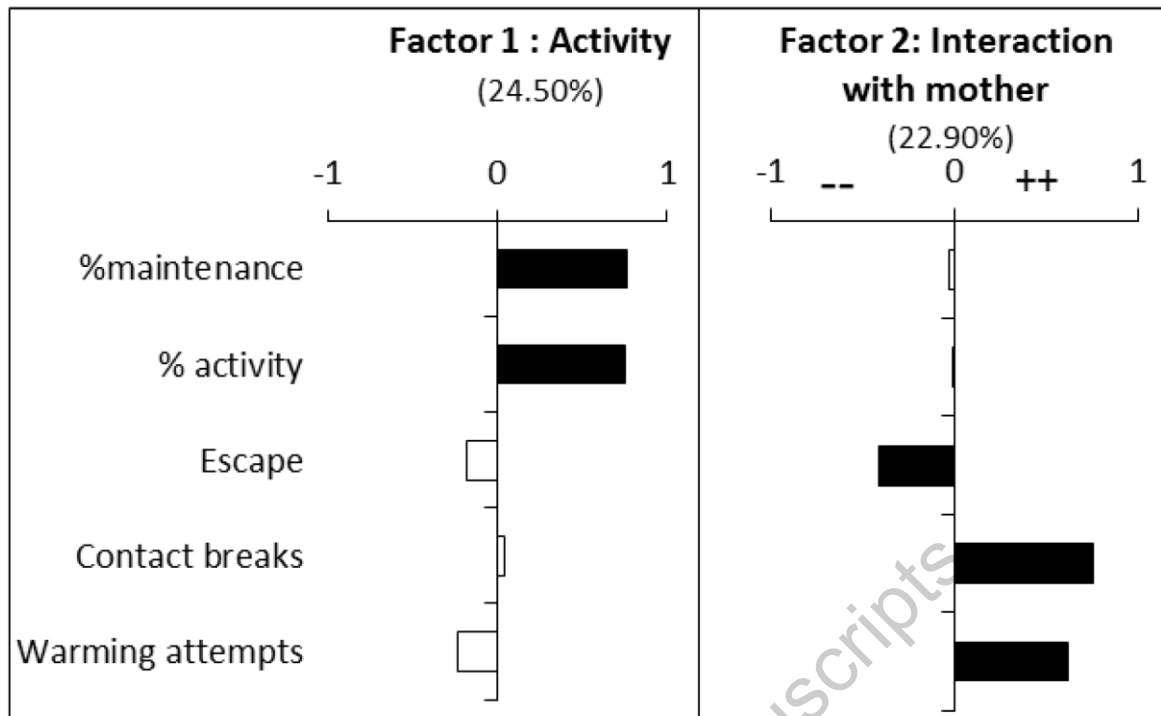


Figure 4: Scores (means \pm SE) on the two axes “Activity” & “Interaction with mother”, in relation to day, according relatedness: unrelated (black bars) and related chicks (white bars). The boxes give the significant results of the GLMMr Test (there are not any interactions effects) and the result of Post-hoc LSD are on the graph: #: $P < 0.10$ & ***: $P < 0.001$

Components

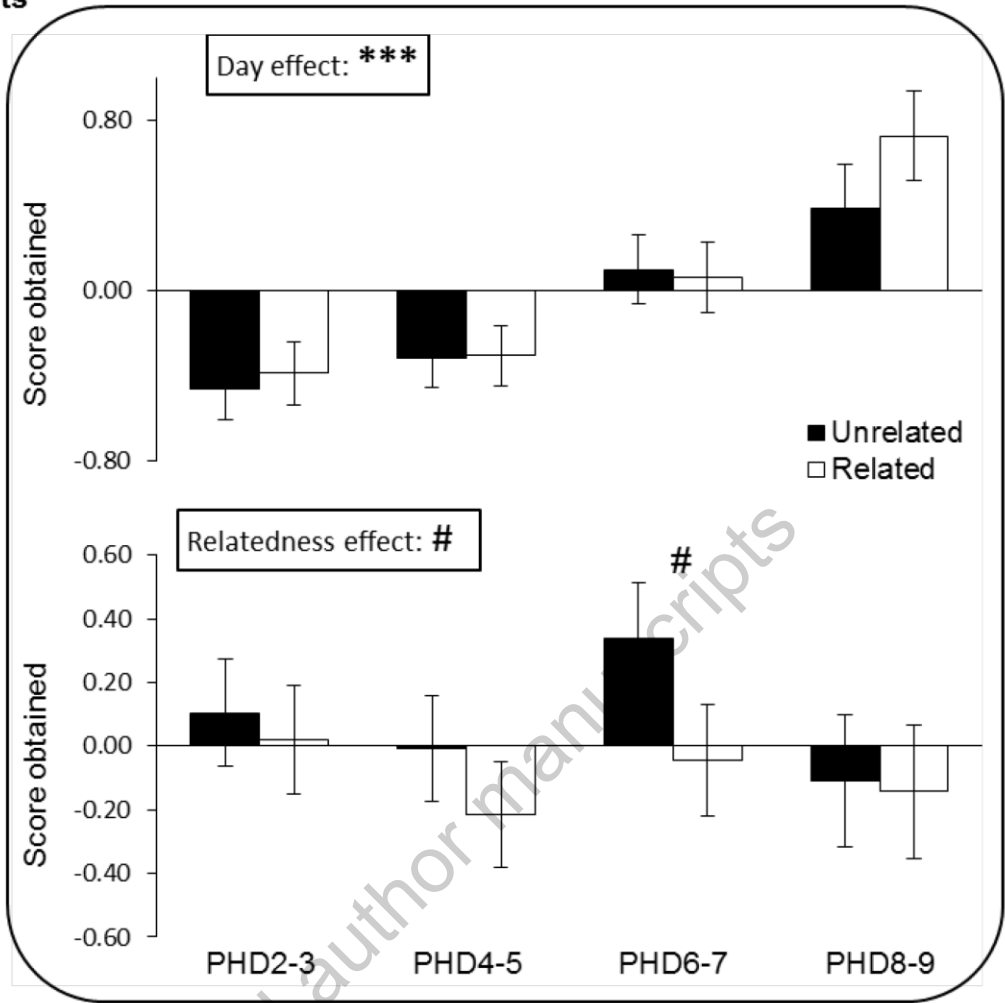


Figure 5: Distance (means \pm SE) between chicks according their relatedness: between unrelated & unrelated (black bars), unrelated and related (hatched bars) & related and related (white bars). GLMMr Test.

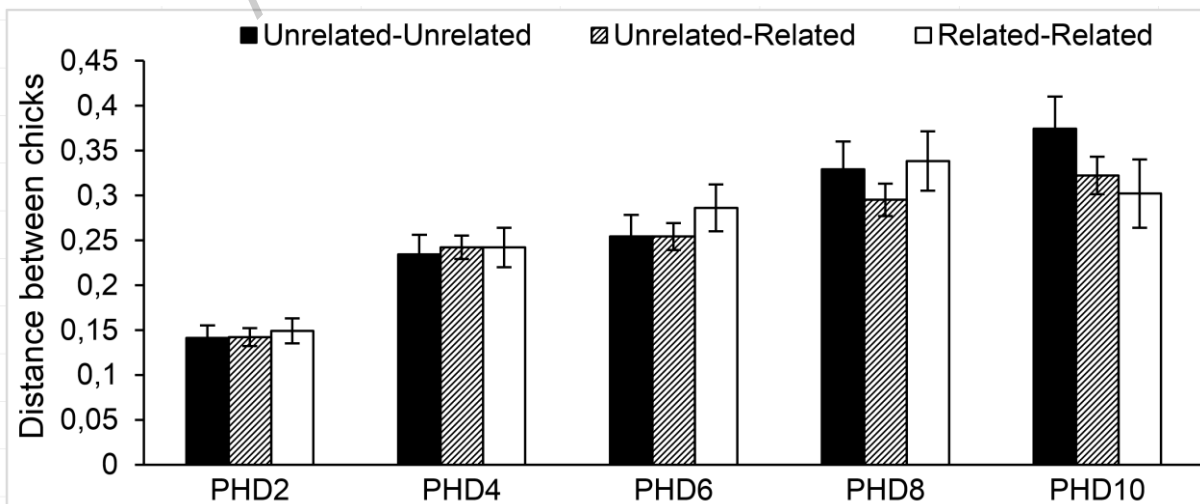


Figure 6: Behavioural traits of chicks described by the 11 main test variables on the first three components of PCA with varimax rotation and the scores (mean \pm S.E.) obtained by chicks according relatedness. The first component represents active or passive emotivity profile (22.16%). The second component is social motivation with conspecifics (14.66%) and the third is social motivation without conspecifics (17.55%): “++” for more social and “- -” for less social motivation. OF: Openfield; NO: Novel Object; SN: Sudden Noise; E: Emergence; RW: Runway test; SS: Social Separation. GLMM Tests.

