

Testing the relationship between clutch size and brood size in the Coot (*Fulica atra*)

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Abstract The time between egg laying and chick fledging is of crucial importance for the survival of young birds. I analyzed breeding output at consecutive phases of growth of young Coots (*Fulica atra*) relative to the clutch size and laying date. Considering the specific breeding biology of the Coot, I tested whether chick survival reveals clutch size-dependent variability. Clutch size did not affect hatching success; it only affected brood size, and that merely temporarily. During the first 20 days after hatching, i.e. during the time of the highest chick mortality, birds with larger clutches lost chicks at a higher rate. As a result, the number of fledged chicks was independent of the initial number of chicks, and pairs with different clutch sizes had a similar number of fledglings. The laying date had no effect. This pattern of age-related chick survival points to the greater role of the type of chick growth (semi-precocial) and behavior in their survival.

Keywords Clutch size · Brood size · Fledging production · Coot · Semi-precocial birds

Introduction

The relationship between clutch size and reproductive success has been widely discussed in the literature. Many hypotheses have been proposed to explain it (Winkler and

Walters 1983; Skutch 1985). For example, in the optimal clutch size (OCH) hypothesis (Charnov and Krebs 1974; Monaghan and Nager 1997), a clutch size exists which maximizes fitness. It was shown, however, that because of gene flow between populations living in different habitats, clutch size can be non-adaptive (Dhondt et al. 1990). Other research has shown that clutch size and reproductive success are unrelated (Rohwer 1985; Lessells 1986; Milonoff et al. 1995; Paasivaara and Pöysä 2007) or that either large or small clutches are advantageous (Verhulst 1995; Lepage et al. 1998; Tinbergen and Sanz 2004; Lengyel 2007). These findings suggest that OCH has no universal application and that it concerns especially precocial birds (Milonoff and Paananen 1993). The individual optimization hypothesis (IOH; Högstedt 1980; Pettifor et al. 1988, 2001) specified and expanded OCH, suggesting that birds individually regulate clutch size. Nevertheless, research to date has not supported IOH unambiguously (Boyce and Perrins 1987; Barber and Evans 1995; Tinbergen and Both 1999).

Shortcomings of the hypotheses mentioned above stem mainly from the fact that they oversimplify and overgeneralize real situations and, as a result, they pass over the complexity of breeding biologies. This problem can be marginalized, however, if we analyze patterns of age-related chick survival in different groups of birds. For example, in altricial birds, chicks are most vulnerable sometime around fledging (Onnebrink and Curio 1991), whereas in precocial birds, chicks are most vulnerable soon after hatching (Colwell et al. 2007). In semi-precocial species in turn, there is no intermediate pattern but one that is similar to that of precocial birds. The difference lies in the fact that the time of chick dependence on parents is much longer in semi-precocial than in precocial birds. Thus, the time of increased chick vulnerability also

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lengthens. Ruthrauff and McCaffery (2005) suggested that spatial clumping of chicks, resulting from insufficient thermoregulation and the inability to self-feed, is one of the main factors increasing brood depredation in precocial birds. Predation, in turn, is the main mortality factor in this group of birds (Colwell et al. 2007). Consequently, we should expect a similar, if not stronger, influence of predation on chick survival in semi-precocial birds and, as a result, a weaker relationship between clutch size and reproductive success.

The European Coot (*Fulica atra*) is a common rail species that inhabits chiefly shallow waters with dense clumps of vegetation. It is a typical semi-precocial species in which the parents feed the chicks for about 30 days. Adults build nest-like platforms for chick brooding and roosting. In Poland, Coots start laying eggs mainly in the second half of April and at the beginning of May. A female lays 7 eggs (3–11) on average, and the female and male incubate them for about 21 days. The chicks fledge and become independent about 60 days after hatching (Cramp 1998). In this paper, I describe effects of clutch size and laying date on age-related survival of Coot chicks from hatching to fledging. I further discuss the possible implications of the breeding biology of the Coot as a typical semi-precocial species.

Methods

Study site

The data on *F. atra* come from a study carried out between April and August of 2002 and 2003 on Słoneczny Górny pond, located in the Milicz fish-ponds reserve. It is one of the largest nature reserves in Poland (51°33'N, 17°21'E) and is a very important breeding area for water birds in Central Europe, protected by the RAMSAR convention. The reserve consists of several clusters of ponds. The Stawno cluster consists of 30 ponds with the area of >1–270 ha. Pond Słoneczny Górny (170 ha) has 13–15 reed islands from which only 5 have solid ground and trees. Along the southwest shore, reeds grow in a strip of up to 200 m wide. Along other shores, they grow irregularly in strips of up to 20 m.

Productivity information

The nests were searched for starting in early spring, i.e. as soon as the Coots started to pair and form territories, and visited at least every second day during egg laying. The eggs were individually marked in all nests with a waterproof pen. In nests where laying had begun before the nests were found, the method of follicle age assessment, by

sinking the eggs in water, was used to assess their age and order of laying. Also, if it was possible, the nest surroundings and water were searched for rejected eggs. A clutch was considered complete if, during two consecutive visits, the number of marked eggs did not change and if, by the second inspection (no later than 2 days after the first one), the nest had not been abandoned. Coots do not remove eggshells but crush them in the nest, incubating other eggs and warming chicks. Therefore, the presence of many small shell fragments crushed inside the nest was sufficient evidence that at least one chick had hatched. The lack of shells or big, uncrushed pieces of shells with the rest of the yolk and/or blood in the nest were evidence of a loss.

In later phases, the chicks were observed and counted until about the 60th day after hatching, equal to the average time of fledging. Counts of chicks per family were assigned to the appropriate 10-day period. In each 10-day period, families were counted at least three times to avoid any oversight, and the number of chicks in the last count was used as the final number for a given 10-day period. The counts of chicks were used in nest history analysis as long as they were credible. Unreliable measurements (data excluded from analysis) concerned situations in which the number of chicks had increased or when measurements were not continuous (at least 10 days without data). In addition, broods were excluded from the analysis if two nests were close to each other and the young were grouped and ungrouped in different combinations. As a result, the number of analyzed nests decreased in consecutive 10-day periods, despite the fact that the excluded pairs were still observed and certainly did not fail, and thus the success of these broods could not have been included as zero.

Breeding Coots are highly territorial birds, aggressively defending their clearly defined territories. There is no exchange of territories between pairs with chicks. Nevertheless, unless territories adjoin, birds can successively expand occupied areas. I did not note any pair with chicks which had moved and settled in a new area. Therefore, each pair could be reliably assigned to a specific area, without the need for capturing and marking. Chicks inhabiting a given territory were counted mostly via direct observation or, in case of insufficient visibility, they were counted directly from the nests. The simplest method is to catch one chick, put it in a nest and cover it with a piece of fabric. Then, after a while, it starts calling silently, attracting the others to swim close to the nest. If it was possible, I determined the cause of chick mortality. I found only 32 dead chicks in or close to the nests; 20 after storms, 10 that died after their parents' death and 2 killed (bitten or pecked to death) and left in the nest. Conversely, I found no symptoms of chick starvation. Marsh Harriers (*Circus aeruginosus*) were regularly seen hunting young Coots, and hundreds of remains were found in inspected nests in the

same area (3 pairs breeding in the same pond). At the same time, more than ten pairs of Marsh Harriers were breeding in nearby ponds and these birds could certainly have been hunting in the studied area.

Statistical analyses

Due to data loss during the season, the variation of chick number with clutch size and laying date was analyzed using linear mixed models (LMM), which can properly handle missing data. The brood-specific numbers of chicks in each 10-day period (1–6) were used as a repeated measure factor, whereas clutch size and laying date were used as covariates. Both the repeated measure factor and covariates were used as fixed estimates. Because of the lowest information criteria, the first-order ante-dependence covariance structure was used as a repeated covariance type (Table 1). For model selection and interpretation, except for Akaike’s Information Criterion (AIC), I used Akaike’s Information Criterion corrected for small sample size (AIC_c), AIC_c differences (Δ_i), Akaike weights (w_i), and maximum likelihood of models (Burnham and Anderson 2002). For all computations, SPSS 16.0 software was used (SPSS 2007).

Results

In total, I found 123 breeding pairs, of which 90 had at least one chick. Including only complete clutches, their sizes in successful and failed nests did not differ significantly (*t* test: *t* = 0.34, *df* = 115, *P* = 0.732). In the following 10-day periods after hatching, I used 38, 28, 22, 18, 18, and 16 nests, respectively. The difference between the clutch sizes of the nests included and excluded was insignificant (*t* test: *t* = 1.23, *df* = 74, *P* = 0.224). The probabilities of chicks still being alive at the end of each 10-day interval (1–6) with respect to brood size at hatching were 0.86,

0.76, 0.55, 0.44, 0.42, and 0.42, respectively. In comparison, the same value for eggs until hatching (compared with clutch size) was 0.97.

The seasonal variation in the number of young in six consecutive 10-day periods with clutch size and laying date was analyzed using LMM. The model with clutch size and laying date as covariates gave higher information criteria than the model with only clutch size (Table 1). This shows that the laying date had no effect on the number of chicks lost before fledging. Conversely, chick age and especially interaction of initial clutch size and chick age were significantly related to the number of chicks per brood (Table 2). This means that brood sizes declined with chick age at different rates depending on clutch size, and that birds with larger clutch sizes lose chicks at a higher rate (Fig. 1). As a result, at fledging all broods had a similar number of young (\bar{x} = 2.75, SD = 0.78), irrespective of their initial number and clutch size.

The estimates of parameters used in the model (Table 3) show that broods declined with time, but only with respect to clutch size. The disproportional decrease in brood size occurred only during the first 20 days after hatching, while in later phases (21–50 days), the broods were not larger than during the sixth 10-day period (Table 3). Taking this into consideration, in the first 10-day period, the broods were larger on average by 2.98 chicks than in the sixth 10-day period, while brood size variability decreased almost twofold (Table 3) (hatching time: SD = 1.48; 6th 10-day period: SD = 0.78; Levene’s test: *F*_{1,90} = 6.32, *P* = 0.014); mostly at the cost of larger broods (Fig. 1).

Because egg losses in Coots were rare during incubation, and hatching success almost always meant complete success (\bar{x} = 97.7% of eggs in successful nests, SD = 8%), while failure meant nest loss, the data on hatching success were not used in the above models. It is important to show, however, that clutch size had no notable effect on hatching success (logistic regression: Wald χ^2 = 1.38, *P* = 0.241).

Table 1 The comparison of linear mixed models (5 strongest models) differing in repeated covariance type and covariates used in analyzing Coot (*Fulica atra*) data

	Max. log (L)	<i>K</i> ^a	AIC	AIC _c	Δ _i	w _i	Covariance type	Model covariates
1	205.70	35	275.70	299.93	10.311	0.006	First-order ante-dependence	Clutch size, laying date ^b
2	211.74	30	271.74	288.80	6.351	0.040	First-order ante-dependence	Clutch size, laying date ^c
3	219.39	23	265.39	274.91	0	0.954	First-order ante-dependence	Clutch size
4	213.39	33	279.87	301.04	14.480	0.001	Unstructured	Clutch size
5	272.26	14	300.26	303.62	34.868	<0.001	First-order auto-regressive	Clutch size

The strongest model is in bold. See “Methods” for details

^a The number of parameters

^b Full factorial model

^c Second degree factorial model

Table 2 LMM analysis of the number of chicks with reference to age (10-day periods after hatching) and initial clutch size

	$df_{(\text{numerator})}$	$df_{(\text{denominator})}$	F	P
Intercept	1	24.348	41.903	<0.001
Age	5	34.812	3.907	0.006
Clutch	1	24.186	0.381	0.543
Age \times clutch	5	33.323	10.280	<0.001

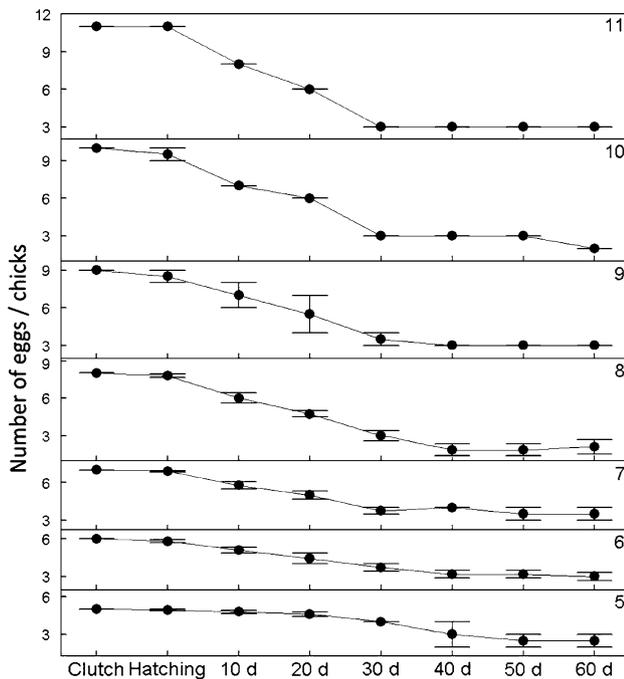


Fig. 1 The numbers of Coot (*Fulica atra*) chicks per nest during consecutive 10-day periods (d days) in groups of nests with a given initial clutch size (annotation on the right). The sizes of groups (with clutch sizes 5–11) during the first 10-day period after hatching were in order: 10, 10, 9, 4, 2, 2, 1. Nests with 3- and 4-egg clutches are not presented because of the lack of reliable data after hatching. Dots Mean, whiskers \pm SE of the mean

Discussion

A marked decline in the number of chicks during the early brood care period is a common phenomenon among precocial and semi-precocial birds (Paasivaara and Pöysä 2007), whereas predation is considered the most frequent cause (Colwell et al. 2007). Since, however, it is difficult to precisely track the fates of each chick, alternative explanations of high chick mortality, such as, for example, laying date, the parents, young and territory quality, cannot be disregarded. Brinkhof et al. (1993) showed that fledging success in the Coot is causally related to timing of breeding. In later research, Brinkhof and Cavé (1997) demonstrated that the seasonal decrease of survival of Coot chicks was limited by food supply during the early brood care

period. I found that laying date did not significantly affect chick survival and nor were there any signs of chick starvation during the brood care period. However, the comparison of both results is difficult because of large differences between habitats and predation intensities. In this study, the survival of Coot chicks negatively depended on clutch size. To date, most research has provided evidence for an opposing relationship where, for example, pre-fledging chick survival increased in enlarged broods and decreased in reduced broods (Lepage et al. 1998; Loonen et al. 1999, Tinbergen and Sanz 2004; Lengyel 2007), or there has been no evidence of brood size-dependent survival (Rohwer 1985; Lessells 1986; Paasivaara and Pöysä 2007). A negative relationship between chick survival and clutch size has only been observed in Semipalmated Sandpipers (*Calidris pusilla*) (Safriel 1975), a precocial bird with specific uniparental care, and Mallards (*Anas platyrhynchos*) (Dzus and Clark 1997). Unlike these species, however, Coot chicks are semi-precocial birds, definitely more dependent on their parents during the first few weeks after hatching.

Because chick mortality in Coots was positively related to the number of chicks per nest, and predation on young Coots was high, I imply that predation was essentially responsible for creating such an atypical relationship. Perhaps it resulted from the additional costs of feeding more chicks and spending less time on the observation of threats, e.g., Coot parents with more chicks will spend more time looking for food with their heads under water, during which they cannot watch out for approaching predators. This can be confirmed by the fact that brood size decline, relative to clutch size, was nonlinear over the period of chick growth and their becoming independent (Fig. 1). If we compare variability within this relationship over time with the course of chick development, we will notice some similarities. During the first 20 days, the chicks are definitely dependent on their parents because of insufficient thermoregulation and the inability to feed themselves. That is why they spend most of the time together, in the nest or near their parents. Starting with the third 10-day period, the chicks begin to self-feed and disperse. Such a process of gradual chick separation from parental care continues until fledging. Hence, if predation was the main cause of higher chick mortality in larger broods, such a relationship would exist provided that the chicks stay together, i.e. no longer than until the third 10-day period after hatching. This, in turn, is reflected by the results (Table 3) and by other research (Arnold 1999; Ruthrauff and McCaffery 2005).

The time of offspring dispersal is critical in terms of predation-caused mortality in birds (Sandercock 1994; Colwell et al. 2007). In Coots, it is of no small importance since the highest chick mortality takes place before

Table 3 Relationship between brood size (dependent variable) and clutch size in six consecutive 10-day periods (age 1–6) after hatching shown as parameter estimates

Parameter	Estimate	SE	df	t	P	95% CI	
						–	+
Intercept	3.470	0.889	18.270	3.904	0.001	1.604	5.336
Age 1	–1.225	0.993	29.014	–1.234	0.227	–3.256	0.805
Age 2	–0.161	1.042	34.912	–0.154	0.878	–2.277	1.955
Age 3	1.407	0.831	20.908	1.693	0.105	–0.321	3.134
Age 4	0.130	0.401	32.510	0.324	0.748	–0.687	0.946
Age 5	–0.345	0.242	15.953	–1.427	0.173	–0.858	0.168
Age 6	0 ^a	0					
Clutch	–0.107	0.120	18.017	–0.895	0.383	–0.358	0.144
Age 1 × clutch	0.602	0.136	30.548	4.430	0.000	0.325	0.879
Age 2 × clutch	0.329	0.143	36.687	2.297	0.027	0.039	0.620
Age 3 × clutch	–0.080	0.111	20.906	–0.719	0.480	–0.312	0.152
Age 4 × clutch	0.005	0.054	32.279	0.093	0.927	–0.104	0.114
Age 5 × clutch	0.056	0.032	15.945	1.725	0.104	–0.013	0.124
Age 6 × clutch	0 ^a	0					

^a This parameter is set to zero because it is redundant

dispersal. During this time, adults build large nests that are used by chicks. These nests are usually scarcely penetrable from their dense surroundings and provide a shelter from waves, but they are well visible from the air. Therefore, Coot chicks are potentially easy prey for Marsh Harriers, and larger broods may even increase predation risk.

Since the numbers of fledged chicks of pairs with different clutch sizes were similar, what was the function of hatchling overproduction? In many species, females lay more eggs than they can normally raise; this has been suggested as serving as a control mechanism for resource availability (Stienen and Brenninkmeijer 2006). In species with asynchronous hatching, however, it might well work as an anti-predatory mechanism. With reference to Coots, this is supported by the fact that they can actively control the survival of their young through brood reduction (Horsfall 1984). As a result, small differences in fledging production among pairs with high clutch size variability could be compensated by better chick quality of pairs with larger clutches. Conversely, small clutch size was shown to be an adaptive response to high predation risk in altricial birds (e.g., Kleindorfer 2007). Skutch (1985) suggested an indirect mechanism in which predation limits the food delivery rate to the nest. My results suggest a direct role of the young in predator attraction, as previously discovered by Safriel (1975). Nevertheless, if Skutch’s hypothesis applies more generally, and adult Coots activity attract predators, we would expect a similar effect of the young. As a result, it might be concluded that if the costs of offspring production in Coots are high then laying small

clutches would be the best option because it would minimize losses. Nevertheless, it is hard to compare the benefits if the real costs are hard to define or are actually unknown (Monaghan and Nager 1997).

This research shows an example of a negative relationship between brood size and chick survival that, at the same time, is the first example of such a phenomenon observed in semi-precocial species. It may point to the fact that there is a cost of having larger clutches, which is strictly related to the species’ breeding biology.

Zusammenfassung

Besteht ein Zusammenhang zwischen Gelegegröße und Anzahl an Jungen bei der Bläßralle (*Fulica atra*)?

Für das Überleben von Jungvögeln ist der Zeitraum zwischen Gelegezeitigung und Ausfliegen von außerordentlicher Bedeutung. Ich habe den Bruterfolg in aufeinander folgenden Zeitabschnitten in der Entwicklung junger Bläßralen relativ zu Gelegegröße und Legedatum untersucht. Unter Berücksichtigung der spezifischen Brutbiologie der Bläßralle habe ich getestet ob die Überlebensrate der Küken auch von der Gelegegröße abhängt. Die Gelegegröße hatte keinen Einfluss auf den Schlupferfolg; sie wirkte sich nur auf die Anzahl an Jungen aus, und das nur zeitweise. Während der ersten 20 Tage nach dem Schlupf, d. h. während der Phase höchster Kükenmortalität, hatten Vögel mit größerem Gelege eine höhere Verlustrate an Küken. Daraus resultierend war die Anzahl flügge

werdender Jungvögel unabhängig von der anfänglichen Anzahl an Küken, und Paare mit unterschiedlicher Gelegegröße hatten die gleiche Anzahl an flüggen Jungen. Das Legedatum hatte keinen Einfluss. Dieses Muster altersabhängiger Überlebensraten bei den Küken zeigt die Bedeutung des Entwicklungstyps (halb nestflüchtend) und des Verhaltens für deren Überleben.

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