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NESTING AND REPRODUCTIVE CHARACTERISTICS OF COOTS *FULICA ATRA* BREEDING ON TWO LAKES IN ALGERIA

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SUMMARY.—*Nesting and reproductive characteristics of Coots* Fulica atra *breeding on two lakes in Algeria.* Variation in dimension of nests (external diameter, cup diameter and height), water depth at nesting sites, clutch sizes, egg sizes and hatching success was studied in Coots *Fulica atra* nesting on two lakes in Algeria in 1996-1997. The main idea of this paper is to provide basic data on the breeding ecology of Coots in the southern part of the species geographic area and to compare breeding characteristics between Lakes Oubeira and Tonga. Water depth at the place of nesting and nest dimensions differed significantly between the lakes, while clutch sizes, hatchling numbers and egg dimensions were not different. Relatively many complete clutches (11%) contained only one egg. The dates of laying onset were significantly different between years 1996 and 1997 on Lake Oubeira but not between Lake Oubeira and Lake Tonga in 1997. A generalised linear model showed that hatching success (the number of eggs hatched per clutch) was dependent on both years and lakes (as factors), laying date, egg volume and water depth at nesting sites but independent of clutch size. Egg dimensions showed significant but not very high repeatabilities (0.35-0.47).

Key words: Algeria, clutch size, Coot, egg size, *Fulica atra,* hatching success.

RESUMEN.—*Nidificación y reproducción de la Focha Común* Fulica atra *en dos lagos de Argelia.* En este trabajo se estudian las variaciones en las dimensiones del nido (diámetro externo e interno y altura sobre el nivel del agua), profundidad del agua en el lugar de construcción del nido, tamaño de puesta, tamaño de los huevos y éxito de eclosión de las Fochas Comunes reproductoras en dos lagos de Argelia durante 1996 y 1997. El objetivo del presente estudio es aportar información básica sobre la ecología reproductiva de la Focha Común en el sur del área de distribución de la especie y comparar las características reproductoras entre las poblaciones de los lagos Oubeira y Tonga. La profundidad del agua en el lugar de ubicación del nido y las dimensiones del mismo difirieron significativamente entre lagos, mientras que no se encontraron diferencias en el tamaño de la puesta, en las dimensiones de los huevos ni en el número de eclosiones. Una parte importante (11%) de las puestas completas estuvo compuesta por un solo huevo. Las fechas de comienzo de la puesta variaron significativamente entre los años 1996 y 1997 en el lago Oubeira pero no variaron entre el lago Oubeira y el lago Tonga en 1997. Mediante modelos generales lineales se determinó que el éxito de eclosión (número de huevos eclosionados por puesta) dependió en ambos años y lagos (factores) de la fecha de puesta, el volumen del huevo y la profundidad del lugar de ubicación del nido, mientras que fue independiente del tamaño de la puesta. Las dimensiones de los huevos mostraron una repetibilidad significativa aunque no muy alta (0,35-0,47).

Palabras clave: Argelia, dimensiones de los huevos, éxito de eclosión, Focha común, *Fulica atra*, tamaño de puesta.

INTRODUCTION

Life-history traits often show a geographic pattern of variation resulting from the influence of local-scale proximate and ultimate factors (e.g. Lack, 1947; Klomp, 1970; Winkler & Walters, 1983). One of the best known aspects of such a geographic pattern is a latitudinally increasing trend in avian clutch size that is most completely explained by Ashmole's (1963) hypothesis (Ricklefs, 1980). In view of this hypothesis, lower latitudes are characterised by less amount of food available per individual in comparison with higher latitudes because the

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former are less seasonal with respect to resource production (Ricklefs, 1980; Winkler & Walters, 1983). If the clutch-size trend is indeed related to food, similar effects on other life-history traits would be expected (Winkler & Walters, 1983).

Coots are socially monogamous relatively, long-lived birds with the oldest ringed individuals being 18 years old; they normally mature in their second calendar year (Cramp, 1980). Coots are highly territorial and aggressive during the breeding season. Incubation lasts 21-24 days, the nestlings are semi-precocial so that parental care (feeding and brooding) is necessary for several weeks (Cramp, 1980).

The Coot breeds on many suitable water bodies in the North African part of the Mediterranean area but nowhere is it very numerous (Etchecopar & Hue, 1964; Snow & Perrins, 1998). As a consequence, there are hardly any data available from this area (Sánchez-Moreno, 1974) to compare with ours and as far as we know this paper is the first description of some wider aspects of the breeding ecology of Algerian Coots.

The main aims of this paper were: (1) to document variation in some basic characteristics of the nesting and reproduction of Coots breeding close to the southern border of its distribution area in the Palearctic; (2) to test the data for potential differences between two lake habitats; (3) to examine within- and between-clutch sources of variation in egg length, breadth, volume and shape; and (4) to determine whether hatching success is related to some aspects of nesting and life-history traits.

Material and methods

The study was carried out on two lakes located in northern Algeria: south of El-Kala, Lake Oubeira (36° 51′ N, 08° 23′ E) in 1996 and 1997 and Lake Tonga (36° 51′ N, 08° 20′ E) in 1997. The lakes are similar in size, about 2200 ha each, and are the most important freshwater bodies of north-eastern Algeria. The littoral vegetation of Lake Oubeira is dominated by the floating sweet-grass *Glyceria fluitans*, bur-reed *Sparganium minimum*, water mint *Mentha aquatica*, common club-rush *Scirpus lacustris* and water chestnut *Trapa natans*. The submerged vegetation is mostly composed of pondweeds *Potamogeton pectinatus* and *P. lucens*. The littoral vegetation belt of Lake Tonga is dominated by common reed *Phragmites australis* and lesser bulrush *Typha angustifolia* with some admixture of common club-rush *Scirpus lacustris*, bur-reed *Sparganium minimum* and *S. erectum* and yellow iris *Iris pseudacorus*. The submerged vegetation of this lake is dominated by pondweeds *P. trichoides*, *P. pectinatus*, *P. coloratus* and white water-lily *Nymphea alba*.

During the breeding season, we searched among emergent vegetation for active nests of Coots. The nests in which egg laying had started were visited every day to record complete clutches and then once a week up to the expected time of hatching (21 days for incubation), when they were again visited every day to record their hatching success by counting the number of chicks hatched. The length (L) and breadth (B) of eggs in all complete clutches were measured by the same person with callipers to the nearest 0.1 mm. Egg volume (V in cm^3) was estimated following Hoyt's (1979) formula: $V = 0.000507*L*B^2$. Egg shape index expressed egg breadth as a per cent of egg length following the formula: $ES = B/L*100$. The following nest and nest site characteristics were also measured (in cm): nest internal and external diameter, nest height and the water depth at the place where the nest was constructed.

Log-transformed nest dimensions were compared between lakes as a collective multivariate variable applying MANCOVA with the depth of water at places of nesting as the covariate. Following Scheiner (1993), MANCOVA was also used to compare between lakes the bivariate variable composed of clutch size and per-clutch mean egg volume with laying date as the covariate. The multivariate analyses of covariance were followed by univariate ANOVAs when necessary.

To test if different factors and variables influence the number of nestlings hatched out of complete clutches of eggs (clutches of at least two eggs were included) we applied the Generalised Linear Modelling approach (Crawley, 1993). This approach provides a correct control over the distribution of error of the response variable (binomial error structure and logit link function was assumed). Accordingly, a generalised linear model was constructed with years and lakes as factors and laying date, clutch size, per-clutch mean egg volume and water depth at nesting sites as covariates. Following Crawley (1993), a maximal model including all the above factors and covariates and the interactions between lakes and the covariates were first fitted using GLIM (NAG, 1985). Then the procedure of backward removal of non-significant terms was applied to produce the final (minimum adequate) model. Overdispersion was corrected by the chi-squared-based scaling of the model, so that changes in deviance resulting from removing a term from the model were interpreted as F statistics (Crawley, 1993).

Egg length, breadth, volume and shape were compared between the lakes using t tests based on per-clutch mean values of the traits rather than traits of individual eggs as observation units. Measurements of individual eggs in clutches with at least two eggs were used in one-way ANOVAs conducted in order to assess intra- and interfemale components of variance in egg traits, which enabled us to calculate repeatabilities (see Lessels & Boag, 1987; Bańbura & Zieliński, 1990, 1998a, 1998b). Repeatabilities were calculated from the components of variance as intraclass correlation coefficients (Sokal & Rohlf, 1981) and their standard errors estimated following Becker (1984).

RESULTS

Descriptive characteristics of nest sizes and reproduction of Coots breeding on Lakes Oubeira and Tonga are presented in Table 1, which characterises also the depth of water at nesting sites. Water at nesting sites was on average deeper in 1996 than in 1997 in Lake Oubeira and both these values were lower than water depth in Lake Tonga in 1997 (Table 1; $F_{2,53}$ = 51.5, P < 0.0001, Sheffe test). An introductory analysis showed that nest dimensions differed between the lakes, but not between years in Lake Oubeira. As different nest dimensions were evidently interdependent, we treated them as components of a multivariate variable. This interdependence is shown by coefficients of correlation between nest height and internal (r_{54} = –0.35; P < 0.01) and external (r_{54} = –0.43; P < 0.001) diameters and between internal and external diameters (r_{54} = 0.70; P < 0.0001). The nest dimensions were also correlated with water depth at nestling sites (r_{54} = 0.45 for internal diameter, r_{54} = 0.58 for external diameter and r_{54} = –0.44 for nest height; P < 0.001 in all cases). Multivariate analysis of covariance with

TABLE 1

Nest and reproductive characteristics of Coots breeding on Lakes Oubeira and Tonga.
[Características reproductivas y de los nidos de la Focha Común en los lagos Oubeira y Tonga (Argelia).]

Variable	*Lake Oubeira*				*Lake Tonga*	
	*1996 (*n *= 17)*		*1997 (*n *= 12)*		*1997 (*n *= 27)*	
	Mean ± SD	*(Min-Max)*	*Mean ± SD*	*(Min-Max)*	*Mean ± SD*	*(Min-Max)*
Water depth (cm) *[Profundidad del agua]*	106.8 ± 41.9	(40-160)	63.3 ± 10.7	(50-80)	154.1 ± 17.6	(113-180)
Nest height (cm) *[Altura del nido sobre el nivel del agua]*	18.4 ± 4.9	(14-35)	19.2 ± 4.0	(14-28)	16.2 ± 2.7	(10-20)
Ext. diameter (cm) *[Diámetro externo]*	29.9 ± 2.6	(25-35)	29.4 ± 1.8	(26-32)	35.9 ± 3.8	(30-49)
Int. diameter (cm) *[Diámetro interno]*	16.6 ± 1.8	(13-20)	16.8 ± 1.6	(14-20)	19.6 ± 2.7	(14-26)
Clutch size *[Tamaño de puesta]*	4.06 ± 1.71	(1-7)	5.08 ± 2.19	(2-11)	4.15 ± 2.30	(1-8)
Hatchling number *[Núm. de huevos eclosionados]*	3.52 ± 2.32	(0-7)	4.67 ± 2.61	(0-11)	2.67 ± 2.69	(0-8)

log-transformed internal and external nest diameters and nest height as the components of a multivariate response variable and depth of water below the nest as the covariate showed that Coots nesting in either lake studied differed with respect to the nest characteristics (Pillai's Trace = 0.3028; *d.f.* = 3,51; $P = 0.0003$). Both internal and external diameters of nests differed between the lakes ($F_{1,53} = 7.26$; $P = 0.009$ for the former and $F_{1,53} = 21.57$; $P = 0.00002$ for the latter). Nest height turned out not to differ between the lakes when the effect of the covariate was controlled for ($F_{1,53} = 0.09$; $P = 0.768$).

In 1996 laying started exceptionally late in Lake Oubeira (mean laying date was 24 May, median 19 May), significantly later than in the same lake in 1997 (mean and median 26 April) and in Lake Tonga in 1997 (mean 3 May, median 6 May) (Kruskal-Wallis ANOVA: $H_2 = 27.15$; $n = 56$; $P < 0.0001$). Because laying date may influence other aspects of reproduction, it was included and its effect was controlled for in the further analysis. As clutch size and egg sizes are often expected to trade off, a multivariate analysis of covariance with clutch size and per-clutch mean egg volume as the components of a multivariate response variable and laying date as the covariate was carried out. It showed no differentiation of Coots inhabiting the studied lakes (Pillai's Trace = 0.0298; *d.f.* = 2,52; $P = 0.456$).

Mean hatchling numbers recorded on Lakes Oubeira and Tonga were not significantly different ($t_{54} = 1.93$; $P = 0.0581$). An influence of different characteristics of nesting and breeding on hatching success is usually expected. Consequently, a generalised linear model for hatching success (the number of chicks hatched out of a clutch of at least two eggs laid) was constructed with the lakes and years as factors and laying date, clutch size, per-clutch mean egg volume and mean water depth at nesting sites as covariates. Interactions of the lake factor with all the covariates were also included, producing maximum model (Table 2). Only the interaction between clutch size and

TABLE 2

Analysis of deviance for generalised linear models explaining the proportion of hatched eggs in Coot clutches composed of at least two eggs in terms of study sites (Lakes Oubeira and Tonga) and years (1996 and 1997) as factors and laying date, clutch size, mean egg volume per clutch and water depth below the nest as covariates. Interactions between the lake factor and the covariates are included.
[Análisis del ajuste de modelos generales lineales para la proporción de huevos eclosionados en puestas de Focha Común compuestas por al menos dos huevos en función del lugar de estudio (lagos Oubeira y Tonga) y del año (1996 y 1997) como factores y de la fecha y tamaño de puesta, el volumen medio de los huevos de cada una y la profundidad del agua bajo el nido como covariantes. Se incluyen además las interacciones entre el factor lago y todas las covariantes.]

Model/Terms	*Deviance*	*df*	*P*
Null model	100.47	49	
Maximum model	53.91	10	0.000000
Final model	51.98	8	0.000000
Residual	48.49	41	
	Change in deviance		
Lake *[Lago]*	14.53	1	0.000445
Year *[Año]*	22.11	1	0.000028
Laying date *[Fecha de puesta]*	0.56	1	0.458532
Clutch size *[Tamaño de puesta]*	1.89	1	0.176669
Egg volume *[Volumen del huevo]*	2.91	1	0.095246
Water depth *[Prof. del agua]*	0.79	1	0.379045
Laying date*Lake *[fecha de puesta*lago]*	15.43	1	0.000330
Clutch size*Lake *[Núm. huevos*lago]*	0.04	1	0.842494
Egg volume*Lake *[Vol. huevo*lago]*	6.34	1	0.015704
Water depth*Lake *[Prof. del agua*lago]*	18.96	1	0.000084

the lake factor and the clutch size variable were removed from the model because they turned out to be the only non-significant terms (Table 2), suggesting that hatching success was independent of clutch size. As a result, a final model was produced that accounted for more than 50% of the total deviance of hatching success.

The lake and year factors, water depth, laying date, and egg size all influenced hatching success either directly or indirectly through its interaction with the lake factor. The interaction between the lake factor and other factors, water depth for example, is complex and may be expected to be still more complex as a result of an influence of the year factor. The year factor could not be used as an interacting factor in the analysis because one of the lakes was studied in only one year. Complexity of these relationships may be demonstrated by comparison of water depth at nesting sites for successful (at least in part) and unsuccessful clutches in all available lake-year combinations, which showed significant differentiation ($F_{5,44}$ = 23.03; P < 0.0001). As shown by the Sheffe test, water depth was not different between successful and unsuccessful clutches on Lake Tonga (means 151.0 cm and 160.2 cm, respectively) but these two values differed from successful Oubeira clutches in 1996 (115.0 cm) and from a homogenous group of unsuccessful Oubeira clutches in 1996 (66.7 cm), in 1997 (60.0 cm) and successful Oubeira clutches in 1997 (63.6 cm). Mean water depth differed between the last group and successful Oubeira clutches in 1996. Consequently, the lake factor is likely to be linked to some non-controlled variables that seem to have influenced hatching success.

Between-lake variation in egg length, breadth, volume and shape was also analysed on the basis of per-clutch mean values as observation units (Table 3). No egg trait differed between the lakes (t_{54} = 0.91 for length and t_{54} = 0.66 for breadth; t_{54} = 0.45 for shape; t-test with separate variance estimation: $t_{47.4}$ = 0.53; P > 0.05 in all cases). The major source of variation in egg traits in the studied Coot populations was differentiation among females. This resulted in relatively low variation within clutches and high variation among clutches, which is shown by significant repeatabilities (Table 4).

Discussion

Coot nest dimensions evidently differed between the investigated lakes. There seem to be two non-exclusive explanations for this fact. First, the size and shape of Coot nests were reported to change with water depth (Cramp, 1980), this report being also true of our study populations. Second, the structure, and conse-

TABLE 3

Egg characteristics of Coots breeding on Lakes Oubeira and Tonga (Algeria). Complete clutches are unit observations, so that the mean values given in this table are based on per-clutch averages of particular traits.
[Medidas de los huevos de las Fochas Comunes reproductoras en los lagos Oubeira y Tonga (Argelia). Las unidades muestrales son las puestas completas, por lo que los valores dados en esta tabla están basados en las medias por puesta de cada medida.]

Egg trait	*Lake Oubeira (*n *= 29)*	*Lake Tonga (*n *= 27)*	*Pooled (*n *= 56)*
	Mean ± SD (Min-Max)	*Mean ± SD (Min-Max)*	*Mean ± SD (Min-Max)*
Length (L) (mm) *[Longitud]*	52.2 ± 2.0 (48.4-58.2)	52.7 ± 1.9 (48.6-56.9)	52.4 ± 1.9 (48.4-58.2)
Breadth (B) (mm) *[Anchura]*	35.0 ± 0.7 (33.7-36.7)	35.1 ± 1.1 (33.2-36.9)	35.0 ± 0.9 (33.2-36.9)
Volume (0.000507*L*B^2) (cm^3) *[Volumen]*	31.9 ± 1.9 (28.5-39.0)	32.2 ± 2.7 (28.5-37.7)	32.0 ± 2.3 (28.5-39.0)
Shape index (B/L*100) *[Índice de forma]*	67.0 ± 2.5 (61.2-72.6)	66.7 ± 2.6 (61.5-72.3)	66.9 ± 2.6 (61.2-72.6)

TABLE 4

Repeatabilities of egg traits of Coots inhabiting the Lakes Oubeira and Tonga (pooled data).
[Repetibilidades de las medidas de los huevos de Focha Común en los lagos Oubeira y Tonga (Argelia).]

Egg trait	*Repeatability*	*SE*	$F_{48,185}$	P
Length *[Longitud]*	0.45	0.071	4.84	0.0000
Breadth *[Anchura]*	0.35	0.073	3.51	0.0000
Volume *[Volumen]*	0.47	0.070	5.16	0.0000
Shape *[Forma]*	0.35	0.073	3.52	0.0000

quently the size and shape of the nest depends also on the plant species used for building it. Nests are usually constructed from dead and live plants found opportunistically by adult birds near the nesting site. Thus the nests built on Lake Oubeira were mostly composed of stems and leaves of *Glyceria fluitans*, *Scirpus lacustris* and *Sparganium minimum*, whereas on Lake Tonga they are mostly constructed from reed *Phragmites australis*. As a more rigid construction material, reed makes Coots construct larger nests. A similar effect was observed in West Siberia by Koshelev (1984). In general, the dimensions of nests observed in Algeria were within the ranges reported in the literature. Cramp (1980) reported the following ranges of nest dimensions for Coots in the Western Palearctic: external diameter, 25-55 cm, cup diameter, 16-30 cm, and height, 8-28 cm. The analogous values for Koshelev's study population were 24-45 cm for external diameter and 16-30 cm for the diameter of the cup.

The start of egg laying in late April and May is typical of North African Coots (Etchecopar & Hue, 1964), but it is later than in most of the Western Palearctic (Snow & Perrins, 1998). Our data showed that the timing of breeding in Algerian conditions may differ from year to year as well as in space, most probably depending on some proximal environmental clues, especially on the highly variable rainfall.

In this study we observed several nests in which only single eggs were laid and incubated (with no signs of partial predation), forming one-egg complete clutches (c. 11% of all clutches). This is exceptional among different Coot populations reported in the literature, where it is suggested that the smallest complete clutches were composed of two eggs (see Koshelev, 1984 for review), although Cramp (1980) gave one egg as the lowest limit of Coots' clutch size. Actually, one-egg complete clutches are rare in bird species with multi-egg clutches; one-egg clutches were for example observed by Arcese *et al*. (1992) in the Song Sparrow *Melospiza melodia*. The largest clutches observed in this study (11 eggs) were smaller than those reported for other populations (even 15 eggs) (Cramp, 1980; Koshelev, 1984). Consequently, the mean clutch size in our study populations (4.32) was lower than the averages reported for the Palearctic (6.5-8.8) (Koshelev, 1984). The average clutch sizes of Coots in the Palearctic including North Africa display a geographic pattern characterised by decreasing clutch size with decreasing latitude, which supports Lack's (1947) generalisation derived from many earlier observations on different avian species.

A negative relation between egg size and clutch size is theoretically expected but rarely demonstrated in birds and other animals (Roff, 1992; Stearns, 1992). Scheiner (1993) showed that multivariate analysis of variance may be a good method to demonstrate a relation between size and number of propagules when a comparison of different habitats/locations is possible. However, we found no indication of such a relationship in our study, as the bivariate centroid composed of clutch size and egg volume did not vary between the lakes.

A comparison of mean egg lengths and breadths for different Coot populations suggests that there probably exists a pattern of geographic variation with Coots breeding in the northern part of the Palearctic laying slightly bigger eggs than those in the south (Alley & Boyd, 1947; Kornowski, 1957; Havlin, 1970; Blum, 1963; Koshelev, 1984). Accordingly, the eggs laid by Coots in our study sites are on average shorter and narrower than in the rest of the Palearctic. Typically for birds, also in Coots differences among females are a major source of variation in different egg dimensions (Lessells *et al*., 1989; Bańbura & Zieliński, 1990; Arnold, 1991; Jover *et al*., 1993; see also Oró *et al*., 1996). However, the values of repeatability reported in the present study, ranging from 0.35 to 0.47, are low as compared to other studies (cf. Bańbura & Zieliński, 1990). It can be inferred from Horsfall's (1984) experimental study on Coots that poor food supply would cause increasing within -clutch variation in egg sizes. As the Algerian lake habitats are not likely to be food-rich, this could in part explain the low repeatability of egg traits. Another possibility is that some clutches contain parasitic eggs dumped by foreign females. The above explanations are not mutually exclusive.

Hatching success in the Algerian Coots proved to be very high, as 188 of 242 eggs laid hatched (77.7%). Analogous values for different areas of the Western Palearctic reported by Cramp (1980) were much lower and ranged from 34% to 49%. Keller (1985) described very high (86%) breeding success for a Polish population of Coots but he did not give figures concerning the percentage of hatched eggs. Aggressive behaviour typical of Coots may be the reason for relatively high breeding success of this species (Jędraszko-Dąbrowska & Dębińska, 1993). Hatching failure almost always resulted from the failure of whole clutches in our study sites and we observed only one case of a single egg failing to hatch in a clutch of six eggs. The hatching failure of total clutches would be expected to result most probably from nest desertion or the death of parents and only in single cases from egg infertility (e.g. Cooke *et al*., 1995). Hence it is especially interesting that hatching success turned out dependent on lake and year factors and on water depth, laying date and egg size but independent of clutch size. This appears to mean that some common but uncontrolled factors influence the timing of breeding, egg size and habitat selection; moreover, all these may differ between years. The between-year differences are likely to be the reason for the lake-laying date interaction being significant. Age is known to affect different aspects of reproduction in birds (see Forslund & Part, 1995; Fowler, 1995 for reviews) and could potentially be a common factor influencing breeding dates. For example, if the age structure of the breeding population differed between years and lakes, so would age-dependent reproductive traits. Different measures of reproductive success were reported to be related to the timing of reproduction in Coots (Brinkhof *et al*., 1997) and the onset of breeding varied with age in some species (e.g. Bańbura & Zieliński, 1998a). Moreover, we could expect that the lakes studied differ in food supply (mostly insects) because of different type of vegetation. Seasonal and spatial habitat-specific variation in food abundance is known to affect both the timing of reproduction and breeding success in Coots (Havlin, 1970; Brinkhof, 1997).

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