BROOD DESERTION IN DUCKS: THE ECOLOGICAL SIGNIFICANCE OF PARENTAL CARE FOR OFFSPRING SURVIVAL

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Abstract

The debate concerning the relative importance of the costs and benefits of parental investment decisions has created considerable controversy. This is especially true in the discussion for duck species, where the link between ending of parental care and offspring survival has not been fully determined. This experimental study tests whether mallard ducklings (*Anas platyrhynchos*; a non-crèching species with maternal care-) achieve maximum survival potential before the typical ending of the hen-brood bond. As mortality rates are at their highest during the first two weeks post-hatching, our experimental investigation of survival was restricted to ducklings from 2 weeks of age until fledging, in non-deserted (ND, control group; n=36) and prematurely abandoned (D, deserted treatment group; n=35) broods under free-ranging conditions. The experiment was conducted over two years to take differences in weather conditions into account. According to age periods, survival rates ranged from 65 to 95% in the D group and from 97 to 100% in the ND. Survival probability of deserted ducklings was 23% lower than that of the control group (p < 0.001) in 15 to 30 day old ducklings but was similar (p > 0.09) thereafter. Assuming that the hen-brood bond is time-disrupted at ~6 weeks post-hatching, our results are consistent with the idea that trade-offs associated with the provision and the consequent ceasing of maternal care have evolved according to the intrinsic ability of ducklings to survive on their own at ~4 weeks post-hatching. The dissipation of the behavioural-hormonal processes underlying the hen-brood bond probably requires a delay between these two events. The maintaining of maternal care for ~4 weeks post-hatching also coincides with the most critical periods of duckling vulnerability after hatching, during which the hen has an important anti-predator role to play.

Introduction

According to life history theory, parental investment has to be balanced between the survival benefits that offspring gain from enhanced parental care and the cost of parenting [1-3]. This trade-off is expressed through specific behavioural and physiological adjustments [2,4]. In migratory birds such as Anatinae, females are alone to rear their young, and physiological constraints linked to nutritional status (body condition) and body moult can interact with parental care [4,5]. Given that brood-rearing hens may be particularly vulnerable to predators and have reduced survival rates [6,7], and that declining habitat quality or increasing resource competition can increase brood-parent conflicts [5,8], the payoffs from attending

or leaving the brood could change according to weather conditions, offspring age and the ducklings' ability to survive on their own [9-11]. Thus, the timing of brood abandonment (i.e., typical timed hen-brood disruption, see [2]) could be related to the brood's age in ways that optimize both duckling survival and female fitness. For instance, it has been shown that attentiveness by mallard hens (*Anas platyrhynchos*) steadily decreases with brood age, and maternal care is clearly disrupted by six weeks post-hatching [4]. At this point in their development, ducklings have almost reached the same size as the hen [4], but remain flightless for 2-3 weeks [12]. Despite the presence of the female, the mortality rate in dabbling ducklings is highest during the first two weeks following hatching, until thermal independence is reached [9,13,14]. It has been argued that in gadwalls (*Anas strepera*), premature brood abandonment (i.e., brood desertion as defined by Székely et al. [2]) during the four weeks following hatching is higher when ducklings are less likely to survive [15]. Furthermore, the "salvage strategy" hypothesis predicts that females with poor body condition are more prompt to desert offspring, potentially to enhance their future survival or reproductive success, whereas the brood size hypothesis proposes that females are less likely to desert larger, more valuable broods (see [15] for review). Amongst Anatinae, neither hypothesis has been consistently supported [15-19]. Nevertheless, alternatively to the idea that parents would desert their offspring when the latter are more unlikely to survive and since the allocation of care should be adaptive, it is also crucial to address the converse assumption that the hen could stop investing in maternal care because the offspring might be able to survive unaided [2,9]. To test this hypothesis, we conducted an experimental study in free-ranging conditions to compare survival rates of radio-marked mallard ducklings staying in the brood (control group: non deserted broods) with deserted ducklings (without maternal care). Moreover, since duckling survival may be related to distance travelled overland [20,21], we also determined whether distances travelled between two consecutive locations among deserted ducklings differed from their non-deserted congeners, and if survival was negatively related to the distances travelled.

Material and methods

Method

Work was conducted in 2005 and 2006 at a mallard breeding area in the Nord region of France (France, 50° 59'N, 2° 35'E). All permits for capturing, marking and releasing the ducklings were issued by the appropriate local governmental administration of the department du Nord. The area is composed of drainage channels (<2 m wide) running through agricultural fields. During spring and summer, the banks of these channels are vegetated with grass and aquatic plants (mainly *Rumex pratensis* and *Phragmites australis*).

Three times a week between early April and early June, observers on foot located newly hatched mallard broods along the channels. Because the mortality rate in ducklings is highest during the first two weeks after hatching [13], only ducklings over 14 days old were captured. This period also corresponds to the age when offspring become cold hardy, having reached their full thermoregulatory capabilities [9]. The hatching date and age of each brood were estimated by comparing duckling body size to that

of the hen and by estimating the ducklings' plumage development stage [22,23]. As broods were located several times per week and each hatching event was recorded, duckling age was estimated with an approximate error of 1-2 days. When a brood was located, brood size was recorded, then the entire brood was slowly pushed towards a fishing net extended across the channel. 1-4 ducklings were randomly captured from each brood, weighed (± 1g) and placed in an opaque box before being immediately equipped with a radio transmitter. Capture and marking operations lasted <20 min. From the time a brood was detected until the release of captured ducklings, the hen flew away and stayed ca. 30 m from the capture site with the remaining not captured offspring. We adapted the non-invasive method described in [24] to attach the radio tag. The tag (TW4 with a specific antenna, Biotrack Inc., Wareham UK) was glued on a ring placed on one leg. To allow tibiotarsus development, the ring was filled with plasticine lining [25]. The radio transmitter and plasticine-filled leg ring weighed 6 grams, i.e., less than 3% of the duckling's body mass. This method of tagging did not visibly impair locomotion. Radio-marked ducklings were not slower than their non-tagged counterparts, and they remained with the brood (details below for the ND group). Moreover, the body mass of the few marked ducks (n = 5 non-deserted and n = 4 deserted) recovered during the following hunting season was within the known body mass range (1100-1500 g) for unmarked wintering mallards with good body condition (see [26]), and no cases of mortality linked to equipment tangling in vegetation were recorded. Finally, with survival probability reaching >0.97 at an age of over 14 days (see results of the present study for non-deserted offspring) this method of tagging did not harm the ducklings and may also be considered as efficient as those based on surgical abdominal or subcutaneous implantations (see [13]).

An experimental "deserted" (D) group was created from the radio-tagged ducklings in each brood. From the ducks captured in a given brood, one tagged duckling was chosen randomly from ≤2 marked ducklings/brood, whereas 2 or 3 ducklings were randomly chosen from >2 marked ducklings/brood. These D group individuals were all immediately and separately released between 600 and 1000 m from their original brood location in suitable habitat (similar water level and vegetation) within the same breeding area but in channels lacking other congeners. Care was therefore taken to put D ducklings in a similar suitable habitat whilst avoiding any brood mixing, which indeed did not occur during the monitoring period. All the released ducklings therefore remained alone over the whole tracking period, without mixing with other congeners. This was possible because channels are extended over long distances. In our experimental design, we preferred scattering the D group ducklings to avoid any risks of brood mixing or adoption rather than simply removing the female from a brood. Indeed, only by discarding the hen, ducklings could benefit from the experience and social relations of other broods or congeners to enhance survivorship. Remaining radio-tagged ducklings from the captured broods were released near the respective points of capture and females, and all joined their brood of origin (non-deserted group, ND). No premature brood abandonments (before week 6 post-hatching) were recorded in the ND group. A total of 79 ducklings were radio-tagged. 4 ND and 4 D ducklings could not be monitored due to the absence of a transmitter signal the day after release and the following days; analyses were therefore restricted to 36 ND and 35 D ducklings of known fate from 39 broods (ND: 1.3±0.3 ducklings/brood in 2005, 1.3±0.4 ducklings/brood in 2006; D: 1.5±0.3 ducklings/brood in 2005, 2.0

± 0.4 ducklings/brood in 2006). Hatching dates for all equipped ducklings ranged between 1st April and 5th June for both years.

Radios transmitted signals for > 90 days. The exact locations (± 10 m) of the ducklings were recorded at least every two days with a portable tracking receiver. Duckling fate was determined by visual contact using binoculars when individuals were still alive, or by retrieving dead ducklings. Duckling survival was monitored for at least 63 days post-hatching, assuming that mallards have fully fledged (i.e. are able to fly) at the age of 9 weeks [27]. In case of mortality by predation, identification of predators was based on remains. For each duckling, we measured straight-line movements (m) by reporting the positions between two consecutive locations on a 1/25000 scale map.

Statistics and calculations

Daily precipitation, and minimum and maximum ambient temperatures were obtained from the National Institute METEOFRANCE for the entire monitoring period (April-July). Before using parametric tests we checked for normality and equality of variance. Mean meteorological data for ten-day periods and year interactions were compared using a two-way ANOVA.

Mallard offspring mortality is highest during the first two weeks after hatching and then remains very low from 30 days of age onwards [13,21]. The hen-brood bond dissipates at ~6 weeks post-hatching [4]. Given these considerations, 3 periods were taken into account for daily survival rate analyses: 15-30 days, 31-42 days and 43-63 days post-hatching respectively. Fisher's Exact Test was used to compare the proportion of dead or alive ducklings within each post-hatching period. On the dataset that included only broods in which several ducklings of the same brood had been tracked, a Generalized Linear Model with a quasibinomial family was used to investigate the effect of the «brood» ducklings belonged, on survival. «Brood» was considered as the dependant variable and survival (dead or alive) was the response variable. This model was fitted to evaluate the possibility that the fates of broodmates were not independent. Since the effect of «brood» was not significant ($F_{1,34}$ = 1.35, p = 0.28) the brood factor was not taken into account in subsequent analyses. In order to check the effect of hatching date, body mass at capture corrected by age (residuals of the linear regression between body mass and age), the mean distance travelled by the ducklings and the size of the groups at release on survival, we also performed a Generalized Linear Model with a quasibinomial family. Survival was the response variable, the state (ND or D) was the dependant factor and the other variables were considered as covariables.

The LogRank survival test was used for each period to detect cumulative survival rate differences between groups. A two-way ANOVA for Repeated Measures was used to compare distances moved between locations according to experimental group and post-hatching period. Brood sizes for the ND group at release were compared between years using the Student T-test and body mass at capture was compared between treatment groups using an ANCOVA with age as the covariable. A two-way ANOVA was used to compare hatching date for years and treatment groups.

All statistical analyses were performed with R, Sigmastat 3.0 (SPSS INC. software) and Minitab 15 software. Values provided are means ± SE. All statistical tests are two-tailed and probability levels < 0.05 were considered as significant.

Results

Mean hatching date did not differ ($F_{1,69} < 3.51$, $p > 0.05$) between treatment groups and years (ND: 24 April ± 3 days and D: 23 April ± 3 days). Brood size of the ND group at release, did not differ between years (t = 0.22, df = 27, p = 0.82) and averaged 6.5 ± 0.5 ducklings. Mean body mass at capture (with age as covariable) was similar between treatment groups ($F_{1,70}$ = 1.10, p = 0.30, D: 287 ± 12g and ND: 249 ± 15g). Mean daily precipitation, minimum and maximum ambient temperatures for each 10-day period differed by years (year x 10-day period interaction, $F_{11,220} > 2.17$, p < 0.02, Table 1).

Table 1. Ranges of daily mean (± SE) rainfall, minimal and maximal temperatures calculated per 10 days period between April and July during 2005 and 2006.

Years	Rainfall, mm	Minimal daily temperature, °C	Maximal daily temperature, °C
2005	0.02 ± 0.02 – 5.12 ± 2.11	6.57 ± 0.61 – 15.24 ± 0.41	12.75 ± 1.21 – 20.33 ± 0.57
2006	0.12 ± 0.10 – 4.84 ± 1.44	6.24 ± 0.62 – 18.39 ± 0.54	10.66 ± 0.65 – 25.51 ± 0.81

The proportion of dead ducklings was higher in group D during the first post-hatching period (Fisher's Exact Test p = 0.001, Fig. 1). No differences were detected for older ducklings (Fisher's Exact Tests, p > 0.30). In both treatment groups, mortality (85%) resulted mainly from predation (e.g. cat, fox, martens), with only two individuals killed by cars.
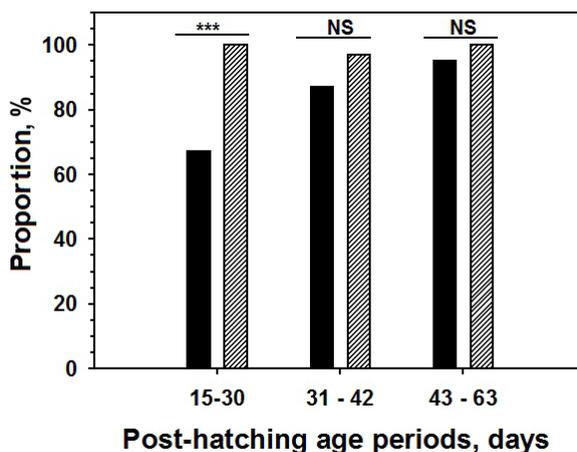

Fig. 1. Proportion (%) of surviving ducklings according to the three post-hatching periods (15-30, 31-41, 42-63 days), and to their status as members of either the non-deserted (ND : dashed bar) or deserted (D : black bar) experimental group. ***: p < 0.001 , NS: Non significant.

D and ND ducklings fledged during the same week, at ~9 weeks old. Cumulative survival rates for the whole post-hatching period (days 15-63) was 0.67 ± 0.08 for D ducklings and 0.97 ± 0.03 for ND ducklings (χ^2 = 11.01, df = 1, p < 0.001). Survival was lower in D versus ND ducklings between 15 and 30 days post-hatching (χ^2 = 12.69, df = 1, p = 0.001, Fig. 2), but survival changes did not differ between treatment groups in the second and the third post-hatching periods (χ^2 < 2.90, df =1, p > 0.09, Fig. 2). Whatever the post-hatching period, survival rates did not differ

between years in the ND and D groups ($\chi^2 < 6.8$, df = 3, p > 0.08). Neither the group size at release, the hatching date nor the body mass (corrected by age) at capture affected survival ($F_{1,70} < 0.70$, p > 0.40).
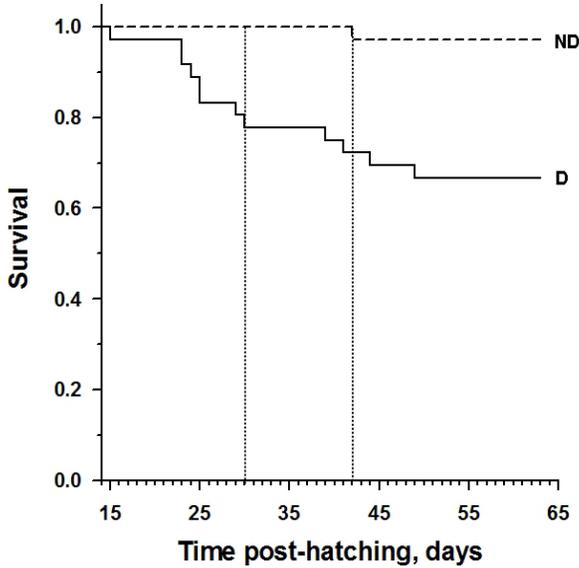

Fig. 2. Cumulative survival rates of duckling mallards according to their age and status: non-deserted (ND) or deserted (D). Vertical dashed lines represent the three age categories (15-30, 31-41, 42-63 days). Changes in survival only differed for the 15-30 days period (see text).

The mean distance between consecutive locations did not differ between D and ND groups ($F_{1,129} = 0.77$, p = 0.38, treatment x period interaction : $F_{2,129} = 2.11$, p = 0.13). However, the distance travelled was twofold lower in the second and third post-hatching periods than during the first period ($F_{2,129} = 23.11$, p < 0.001, Fig. 3). Overall, survival was not affected by the mean distance travelled ($F_{1,55} = 0.25$, p = 0.62).
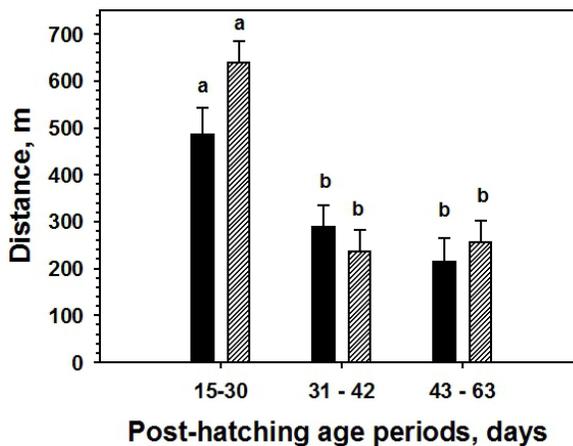

Fig. 3. Mean (± SE) distance (m) between consecutive locations travelled by mallard ducklings according to their age class and status: non-deserted (ND : dashed bar) or deserted (D : black bar). Values sharing the same letter are not significantly different (p > 0.05).

Discussion

This work with free-ranging, radio-marked mallard ducklings yields new insights into the ecological significance of parental care duration. Specifically, our results are consistent with an earlier hypothesis that the timed ending of maternal care and typical brood abandonment in mallards (three weeks before fledging, [4,12]) coincides with an intrinsic ability of growing ducklings to survive unaided (see [2,9]). Extending maternal care beyond this critical period of early duckling development could compromise the female's fitness, potentially affecting her ability to moult, regain body condition or to engage in future reproduction. Although the aim of our experiment design was not primarily to mimic a natural situation, this case of deserted ducklings can nevertheless be considered as an extreme natural situation of premature abandonment. Indeed, broods and rearing hens are frequently subjected to high mortality risks or disturbances due to predation (raptors, mustelidae, foxes, pikes) which can result in partial brood destruction or duckling scattering, resulting in a loss of maternal care before the typical ending of parental care [6,7,20,28,29]. After such brood disorganisation, ducklings can be separated from the hen and other broodmates and/or forced to move toward other sites with very few or no social interactions, which are assumed to be an important factor during development [13,20,30].
Survival rates of ND ducklings reported here are similar to those described for North American mallards [9,10,13,21] and other duck species [21,31,32]. This confirms that if the hen is with the brood, the survival probability of two week-old ducklings is very high once their thermoregulatory ability and cold hardiness is attained [9]. Conversely, deserted ducklings released alone had a significantly lower survivorship during the 15-30 days post-hatching period, whatever the year of breeding. These results give a new insight into the understanding of parental investment, and complete information gained through non experimental studies documenting survival rates in naturally deserted broods [15,33]. In natural conditions, deserted ducklings usually stay with their broodmates or gather with other congeners, and may therefore gain survivorship from the protective role and social relations associated to large group sizes, which may counterbalance the sudden loss of maternal care (See [11,34]).
The present findings on survival of radio-marked ducklings according to age classes also reinforce previous data showing that duckling survival is consistently high after 30 days post-hatching [13,21,34-36]. Thus, survival rate after one month post-hatching could be considered as an index of reproductive output, whatever the maternal care experience of ducklings (ND or D). At this age, mallard ducklings are in class IIB for feather growth ("mostly feathered" [22]) and the rate of body mass gain is at the inflection point. Structural growth is almost complete [27,37], and offspring are therefore likely less vulnerable to the effects of an energetic or nutritional stress on growth and are physically more capable of escaping from predators. These results globally emphasize the idea that intrinsic factors, and especially physical condition linked to age, may influence duckling survival (see [11]). The complex phenomenon of ceasing parental care results from the combined effects of endocrine adjustments by the hen (decreased release of prolactin, the hormone that regulates parental care behaviour) and external behavioural stimuli signalled by the ducklings such as growth and behavioural changes [4,38-40]. Therefore, in precocial species with uniparental care, it may generally be assumed that the spontaneous and more

typical progressive process of offspring abandonment occurs after ducklings have reached their intrinsic capacity to take care for themselves [2,11]. A delay between these two events is probably necessary to enable the behavioural-hormonal processes underlying the hen-brood bond to dissipate [15]. Interestingly, the findings of this study substantially support the idea that the typical timing of parental care disruption corresponds to a concomitant maximization of offspring fitness, i.e. parents abandon the brood after the young become independent (see [2,9]). If the rearing of young is costly to hens and if offspring-parent conflicts increase with duckling growth in any way [4,6,7], it may be adaptively advantageous for them to abandon their broods when duckling survival no longer depends on maternal care. Indeed, the decision to abandon the brood may give the female an opportunity to allocate more time and resources to self-maintenance activities, especially when nesting occurs late in the breeding season (see [41]). In Anatinae species, several factors (brood success, brood size) may trigger brood desertion before the typical ending of parental care (see [15] for review). Alternatively, our results imply that offspring desertion could have an adverse effect on brood survival if it occurs within a month after hatching.

It has been argued that ducklings travelling longer distances overland may have a lower survival, but results are contradictory [21]. In the present study, survival was lower in D groups compared to ND groups during the first 15-30 day period. Even if the distance travelled is more important during the first period for D and ND ducklings, it was not different between those treatment groups. This higher locomotor activity for 15-30 days ducklings could be associated to the need to forage intensively during the period of high growth rate [27,37,42]. But overall, we show that survival was not affected by the distance travelled. Contrary to what could usually be expected, these results do not support the idea that distance travelled negatively affects the survival of ducklings aged two weeks or more. Therefore, it is possible that at this age, energetic costs or predation risks associated with longer movements were relatively benign. Higher mortality in D ducklings during the 15-30 day-old period could therefore result from greater vulnerability to predators, regardless of distances moved. This highlights the important protection role played by the hen for younger ducklings, and is in accordance with the alert, unifying and leadership behaviours displayed by hens with ducklings during the first month post-hatching [4].

Duckling survival is positively related to the body mass of newly-hatched ducklings and to growth rate shortly after hatching [11,42]. Since our results for older ducklings (>2 weeks) in ND and D groups did not show any relation between survival and body mass at capture, the findings of [11,42] may be mostly applicable for the first two weeks after hatching. We do not believe that the consistently high survival we observed after one month of age can be due to ducklings having encountered exceptionally favourable habitat conditions: the mean daily body mass increase (growth rate) of 10-40 days old non-deserted ducklings obtained from the same population, during the same years of this study (Boos, unpublished data), was lower than growth rates reported in other mallard populations [27,43].

Interestingly, despite its importance in duck population growth rates, duckling survival is one of the most poorly quantified components of the annual cycle (see [10]). If hens prematurely abandon the brood one month after hatching (i.e. about 10-15 days before parental care typically ends) because of abnormal physiology, stress, disturbance or predation, this would apparently have no significant impact on the

reproductive output as ducklings have become able to survive on their own. It has been described that brood desertion among goldeneye (*Bucephala clangula*) had no significant effect on the survival rate of ducklings at a given age [33]. Nevertheless, this analysis relied on two age classes (up to about 23 days and 24-45 days old respectively) and was restricted to deserted ducklings staying with broodmates for which social relations and a larger brood size are assumed to enhance survivorship (see [11,41]). Furthermore, Aythini offspring are considered to be independent earlier than dabbling ducklings due to their more efficient diving capabilities [9]. However, exactly how far a sudden loss of maternal care before the typical ending of the hen brood-bond may affect survival of the young -and therefore recruitment- still remained to be established; especially in mallards, the most numerous and widespread dabbling duck species in the northern hemisphere. Our data provides substantial new evidence that the care hens give to their offspring before week four post-hatching plays an important demographic role, namely by enhancing recruitment.

Conclusion

This experimental study of free-ranging mallard ducklings demonstrates that the intrinsic ability of offspring to survive on their own may be attained before the known timed disruption of the hen-brood bond. This is consistent with the view that a life history trade-off may underlie the reduction in maternal care and typical timing of complete brood abandonment. Overall, these findings also help to understand when the hen's anti-predator or other protective roles are needed most. However, because brood survival is positively related to habitat quality [8,10,14,44] it may be possible that the differences observed in survival rates between deserted and non-deserted ducklings during the 15-30 day post-hatching period may be less pronounced in more suitable environmental conditions (see [45]). Further investigations are needed to evaluate this assumption.

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