Breeding biology of two sympatric coots with contrasting conservation status

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Capsule Red-knobbed Coots *Fulica cristata* and Common Coots *Fulica atra* have similar breeding biology except in chick survival, which was significantly lower in Red-knobbed Coots.

Aims To provide information on the breeding biology of Red-knobbed Coots in Spain and to compare this with similar data for Common Coots.

Methods During two consecutive breeding seasons, clutch size, egg size, brood size and chick survival of Red-knobbed and Common Coots were studied in nearly all of the lagoons in which Red-knobbed Coots were breeding.

Results Clutch size was similar in the two species. Egg volume varied between years within species. Both species had similar brood sizes but chick survival differed significantly, being lower in Red-knobbed Coots (36% and 55% in 2002 and 2003, respectively) than in Common Coots (93% and 91% in 2002 and 2003, respectively). The number of fledglings per pair was lower in Red-knobbed Coots (0.9 and 2.1 in 2002 and 2003, respectively) than in Common Coots (2.2 and 3.0 in 2002 and 2003, respectively).

Conclusion The disparity in productivity between Red-knobbed and Common Coots in the lagoons of southern Spain is mainly due to differential chick survival rates. These differences could be the key factor that has led to their currently different conservation status in Spain.

RED-KNOBBED COOTS *FULICA CRISTATA* AND SYMPATRIC COMMON COOTS *FULICA ATRA* WERE ABUNDANT AND WIDELY DISTRIBUTED IN SPAIN UNTIL THE BEGINNING OF THE 20TH CENTURY (CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998, AMAT & RAYA 2004). HOWEVER, RED-KNOBBED COOTS EXPERIENCED A DRAMATIC POPULATION DECLINE DURING THAT CENTURY, DISAPPEARING FROM THE CENTRAL AND EASTERN REGIONS OF SPAIN (BERNIS 1964, FERRER 1981). CURRENTLY, RED-KNOBBED COOTS HAVE A VERY UNFAVOURABLE CONSERVATION STATUS IN THEIR EUROPEAN RANGE (IUCN 1994), BREEDING IN ONLY A FEW LAGOONS IN SPAIN (CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998, AMAT & RAYA 2004), ALTHOUGH THEY ARE LOCALLY COMMON TO ABUNDANT IN SUB-SAHARAN AFRICA (WETLANDS INTERNATIONAL 2002). IN CONTRAST, COMMON COOTS HAVE DISPLAYED A VERY DIFFERENT POPULATION TRAJECTORY IN THE PAST CENTURY, AND STILL REMAIN WIDESPREAD AND ABUNDANT IN SPAIN (CRAMP & SIMMONS 1980, FERNÁNDEZ-PALACIOS & RAYA 1991, TAYLOR & VAN PERLO 1998).

THE POPULATION DECLINE OF RED-KNOBBED COOTS HAS

BEEN ATTRIBUTED TO EXCESSIVE HUNTING AND EGG COLLECTION (VALVERDE 1960), AND DEGRADATION AND LOSS OF HABITATS (AMAT & RAYA 2004). HOWEVER, IT IS NOT CLEAR WHY THE SAME FACTORS DID NOT SIMULTANEOUSLY AFFECT COMMON COOTS. DISPARITY IN PRODUCTIVITY BETWEEN THE TWO SPECIES COULD BE AN IMPORTANT FACTOR (LACK 1968, ALONSO 1984, NORMENT 1992, SIRIWARDENA ET AL. 1998), AND MORE SPECIFICALLY DIFFERENCES IN THE ABILITY TO ACQUIRE RESOURCES COULD DIFFERENTIALLY AFFECT BREEDING PERFORMANCE IN THE TWO SPECIES (MARTIN 1987, BRINKHOF & CAVÉ 1997).

THIS STUDY PROVIDES BASIC INFORMATION ON THE BREEDING BIOLOGY OF RED-KNOBBED COOTS IN SPAIN, AND INVESTIGATES WHETHER DIFFERENCES IN PRODUCTIVITY MAY BE CAUSING THE CURRENT DIFFERENT CONSERVATION STATUS OF THE TWO COOT SPECIES IN THIS COUNTRY. FOR THIS PURPOSE, KEY BREEDING PARAMETERS HAVE BEEN COMPARED, FROM PAIR ESTABLISHMENT TO CHICK SURVIVAL, IN NEARLY ALL LAGOONS IN WHICH RED-KNOBBED COOTS BREED SYMPATRICALLY WITH COMMON COOTS. THE RELATIONSHIP BETWEEN THE MEAN TIME SPENT FORAGING BY ADULTS AND THE MEAN NUMBER OF CHICKS RAISED PER BROOD IN BOTH SPECIES HAS ALSO BEEN ANALYSED.

METHODS

Study area

BREEDING BIOLOGY WAS STUDIED IN 16 LAGOONS IN ANDALUSIA, IN THE MEDITERRANEAN CLIMATE ZONE REGION OF SOUTHERN SPAIN (TABLE 1) (ROMERO ET AL. 1998). THE LAGOONS ARE BRACKISH AND SHALLOW, AND ANNUAL WATER LEVELS DEPEND ON RAINFALL. THUS, LAGOONS SHOW A MARKED SEASONALITY AS WELL AS STRONG VARIATIONS IN WATER LEVELS BETWEEN YEARS (AMAT 1984). IN 2002 AND 2003, WHEN THIS STUDY WAS CONDUCTED, TOTAL ANNUAL RAINFALL WAS, RESPECTIVELY, 550 MM AND 760 MM. ACCORDINGLY, WATER LEVELS WERE LOWER IN 2002 THAN IN 2003, AND 57% OF LAGOONS DRIED OUT BY THE END OF AUGUST IN 2002, BUT ALL REMAINED WET IN 2003.

NEARLY ALL THE STUDY LAGOONS ARE PROTECTED AREAS SURROUNDED BY CULTIVATED FIELDS. THE MAIN SUBMERGED MACROPHYTES SUITABLE AS FOOD FOR COOTS ARE *POTAMOGETON PECTINATUS*, *RUPPIA* SPP., *CHARA* SPP., *ZANNICHELLIA OBTUSIFOLIA* AND *MYRYPHYLLUM* SPP. THE MAIN EMERGENT MACROPHYTES IN WHICH COOTS USUALLY BUILD THEIR NESTS ARE *PHRAGMITES AUSTRALIS*, *TAMARIX AFRICANA*, *JUNCUS ACUTUS*, *SCIRPUS MARITIMUS* AND *TYPHA DOMINGENSIS*.

Field methods

EACH LAGOON WAS VISITED TWICE A MONTH DURING THE NON-BREEDING PERIOD, AND AT LEAST ONCE A WEEK DURING THE BREEDING PERIOD. IN THE LAGOONS WHERE BOTH COOT SPECIES WERE BREEDING (TABLE 1), I SEARCHED FOR COOT NESTS AND ESTIMATED THE EMERGENT VEGETATION HEIGHT AS THE AVERAGE OF THREE MEASUREMENTS MADE AROUND THE NEST (<50 CM). I ALSO CLASSIFIED THE VEGETATION COVER OF THE NEST INTO THE FOLLOWING CATEGORIES: 0, THE NEST WAS UNCOVERED; 1, 1-50% OF THE EXTERNAL DIAMETER OF THE NEST COVERED BY EMERGENT VEGETATION; 2, BETWEEN 51 AND 90% COVERED; 3, >90% COVERED.

I VISITED EACH NEST AT LEAST ONCE DURING THE INCUBATION PERIOD TO RECORD CLUTCH SIZE AND MEASURE EGG DIMENSIONS (LENGTH AND WIDTH) TO THE NEAREST 0.1 MM WITH A DIGITAL CALLIPER. I MONITORED THE BROODS AND COUNTED THE NUMBER OF CHICKS PER PAIR FROM HATCHING UNTIL THE CHICKS WERE 60 DAYS OLD. FAMILY GROUPS WERE ALWAYS TOGETHER AND STAYED IN THE SAME LOCATION AT LEAST UNTIL CHICKS WERE 60 DAYS OLD, WHEN THEY ARE NO LONGER FED BY PARENTS (HORSFALL 1984A, AMAT 1995). ALTHOUGH DETERMINING THE EXACT NUMBER OF CHICKS HATCHED IN EVERY NEST WAS IMPRACTICAL, THE WEEKLY MONITORING PROGRAMME RECORDED THE NUMBER OF CHICKS IN THE FEW DAYS POST-HATCHING (LESS THAN SIX DAYS) WHILE THEIR PARENTS WERE FEEDING THEM. THE FOLLOWING CATEGORIES OF

Table 1. Number of Red-knobbed Coot individuals observed and number of Red-knobbed Coot pairs breeding in the study lagoons during 2002 and 2003.

Lagoon	2002		2003	
	Individuals	Breeding pairs	Individuals	Breeding pairs
Medina ^a	19	8	33	11
Jellí ^b	0	0	4	1
Montellano	0	0	0	0
Comisario	0	0	0	0
Salada de Zorrilla ^b	4	0	9	3
Dulce de Zorrilla ^a	12	4	7	1
Hondilla ^a	10	4	11	5
Galiana ^b	0	0	2	1
Pilón	0	0	0	0
Peña	0	0	0	0
Taraje	0	0	0	0
Cigarrera	0	0	0	0
Dehesa de Abajo ^a	10	5	13	5
Portil	2	0	1	0
Primera de Palos	2	0	3	0
Calatilla ^a	2	1	3	1

^aBreeding parameters studied in 2002 and 2003. ^bBreeding parameters studied only in 2003.

CHICK AGE WERE ESTABLISHED: AGE 0, CHICKS LESS THAN SIX DAYS OLD; AGE 15, CHICKS 6-15 DAYS OLD; AGE 30, CHICKS 16-30 DAYS OLD; AGE 45, CHICKS 31-45 DAYS OLD; AGE 60, CHICKS 46-60 DAYS OLD.

FINALLY, IN FIVE LAGOONS I RECORDED THE TIME SPENT FORAGING BY BREEDING ADULTS. FOCAL SAMPLING WAS USED (ALTMANN 1974), IN WHICH THE ACTIVITIES OF THE FOCAL INDIVIDUAL WERE CONTINUOUSLY RECORDED DURING THREE-MINUTE SAMPLING PERIODS. FOCAL INDIVIDUALS OF EACH COOT SPECIES FORAGING IN THE SAME AREA WERE ALTERNATELY RECORDED. THE DURATION OF EACH ACTIVITY WAS MEASURED TO THE NEAREST 0.1 SECOND AND I DISTINGUISHED BETWEEN 'FORAGING ACTIVITIES' AND 'OTHER ACTIVITIES' (E.G. LOCOMOTION, PREENING). SUBSEQUENTLY, I ANALYSED THE RELATIONSHIP BETWEEN THE MEAN TIME SPENT FORAGING BY BREEDING ADULTS IN A LAGOON AND THE MEAN NUMBER OF FLEDGLINGS PER PAIR OBSERVED IN THE SAME LAGOON. OBSERVATIONS WERE MADE EACH DAY IN A DIFFERENT LAGOON BETWEEN 08:00 AND 18:00 HOURS (GMT+2 HOURS) DURING THE THIRD WEEK OF APRIL. AT MOST, I RECORDED THE SAME BIRD ONCE IN THE MORNING AND ONCE IN THE AFTERNOON. THE TOTAL NUMBER OF FOCAL OBSERVATIONS CONDUCTED WAS 139 AND 205 FOR RED-KNOBBED AND COMMON COOTS, RESPECTIVELY.

Statistical analysis

ALL SECOND BROODS WERE REMOVED FROM THE ANALYSES.

THE ESTIMATES OF VEGETATION COVER AT THE NEST WERE ANALYSED BY χ^2 TEST. TWO-WAY ANOVAS WERE USED TO EVALUATE THE EFFECTS OF YEAR, SPECIES AND THEIR INTERACTION ON EMERGENT VEGETATION HEIGHT AROUND THE NEST (SQUARE-ROOT TRANSFORMED), AND CLUTCH AND BROOD SIZE (SQUARE-ROOT TRANSFORMED). THE VOLUME OF THE EGGS WAS ESTIMATED USING THE EQUATION $V = 0.51 \times LB^2$ (HOYT 1979), WHERE L IS THE LENGTH AND B IS THE BREADTH (MAXIMUM DIAMETER). THE VOLUME OF THE EGGS WAS AVERAGED BY NEST AND THE EFFECT OF SPECIES, YEAR AND THEIR INTERACTIONS ON MEAN EGG VOLUME WAS ANALYSED BY USING TWO-WAY ANCOVA INCLUDING CLUTCH SIZE AS A COVARIATE.

I ESTIMATED CHICK SURVIVAL RATE AS THE PROPORTION OF CHICKS IN A BROOD THAT SURVIVED TO DAY 60, AND ANALYSED THE INTER-SPECIFIC AND ANNUAL VARIATION ON CHICK SURVIVAL RATE (ARCSINE TRANSFORMED) USING TWO-WAY ANOVA. THE SLICE OPTION WAS USED TO STUDY ALL SIGNIFICANT SPECIES*YEAR INTERACTIONS TO COMPARE THE LEVELS OF ONE FACTOR WHILE HOLDING THE OTHER FACTOR FIXED. FINALLY, I CALCULATED THE MEAN PERCENTAGE OF TIME THAT THE ADULTS SPENT FORAGING RELATIVE TO THE TOTAL TIME OF OBSERVATION IN EACH STUDIED LAGOON, AND ANALYSED ITS RELATIONSHIP WITH THE MEAN NUMBER OF FLEDGLINGS PER PAIR OBSERVED BY USING A SPEARMAN CORRELATION. STATISTICA 6.0 (STATSOFT INC., TULSA, OKLAHOMA) WAS USED THROUGHOUT.

RESULTS

RED-KNOBBED COOTS BREED IN SIX LAGOONS IN 2002 (BREEDING POPULATION SIZE 22 PAIRS) AND EIGHT LAGOONS IN 2003 (BREEDING POPULATION SIZE 28 PAIRS) (TABLE 1). IN CONTRAST, COMMON COOTS BREED IN ALL LAGOONS OF THE STUDY AREA IN BOTH YEARS.

THE EGG-LAYING PERIOD OF BOTH COOT SPECIES WAS LARGELY COINCIDENT BUT SHORTER IN 2002 THAN IN 2003. IN RED-KNOBBED COOTS IT SPANNED FEBRUARY-MAY IN 2002 AND MARCH-AUGUST IN 2003 (IN 2002 THE INTERQUARTILE RANGE WAS FROM THE SECOND FORTNIGHT OF APRIL TO THE FIRST FORTNIGHT OF MAY; IN 2003 THE INTERQUARTILE RANGE WAS FROM THE FIRST FORTNIGHT OF MAY TO THE SECOND FORTNIGHT OF JUNE). COMMON COOTS LAID CLUTCHES BETWEEN FEBRUARY AND JUNE IN 2002 AND BETWEEN LATE JANUARY AND SEPTEMBER IN 2003 (2002, INTERQUARTILE RANGE FROM THE SECOND FORTNIGHT OF APRIL TO THE SECOND FORTNIGHT OF MAY; 2003, INTERQUARTILE RANGE FROM THE SECOND FORTNIGHT OF MAY TO THE SECOND FORTNIGHT OF JUNE). I DID NOT OBSERVE DOUBLE-BROODING IN RED-KNOBBED COOTS DURING 2002, AND ONLY ONE PAIR RENESTED FOLLOWING NESTLING FAILURE. IN 2003, FOUR PAIRS OF RED-KNOBBED COOTS DOUBLE-BROODED, BUILDING ANOTHER NEST FOR THE

SECOND CLUTCH IN THE SAME TERRITORIES. DOUBLE-BROODING WAS OBSERVED IN COMMON COOTS IN BOTH 2002 AND 2003, ALTHOUGH NO RECORD WAS MADE OF THE EXACT NUMBER OF PAIRS IN WHICH THIS OCCURRED.

Nest-site characteristics

DURING THE TWO STUDY YEARS, THE OCCUPATION OF THE TERRITORIES STARTED AT THE BEGINNING OF JANUARY IN THE TWO SPECIES, AND BOTH APPARENTLY PREFERRED TERRITORIES WITH AN AREA OF OPEN WATER ADJACENT TO A PATCH OF ABUNDANT EMERGENT VEGETATION.

NESTS WERE MORE FREQUENTLY ANCHORED TO ABUNDANT EMERGENT VEGETATION (FIG. 1) IN RED-KNOBBED ($\chi^2_3 = 9.4$, $P < 0.05$ AND $\chi^2_3 = 26.8$, $P < 0.001$ IN 2002 AND 2003, RESPECTIVELY) AND COMMON COOTS ($\chi^2_3 = 10.9$, $P < 0.05$ AND $\chi^2_3 = 127.2$, $P < 0.001$ IN 2002 AND 2003, RESPECTIVELY). OVERALL, 66% OF THE NESTS OF RED-KNOBBED COOTS WERE ANCHORED TO *PHRAGMITES AUSTRALIS*, 25% TO *JUNCUS ACUTUS*, AND 9% TO OTHER PLANT SPECIES (E.G. *SCIRPUS MARITIMUS*, *TAMARIX AFRICANA*, *TYPHA DOMINGENSIS*). IN COMMON COOTS, 56% OF THE NESTS WERE ANCHORED TO *PHRAGMITES AUSTRALIS*, 24% TO *TAMARIX AFRICANA*, 11% TO *JUNCUS ACUTUS*, AND 9% TO OTHER PLANT SPECIES (E.G. *SCIRPUS MARITIMUS*, *TYPHA DOMINGENSIS*).

EMERGENT VEGETATION HEIGHT (MEAN $\pm$ SE) AT THE SITES WHERE RED-KNOBBED COOTS ANCHORED THEIR NESTS WAS 207.6 ± 17.46 CM AND 222.1 ± 10.27 CM IN 2002 AND 2003, RESPECTIVELY. IN COMMON COOTS, THE HEIGHT WAS 190.6 ± 16.74 CM AND 197.8 ± 5.35 CM IN 2002 AND 2003, RESPECTIVELY. DIFFERENCES WERE NOT STATISTICALLY SIGNIFICANT BETWEEN SPECIES OR YEAR ($P > 0.09$ IN ALL CASES).

Figure 1. Proportion of nests observed for each vegetation cover class in Red-knobbed (RKC) and Common Coots (CC) in 2002 and 2003. Sample sizes are in parentheses.

Breeding parameters

AVERAGED BREEDING PARAMETERS BASED ON ABOUT 40 PAIRS OF RED-KNOBBED COOTS AND ABOUT 160 PAIRS OF COMMON COOTS MONITORED DURING 2002 AND 2003 ARE REPORTED IN TABLE 2.

CLUTCH SIZE WAS SIMILAR BETWEEN SPECIES AND YEARS (TABLE 2). EGG VOLUME WAS LARGER IN 2003 THAN IN 2002 IN BOTH RED-KNOBBED AND COMMON COOTS ($F_{1,99} = 19.7$, $P < 0.001$, TABLE 2). INITIAL BROOD SIZE WAS SIMILAR BETWEEN SPECIES, AND BOTH SHOWED A LARGER INITIAL BROOD IN 2003 THAN IN 2002 ($F_{1,198} = 40.49$, $P < 0.001$). THE SPECIES'YEAR INTERACTION WAS NOT SIGNIFICANT.

THE CHICKS OF EACH SPECIES EXHIBITED A DIFFERENT PATTERN OF SURVIVAL AFTER HATCHING. IN COMMON COOTS NEARLY ALL CHICKS REACHED AGE CLASS 60 (93% AND 91% IN 2002 AND 2003, RESPECTIVELY) WHEREAS IN RED-KNOBBED COOTS ONLY 36% OF THE CHICKS IN 2002 AND 55% OF THE CHICKS IN 2003 SURVIVED TO DAY 60 (FIG. 2). SLICING OF THE SIGNIFICANT SPECIES'YEAR INTERACTION ($F_{1,184} = 5.8$, $P = 0.02$) INDICATED THAT DIFFERENCES IN CHICK SURVIVAL RATE BETWEEN YEARS WERE ONLY SIGNIFICANT IN RED-KNOBBED COOTS ($F_{1,184} = 5.8$, $P = 0.02$), WITH A HIGHER CHICK SURVIVAL RATE IN 2003 THAN IN 2002 (TABLE 2). MOREOVER, DIFFERENCES IN CHICK SURVIVAL RATE BETWEEN SPECIES WERE SIGNIFICANT IN THE TWO YEARS ($F_{1,184} = 71.2$, $P < 0.001$ AND $F_{1,184} = 53.9$, $P < 0.001$ IN 2002 AND 2003, RESPECTIVELY), WITH CHICK SURVIVAL LOWER IN RED-KNOBBED THAN IN COMMON COOTS IN THE TWO STUDY YEARS (TABLE 2). ALTOGETHER, THE NUMBER OF FLEDGLINGS PER PAIR (TABLE 2) WAS LOWER IN RED-KNOBBED THAN IN COMMON COOTS ($F_{1,184} = 31.1$, $P < 0.001$), AND LOWER IN 2002 THAN IN 2003 IN THE TWO SPECIES ($F_{1,184} = 29.9$, $P < 0.001$).

THERE WAS A STATISTICALLY SIGNIFICANT NEGATIVE CORRELATION IN RED-KNOBBED COOTS BETWEEN MEAN NUMBER OF CHICKS RAISED PER PAIR AND THE MEAN TIME THAT ADULTS SPENT FORAGING ($\lambda_1 = -0.743$, $P = 0.03$, $N = 8$ LAGOONS, FIG. 3). HOWEVER, THIS CORRELATION WAS NOT STATISTICALLY

SIGNIFICANT IN COMMON COOTS ($\lambda_1 = -0.521$, $P = 0.18$, $N = 8$ LAGOONS, FIG. 3).

DISCUSSION

IN SOUTHERN SPAIN, THE POPULATION OF RED-KNOBBED COOTS IS ENDANGERED AND IT IS ALSO AT THE EDGE OF THE SPECIES DISTRIBUTION RANGE (CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998, AMAT & RAYA 2004). THE SPECIES, HOWEVER, DOES NOT FACE CONSERVATION PROBLEMS IN ITS SUB-SAHARAN RANGE AND POPULATION IS INCREASING IN SOME AREAS (E.G. SOUTHERN AFRICA, WETLANDS INTERNATIONAL 2002). COMMON COOTS ARE A CLOSELY RELATED SPECIES (LIVEZEAY 1998), ABUNDANT IN EUROPE, AND LIVING IN SYMPATRY WITH RED-KNOBBED COOTS IN THE STUDY AREA. THE RESULTS PRESENTED HERE SHOW A DISPARITY IN PRODUCTIVITY BETWEEN THESE TWO SPECIES, MAINLY ATTRIBUTABLE TO DIFFERENTIAL CHICK SURVIVAL RATES. IT SEEMS PROBABLE THAT THESE ARE RELATED TO A DIFFERENCE IN THE ABILITY OF THESE TWO COOT SPECIES TO ACQUIRE RESOURCES DURING THE BREEDING PERIOD AT THE SAME SITES.

A LARGELY COINCIDENT EGG-LAYING PERIOD AND THE ABSENCE OF DIFFERENCE IN CLUTCH SIZE BETWEEN THE TWO STUDY SPECIES DOES NOT APPEAR TO HAVE CONTRIBUTED TO THE CONTRAST IN THEIR PRODUCTIVITY IN THE STUDY AREA. THE LAYING PERIOD OF COMMON COOTS, SPANNING LATE JANUARY TO SEPTEMBER, WAS SIMILAR TO THAT REPORTED IN OTHER EUROPEAN REGIONS (FEBRUARY-SEPTEMBER, CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998). IN RED-KNOBBED COOTS, HOWEVER, THE LAYING PERIOD OBSERVED STRETCHED FROM FEBRUARY TO AUGUST AND WAS MARKEDLY SHORTER THAN IN ITS SUB-SAHARAN RANGE, WHERE BIRDS USUALLY LAY EGGS ALL YEAR ROUND (CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998). THESE DATA SUGGESTED A REDUCED PRODUCTIVITY OF RED-KNOBBED COOTS IN THE STUDY AREA, WHERE SECOND BROODS WERE NOT FREQUENTLY OBSERVED.

THE CLUTCH SIZE OF BOTH SPECIES AVERAGED SIX EGGS AND

Table 2. Reproductive parameters (mean $\pm$ sd) of Red-knobbed and Common Coots in southern Spain during 2002 and 2003.

	Red-knobbed Coot		Common Coot	
	2002	2003	2002	2003
Clutch size	5.9 $\pm$ 1.28 (13) ^a	5.8 $\pm$ 1.39 (27) ^a	5.6 $\pm$ 1.50 (30) ^a	6.1 $\pm$ 1.26 (129) ^a
Egg volume (cm ³)	33.52 $\pm$ 3.46 (10) ^a	37.97 $\pm$ 2.88 (27) ^b	34.11 $\pm$ 3.12 (22) ^a	36.08 $\pm$ 3.08 (45) ^b
Initial brood size	2.4 $\pm$ 0.88 (15) ^a	3.7 $\pm$ 1.15 (28) ^b	2.4 $\pm$ 0.68 (46) ^a	3.4 $\pm$ 1.08 (113) ^b
Fledglings /pair	0.9 $\pm$ 1.06 (15) ^a	2.1 $\pm$ 1.62 (26) ^b	2.2 $\pm$ 0.57 (46) ^c	3.0 $\pm$ 1.10 (101) ^d
Chick survival*	0.36 $\pm$ 0.44 (15) ^a	0.55 $\pm$ 0.27 (26) ^b	0.93 $\pm$ 0.16 (46) ^c	0.91 $\pm$ 0.16 (101) ^c

Sample sizes (number of pair studied) are in parentheses. Means with the same superscript letter were not significantly different at the 5% confidence level (two-way ANOVA). *Mean proportion of chicks in a brood that survived to day 60 (see Methods).

Figure 2. Chick survival patterns from age 0 to age 60 in Red-knobbed (RKC) and Common Coots (CC) during 2002 and 2003 in the study lagoons. See Methods for chick age classification.

Figure 3. Relationship between the mean number of fledglings per pair and the average time spent foraging by adults in Red-knobbed (RKC) and Common Coots (CC). Each data point denotes a lagoon.

WAS WITHIN THE RANGE OF DATA FOR RED-KNOBBED COOTS IN THEIR SUB-SAHARAN RANGE (FIVE TO SEVEN EGGS, CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998), BUT ON THE LOWER SIDE OF DATA REPORTED FOR COMMON COOTS IN EUROPE (SIX TO TEN EGGS, CRAMP & SIMMONS 1980, TAYLOR & VAN PERLO 1998).

EGG-LAYING PERIOD AND CLUTCH SIZE ARE TWO LIFE-HISTORY TRAITS THAT DEPEND ON HABITAT CONDITIONS (LACK 1954, PERRINS & BIRKHEAD 1983, MARTIN 1987, DERVIEUX ET AL. 1990, EVANS ET AL. 2005, WEGGLER 2006). THEREFORE, A SHORTER EGG-LAYING PERIOD IN RED-KNOBBED COOTS AND A REDUCED CLUTCH SIZE IN COMMON COOTS BOTH INDICATE THAT THE STUDY LAGOONS IN SOUTHERN SPAIN MIGHT NOT BE CURRENTLY OPTIMUM HABITATS FOR COOTS.

BROOD MORTALITY DUE TO STARVATION IS THE MAIN FACTOR DETERMINING BROOD SIZE IN COOTS (HORSFALL 1984A, AMAT 1995). IN THIS STUDY, BOTH COOT SPECIES SHOWED A SIMILAR BROOD SIZE, ALTHOUGH THEY DIFFERED IN CHICK SURVIVAL. THE CHICK SURVIVAL RATE FOR COMMON COOTS (93% AND 91% IN 2002 AND 2003, RESPECTIVELY) WAS SIMILAR TO THAT FOUND IN THE UK (HORSFALL 1984A), AND MOST OF THE CHICKS SURVIVING THE FIRST FEW DAYS AFTER HATCHING ALSO SURVIVED UNTIL FLEDGING. HOWEVER, CHICK SURVIVAL WAS MUCH LOWER IN RED-KNOBBED COOTS BREEDING SIMULTANEOUSLY (36% AND 55% IN 2002 AND 2003, RESPECTIVELY), AND IN THE SAME LAGOONS A LARGER PROPORTION OF CHICKS SURVIVING THE FIRST FEW DAYS AFTER HATCHING DID FINALLY DIE. ABSENCE OF DIFFERENCES IN NEST-SITE CHARACTERISTICS BETWEEN THE TWO SPECIES DID NOT SUPPORT A HIGHER PREDATION RISK FOR CHICKS OF RED-KNOBBED COOTS (ALONSO ET AL. 1991, HIPFNER ET AL. 2001, BATÁRY ET AL. 2004). HOWEVER, THE NEGATIVE RELATIONSHIP BETWEEN THE TIME SPENT FORAGING BY ADULTS AND THE NUMBER OF FLEDGLINGS PER PAIR FOUND ONLY IN RED-KNOBBED COOTS SUGGESTED THAT CHICK SURVIVAL OF THIS SPECIES WAS LIMITED BY FOOD AVAILABILITY IN THE STUDY LAGOONS (LACK 1954, MARTIN 1987, BRINKHOF & CAVÉ 1997, GILL ET AL. 2002).

SOME OF THE BREEDING PARAMETERS DID VARY BETWEEN THE TWO STUDY YEARS, WITH CONTRASTING RAINFALL AND WATER LEVELS IN THE LAGOONS, SUGGESTING THAT PRODUCTIVITY IN COOTS ALSO DEPENDS ON HABITAT CONDITIONS (BRINKHOF & CAVÉ 1997, HALSE & JAENSCH 1989). IN PARTICULAR, RED-KNOBBED COOTS HAD FEWER BREEDING ATTEMPTS THAN SYMPATRIC COMMON COOTS AND ONLY SOME PAIRS INITIATED SECOND BROODS IN 2003, THE RAINIEST YEAR. EGG VOLUME WAS ALSO HIGHER IN 2003 FOR THE TWO SPECIES, SUGGESTING THAT FEMALES FOUND BETTER CONDITIONS IN THIS YEAR (HORSFALL 1984B, MARTIN 1987, LU & ZHENG 2003, JOHNSON ET AL. 2006). THE ABSENCE OF DIFFERENCES IN CLUTCH SIZE BETWEEN YEARS SUGGESTS THAT BOTH RED-KNOBBED AND COMMON COOTS REDUCED EGG SIZE INSTEAD OF CLUTCH SIZE UNDER ADVERSE HABITAT CONDITIONS (JOHNSON ET AL. 2006). IN ADDITION, INITIAL STARVATION MORTALITY WITHIN BROODS WAS LOWER IN 2003, AND THE TWO COOT SPECIES SHOWED LARGER INITIAL BROOD SIZES IN THIS YEAR. HOWEVER, THE EFFECTS OF YEAR VARIATION IN CHICK SURVIVAL RATE WERE ONLY SIGNIFICANT FOR RED-KNOBBED COOTS, RECORDING AN INCREASE OF 19% IN THE RAINIEST YEAR.

I REPORT HERE A DISPARITY IN PRODUCTIVITY BETWEEN RED-KNOBBED AND COMMON COOTS IN SOUTHERN SPAIN THAT COULD BE A CONTRIBUTORY FACTOR IN THEIR DIFFERENTIAL CONSERVATION STATUS. PRODUCTIVITY OF RED-KNOBBED COOTS WAS APPARENTLY MORE SENSITIVE TO VARIATION IN

HABITAT CONDITIONS. THIS SUPPORTS THE SUGGESTION THAT THE DEGRADATION AND LOSS OF HABITATS DUE TO RECENT CHANGES IN AGRICULTURAL PRACTICES COULD HAVE NEGATIVELY AFFECTED THE PRODUCTIVITY OF RED-KNOBBED COOTS (AMAT & RAYA 2004), AND THUS MAY PARTIALLY EXPLAIN THEIR RECENT POPULATION DECLINE IN SPAIN. HOWEVER, ADULT SURVIVAL RATES ARE ALSO A DETERMINANT OF POPULATION DYNAMICS (HIRALDO ET AL. 1996, SIRIWARDENA ET AL. 1998, JENOUVRIER ET AL. 2005, MORALES ET AL. 2005), AND EXCESSIVE HUNTING WAS ALSO SUGGESTED AS A POTENTIAL CAUSE OF THE RED-KNOBBED COOT POPULATION DECLINE (VALVERDE 1960). ESTIMATES OF ADULT SURVIVAL RATES IN THE STUDY AREA ARE ONGOING, USING COOTS MARKED WITH PLASTIC NECK COLLARS. THESE STUDIES WILL HELP TO ELUCIDATE THE RELATIVE IMPORTANCE OF ADULT MORTALITY AND PRODUCTIVITY IN RED-KNOBBED AND COMMON COOT POPULATION GROWTH RATES, AND PREDICT THEIR LONG-TERM TRAJECTORIES.

ACKNOWLEDGEMENTS

I AM GRATEFUL TO CONCHITA ALONSO, JAIME A. NIETO, ANTONIO VALERO, ALONSO VARO AND MANOLO VAZQUEZ FOR HELPING WITH THE FIELDWORK, AND TO JUAN A. AMAT, CONCHITA ALONSO, JORDI FIGUEROLA, ANDY J. GREEN AND TWO ANONYMOUS REFEREES FOR HELPFUL COMMENTS ON THIS MANUSCRIPT. THE CONSEJERÍA DE MEDIO AMBIENTE, JUNTA DE ANDALUCÍA, IS ACKNOWLEDGED FOR ALLOWING ME TO WORK WITHIN THE PROTECTED LAGOONS AND PROVIDING FACILITIES, AND JOSÉ GALINDO AND PEDRO FOR PROVIDING DATA OF RAINFALL. THE STUDY WAS FUNDED BY CONSEJERÍA DE MEDIO AMBIENTE, JUNTA DE ANDALUCÍA, AND CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS, CO-FINANCED WITH FEDER FUNDS FROM THE EUROPEAN UNION.

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