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AVIAN REPRODUCTION IN A MEDITERRANEAN CONTEXT: CONTRIBUTIONS OF ORNITHOLOGICAL RESEARCH IN SPAIN

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SUMMARY.—*Avian reproduction in a Mediterranean context: contributions of ornithological research in Spain.*

Aims: To review the studies of avian breeding biology conducted by Spanish researchers in the last decades, emphasizing the Mediterranean aspects of avian reproduction. The main topics covered are life history evolution, sexual selection and host-parasite interactions, including brood parasitism.

Results and Conclusions: Avian breeding biology has been strongly influenced by the dominance in the literature of north temperate studies at least since David Lack. There is some evidence that studies of Mediterranean populations may bridge the life history gap between tropical and north temperate populations. Fecundity seems to be lower in the Mediterranean than farther north, while adult survival could be higher due to benign winter climates or shorter migration routes. Multi-broodedness may be more common and lead to reduced clutch sizes. Nest predation may also be higher and more similar to the tropics in the Mediterranean. Parasites may not be a secondary determinant of breeding success and adult survival, but exert a relentless selective pressure on breeding adaptations of Mediterranean birds. Thermal constraints imposed by hot and dry summers may affect the duration of breeding seasons, the number of broods and hatching asynchrony through effects of temperature at laying on egg viability. Spanish studies have revealed bizarre male displays of vigour as well as geographic variation in the sexual implications of some ornaments studied farther north. Parasite-mediated sexual selection could be stronger in Mediterranean populations. Spanish researchers have revealed a new model system in the study of brood parasitism, which has contributed an improved understanding about the intricacies of host-parasite behavioural interactions and about the speed and scale of evolutionary arm-races.

Key Words: breeding biology, brood parasitism, climate, geography, latitude, life history, Mediterranean, parasites, sexual selection, Spain.

RESUMEN.—*La biología reproductiva de aves en el ámbito del Mediterráneo: contribuciones de la investigación ornitológica española.*

Objetivos: Revisar los estudios de biología reproductiva de aves realizados por investigadores españoles durante las últimas décadas, haciendo énfasis en los aspectos mediterráneos de las adaptaciones reproductivas. Los principales temas tratados son la evolución de las estrategias vitales, la selección sexual y las interacciones parásito-hospedador, incluido el parasitismo de puesta.

Resultados y Conclusiones: La biología reproductiva de aves ha estado fuertemente influida por el predominio en la bibliografía de estudios de zonas templadas del hemisferio Norte, al menos desde los trabajos publicados por David Lack. Existen evidencias de que los estudios de poblaciones mediterráneas pueden contribuir a rellenar el vacío existente en cuanto a estudios sobre estrategias vitales entre poblaciones tropicales y de zonas templadas del norte. La fecundidad parece ser menor en las zonas mediterráneas que en latitudes más norteñas, mientras que la supervivencia adulta podría ser mayor en los ambientes mediterráneos debido a condiciones invernales más benignas o a rutas migratorias más cortas. Múltiples puestas por temporada podrían ser más frecuentes en las zonas mediterráneas y conducir a tamaños de puesta más reducidos. La depredación de nidos podría ser también mayor en el Mediterráneo que en las zonas más norteñas, siendo por tanto más similar a lo que se encuentra en los trópicos. Los parásitos, seguramente no son un factor secundario en determinar el éxito reproductor y la supervivencia, ejerciendo una presión selectiva constante e importante sobre las adaptaciones reproductivas de aves mediterráneas. Las constricciones térmicas impuestas por veranos secos y calurosos pueden afectar a la duración de la temporada reproductiva, al número de puestas y a la asincronía de eclosión a través de los efectos de la temperatura durante la puesta sobre la viabilidad de los huevos. Estudios realizados en España han descubierto curiosas exhibiciones de vigor realizadas por los machos así como variación geográfica en las implicaciones sexuales de algunos ornamentos estudiados más al norte. La selección sexual mediada por parásitos podría ser más importante en poblaciones mediterráneas. Investiga-

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dores españoles han revelado un nuevo modelo en el estudio del parasitismo de cría que ha contribuido a una mejor comprensión de la complejidad de las interacciones conductuales entre parásitos y hospedadores, aportando información que ha modificado las ideas previas existentes sobre la velocidad y escala de las carreras de armamento evolutivas.

Palabras clave: Biología reproductiva, clima, España, estrategia de vida, geografía, latitud, Mediterráneo, parásitos, parasitismo de puesta, selección sexual.

INTRODUCTION

The study of avian reproduction has constituted traditionally one of the most productive and attractive research fields in ornithology. The fascination with the spectacular displays and ornaments exhibited by breeding birds and the relative easiness for observing them in climatologically favourable conditions may explain that natural history since Aristotle has shown a marked interest in avian reproductive biology. Darwin (1859, 1871) used frequently birds to exemplify the process of adaptation through natural selection and focussed a large part of his discussion of sexual selection on birds. Given that Darwinian selection is based on differential reproductive success throughout life, the study of avian reproduction may reveal adaptation and allow an empirical approach to the elusive concept of 'fitness' in the wild. The enormous diversity of life history traits and mating systems exhibited by birds has constituted an inexhaustible source of comparative analyses in the search for adaptation and for the trace of evolution ever since Darwin (Lack, 1968; Bennett & Owens, 2002).

Ornithologists, both amateur and professional, have collected vast amounts of information on reproductive traits which have been the substrate of analyses and generalisations. David Lack (1954, 1966) was one of the pioneers in the study of avian reproduction and had a tremendous influence not only on ornithology but for the whole field of ecology and evolution. His adherence to strict individual selection was one of the main supports for the revival of Darwinian principles in ecology in the 1960s and 1970s, whose outcome were the fields of evolutionary and behavioural ecology. His papers and books constituted a solid foundation for subsequent research efforts. Lack focussed his own research on species breeding in North temperate areas given the geographic bias in the amount of information collected. For historic and cultural reasons, a few countries in Europe and North America had traditionally concentrated most of the researchers and naturalists studying birds, and almost any other type of organism as well (Mayr, 1982). The cause of these cultural biases in the study of natural history has not been well studied, but they can be traced far back in history (Mayr, 1982). Whatever the reason, the fact remains that natural history has been and is still dominated by a few countries based in temperate areas of the Northern hemisphere. Mediterranean, tropical and south temperate regions were visited by naturalists from these countries, and thereby contributed to the great store of information on geographic patterns and trends in breeding biology. Two other pioneers of the study of avian breeding like Ron Moreau and Alexander Skutch (Ricklefs, 1999) based their research in the tropics and thereby contributed to broaden the foundation of the field.

In the last decades, scientific research groups from countries which had not contributed greatly to the natural sciences in the past have rapidly increased the rate and quality of their published production. This increase has been associated to rapid economic development and to official policies tending to support international peer-reviewed publication and improved contacts with the international scientific community. Spain is one example of this increase in scientific publication (from 1.6 to 2.7% of global scientific production in the last decade). However, papers on birds of Mediterranean habitats still constitute a very small proportion (< 1%) of the ornithological literature (Bautista & Pantoja, 2000). Until 1990, breeding biology *sensu lato* was covered by less than 10% of articles in the Spanish ornithological journal Ardeola (Potti & Moreno, 1996). A significant presence of Spanish researchers in foreign ornithological journals started at the end of the 1980's (Potti & Moreno, 1996). Thus, it is not surprising that a review of Spanish contributions to the study of avian breeding should focus on the last two decades. Given the limited

local tradition in natural history in countries like Spain, the paradigms of North temperate avian ecology have been incorporated whole to research on Mediterranean species and habitats. This adaptation to models derived for different conditions than those experienced locally has led in some cases to dissociations between expectations and the real world. This has in turn changed somewhat the perspective of Spanish ornithology, contributing to the development of a certain Mediterranean view of avian breeding adaptations. I will hereafter review three aspects of avian reproduction where a Mediterranean view can be detected, without trying to be exhaustive in coverage. These are life history evolution, sexual selection and host-parasite interactions, including brood parasitism. Spanish researchers have been increasingly active in these fields, some of their results contributing to a geographic broadening of perspectives in avian ecology. Only studies implying this potentially new perspective will be reviewed. Thus, many excellent studies by Spanish ornithologists which do not contribute to a geographic comparison with ornithology farther north are not contemplated.

Mediterranean populations: bridging the tropics-north temperate life history gap?

Some of the main paradigms of geographic variation in avian life histories were based on observations of North temperate patterns. Thus, the long days in the North during spring (Lack, 1954) or the high mortalities experienced by birds during the harsh Northern winters (Ashmole, 1963) were used to explain latitudinal clines in fecundity of resident species, brood size was modelled as implying energy savings in thermoregulation and the onset of incubation was studied without consideration of viability losses due to high temperatures stimulating premature embryo development. Recently, this focus on adaptation to North temperate conditions and the disregard for conditions in the tropics has been criticized (Stutchbury & Morton, 2001). The tropics harbour a majority of avian species, so the geographic paradigm in avian ecology seems to be both flawed and partial. Mediterranean conditions occupy a somewhat intermediate position in this regard. Seasons are less marked than farther north, daylength fluctuates less, conditions can be warm in spring and lead to heat stress rather than its opposite, and winters are not as harsh for residents. Breeding seasons are often longer than in the North, with consequent changes in the number of broods that can be raised. Like in the tropics, Mediterranean regions constitute wintering as well as breeding areas. However, seasonality is more marked than in the tropics, implying a clear-cut breeding season. The question is if the paradigms based on North temperate populations are adequate for studying breeding adaptations in Mediterranean regions. Here, we will present a Mediterranean view of avian life histories, focussing on contributions by Spanish researchers.

In contrast to very general predictions about latitudinal trends in breeding phenology, some populations of both resident and migratory species in Spain breed later than populations farther north (Sánchez-Aguado, 1984; Soler & Soler, 1987; Potti *et al*., 1987). Baker (1938) also suggested that the tendency of laying dates to increase with latitude is inverted in the Mediterranean. Also, the temperature dependence of laying dates is not the same in some Spanish populations as in central Europe (Sánchez-Aguado, 1984). Sanz (1997, 1998) has reviewed the latitudinal trends in laying date and clutch size for two passerines breeding from North Africa to Scandinavia. He has found a quadratic association with latitude for both variables, confirming Lack's evidence in a large geographic context (Fig. 1). Breeding phenology is earliest and clutch size largest around 50°N for the migratory Pied Flycatcher *Ficedula hypoleuca* while the resident Great Tit *Parus major* lay earliest in the Mediterranean and produce the largest clutches at 60°N. Thus, Spanish populations of these well-studied nest-box breeding species have relatively small clutches and do not breed earlier than some populations farther north. However, Great Tits are multibrooded, which complicates the analysis of seasonal trends. In a later study, Sanz *et al*. (2000) explored the latitudinal variation in the energetics of breeding Great Tits from Spain to Northern Finland. They found that daily energy expenditure while feeding nestlings was lowest for Spanish birds and that they used all available daylight hours for this activity, while Great Tits farther north had a working day shorter than the daylight period and higher parental ef-

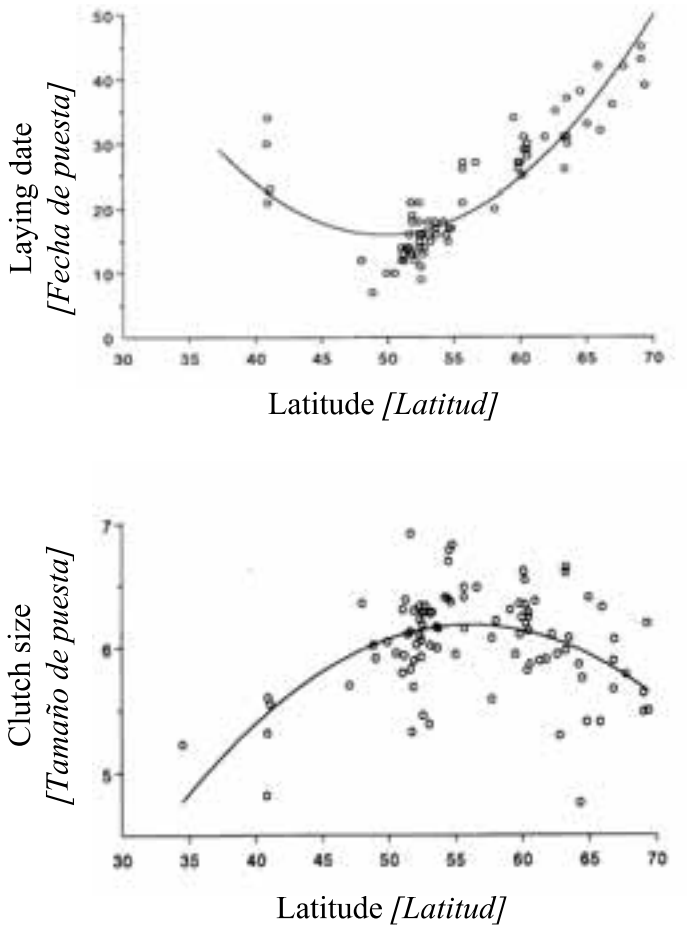

FIG. 1.—Mean laying date (1 = 1 May) and mean clutch size of Pied Flycatcher *Ficedula hypoleuca* populations in relation to latitude across Europe (Reprinted from Sanz (1997) *Ibis*, 139: 107-114, with permission from Blackwell Publishing Ltd.).
[Fecha media (1 = 1 mayo) y tamaño medio de puesta de poblaciones de Papamoscas Cerrojillo Ficedula hypoleuca *en relación con la latitud en Europa (Reproducido de Sanz (1997) con permiso).]*

forts. A tentative conclusion from these analyses is that the clutch size of Mediterranean tits may be constrained by the hours of daylight available, which is not the case for central and north European populations (Sanz, 1999). Blondel *et al*. (1987) have stressed the variation in clutch size of another insectivorous passerine, the Blue Tit *Parus caeruleus,* in the Mediterranean region, especially the contrast between insular populations breeding in Corsican evergreen oak forests and mainland ones occupying deciduous forests. Gil-Delgado *et al*. (1992) have shown in a study of Blue Tits in Spanish mainland evergreen oak forests, that the difference between the two types of forests can be attributed to habitat effects rather than to insular/mainland differences (see also Fargallo, 2004). Mediterranean evergreen oak forests are exceptionally poor habitats for breeding tits, comparing unfavourably even with pine plantations (Maícas-Catalán & Fernández-Haeger, 1996). The typical seasonal decline in clutch size found in temperate single-brooded populations is not found in these populations (Gil-

Delgado *et al*. 1992; Maícas-Catalán & Fernández-Haeger, 1996), indicating unpredictable food resources in this typical Mediterranean habitat.

Ashmole's (1963) hypothesis postulates higher winter mortality rates in the north for resident species, but information about survival rates in Mediterranean populations is scant (*e.g*. Asensio & Carrascal, 1990; Senar & Copete, 1990; Cuadrado, 1994). Herrera (1978) also proposed that conditions during the non-breeding season could limit resident populations in the Mediterranean. In support of Ashmole, clutch size appears to be largest and survival lowest in the most seasonal areas of Spain for two passerine species (Pérez-Tris & Tellería, 2002; Fig. 2). Sanz (2001) has shown a significant negative latitudinal trend in survival rates

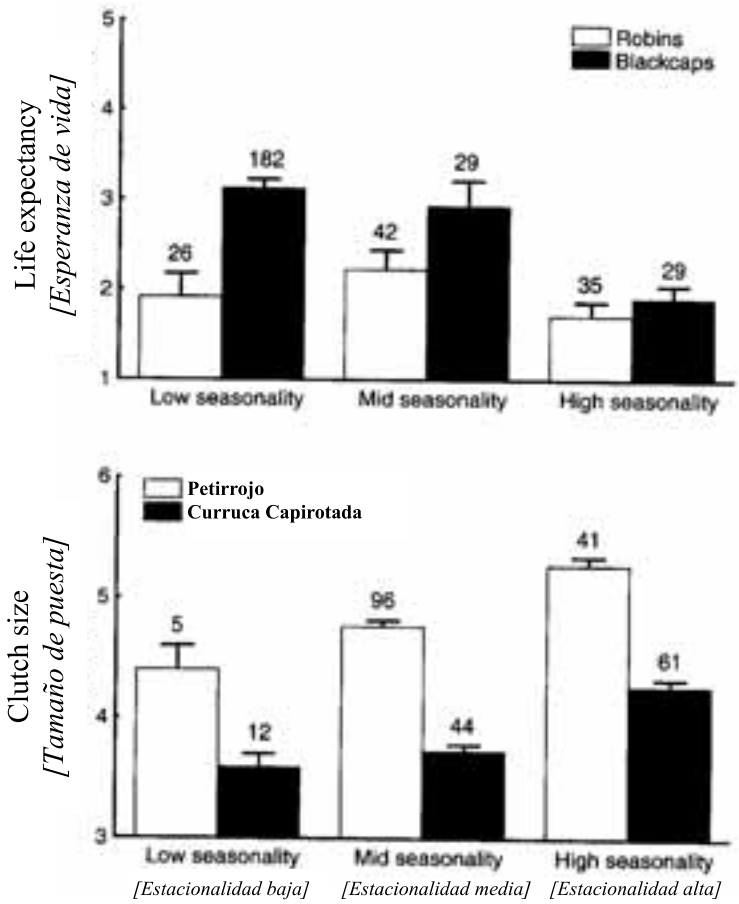

FIG. 2.—Regional and interspecific variation in life expectancy (years) and clutch size of Robins *Erithacus rubecula* and Blackcaps *Sylvia atricapilla* (means, standard errors and sample sizes), in relation to the changing degree of seasonality in the Iberian Peninsula. In both species, means differed between the region with the highest seasonality (Northern plateau) and the other areas (Tukey's test: life expectancy $P < 0.05$; clutch size $P < 0.005$) (Reprinted from Pérez-Tris & Tellería (2002) *Acta OEcologica*, 23: 13-21, with permission from Elsevier).

[Variación regional en esperanza de vida (años) y tamaño de puesta de Petirrojos Erithacus rubecula *y Currucas Capirotadas* Sylvia atricapilla *(medias, errores estándar y tamaños de muestra), en relación con el grado de estacionalidad en la península Ibérica. En ambas especies, las medias difieren entre la región de mayor estacionalidad (meseta Norte) y las otras (test de Tukey: esperanza de vida $P < 0,05$; tamaño de puesta $P < 0,005$ (Reproducido de Pérez-Tris & Tellería (2002) con permiso).]*

across Europe for female Pied Flycatchers, although the very low return rates for Scandinavian populations in his data set include breeding dispersal. Sanz & Moreno (2000) have revealed a late onset of senescence in a Spanish population of Pied Flycatchers compared with populations farther north. They argue for an effect of shorter migration routes on survival rates, which in turn would modulate senescence. This intriguing hypothesis postulates increased survival rates in the Mediterranean for birds wintering in tropical Africa. More information is needed about geographical variation in survival rates across Europe to evaluate if mortality is lower in the south. Higher adult survival in Mediterranean populations could have selected for the lower clutch sizes found (Martin, 2002). Alternatively, low fecundities imposed by the environment could have led to reductions in reproductive costs and correspondingly low mortalities.

The latitudinal trend in clutch size should not be confused with annual or lifetime fecundity, given the important effect on these variables of breeding season duration. Unfortunately, studies on variation in lifetime reproductive success in Spanish avian populations are still scarce (Forero *et al*., 2002). Breeding seasons in Iberia frequently allow repeated breeding (De Lope, 1983; Sánchez-Aguado, 1984; Pajuelo *et al*., 1992; Sanz *et al*., 1993; Soler, M. *et al*., 1995a). The need to be able to relay after predation events may be a crucial determinant of small clutches (Milonoff, 1989; Suárez & Manrique, 1992), and with prolonged breeding seasons the optimal clutch size in each attempt may decrease (Farnsworth & Simons, 2001). Multi-broodedness may actually reinforce latitudinal trends in clutch size by favouring smaller clutches. The typically quadratic seasonal pattern in clutch size is based on selection for small clutches for pairs starting early and being able to raise several broods and for larger clutches for later-breeding single nesters (Crick *et al*., 1993; Soler, M. *et al*., 1995a; Fig. 3). Breeding seasons of some passerines exceed three months in some Mediterranean populations studied (De Lope, 1983; Sánchez-Aguado, 1984; Pajuelo *et al*., 1992; Soler, M. *et al*., 1995a), and nest predation may be important in

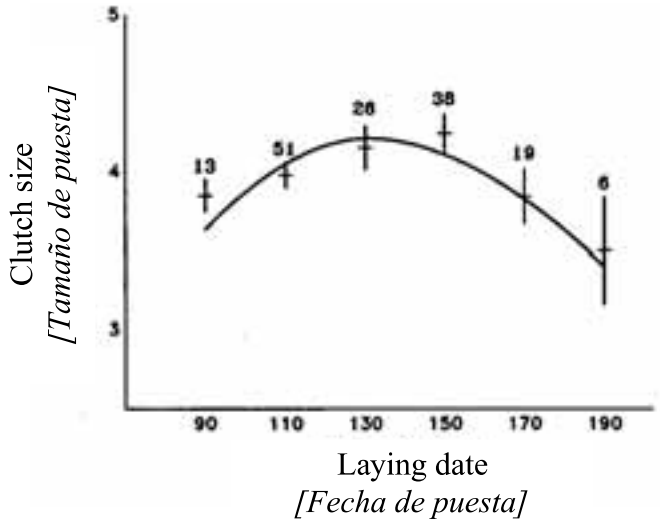

FIG. 3.—Mean clutch sizes (± SE) laid for 20-day periods throughout the 4-month laying season (1 = 1 January) in a Black Wheatear *Oenanthe leucura* population in southern Spain. The quadratic regression function of clutch size on laying date ($y = -1.17 + 0.08\ x - 0.0003\ x^2$, $P < 0.001$) is also depicted (Reprinted from Soler, M. *et al*. (1995a) *Journal für Ornithologie*, 136: 17-27, with permission from the Editor-in-chief of the Journal). *[Tamaños de puesta medios (± error estándar) por períodos de 20 días durante los 4 meses de temporada de puesta (1 = 1 enero) en una población de Collalba Negra* Oenanthe leucura *del Sur de España. También se presenta la función de regresión cuadrática ($y = -1{,}17 + 0{,}08\ x - 0{,}0003\ x^2$, $P < 0{,}001$) (Reproducido de Soler, M. et al. (1995a) con permiso).]*

the Mediterranean depending on habitat (De La Cruz *et al*., 1990; Suárez & Manrique, 1992; Belda *et al*., 1995; Yanes & Suárez, 1995; Fraga & Amat, 1996; Ponz *et al*., 1996; Martín-Vivaldi *et al*., 1999). The proportion of pairs laying second clutches declines with latitude in Great Tits and Barn Swallows *Hirundo rustica* presumably as a consequence of changes in the duration of breeding seasons (De Lope, 1983; Sanz, 1998). However, the proportion of pairs laying second clutches is lower in Spain than farther north for the House Martin *Delichon urbica* which may be related to thermal constraints (Pajuelo *et al*., 1992). In the Blackbird *Turdus merula*, Mediterranean populations do not seem to enjoy a longer breeding season than British ones owing to relatively late breeding onset (Gil-Delgado & Lacort, 1996). For multi-brooded species, annual reproductive success is better explained by number of breeding attempts than by clutch size in each attempt (Sanz *et al*., 1993, Soler, M. *et al*., 1995a). We should expect smaller clutches in Mediterranean populations of multi-brooded species than farther north (but see De Lope, 1983 for Barn Swallows), although no inter-specific comparative study has yet been conducted on this aspect.

Thermal constraints on breeding success may operate differently in Mediterranean environments than farther north, as the incidence of rainy weather may have beneficial effects (Lucio, 1990; Redpath *et al*., 2002). For species with ranges centred on northern latitudes, Mediterranean climatic conditions may operate by limiting reproductive success, while the same conditions do not affect species with ranges centred in the Mediterranean (García & Arroyo, 2001). Moult-breeding overlaps are larger in Spanish Pied Flycatcher populations than in Scandinavia, possibly due to constraints imposed by dry and hot Mediterranean summers (Hemborg *et al*., 2001). Nestlings may suffer more from thermal stress at high temperatures than from exposure (Nager & Wiersma, 1996). Reduced incidence of second clutches in Spanish House Martin populations may be due to constraints imposed by hot summers (Pajuelo *et al*., 1992). Temperatures above 25 °C during the laying period may induce embryonic development before the onset of full incubation (Webb, 1987), and these temperatures may occur frequently in some habitats and seasons in the Mediterranean. The egg viability hypothesis for the evolution of hatching asynchrony in altricial birds posits that embryo mortality increases with the number of days the eggs are left unincubated after laying (Arnold *et al*., 1987). Veiga (1992) showed in House Sparrows *Passer domesticus* that eggs lost viability when unattended, and that this effect increased with the advancing season with concomitant higher temperatures. Asynchronous nests in this population had a greater probability of hatching the early laid eggs successfully and hatching duration was positively affected by ambient temperature (Veiga & Viñuela, 1993; Fig. 4). In the Black Kite *Milvus migrans*, a delayed onset of incubation reduced egg viability of first-laid eggs, especially when ambient temperature during the laying period was high (Viñuela, 2000). Koenig (1982) showed a general increase in egg hatchability with increasing latitude and explained it as due to selection for higher fecundity. However, it may in part be due to egg viability losses in areas with high temperatures at laying. Although alternative hypotheses cannot be excluded, the evidence presented in these studies predicts that egg viability constraints will be more important for explaining hatching asynchrony and resulting size hierarchies in broods in the Mediterranean than other selective pressures.

The impact of parasites on parental fitness has received a great deal of attention by avian biologists in the context of the operation of reproductive costs (Møller, 1997). However, parasites are still treated as a minor factor affecting bird population dynamics (see Newton, 1998 for a recent example), following the tradition initiated by Lack. To what degree is this vision based on the low prevalences and infection intensities found in most north temperate populations? Intensive studies of bird-parasite interactions in the Mediterranean have revealed in most cases rich parasite faunas (Merino *et al*., 1997; Fargallo & Merino, 2000), high prevalence in adults (Fargallo & Merino, 1999; Merino *et al*., 1997) and moderate prevalence in nestling birds (Merino & Potti, 1995a, 1996; Soler, J. J. *et al*., 1999a). However, other studies have revealed low prevalences of hematozoa (Blanco *et al*., 1997; Forero *et al*., 1997; Jovani *et al*., 2002). Despite some scepticism about the validity of purely observational studies (Bauchau, 1997), ectoparasites in the Me-

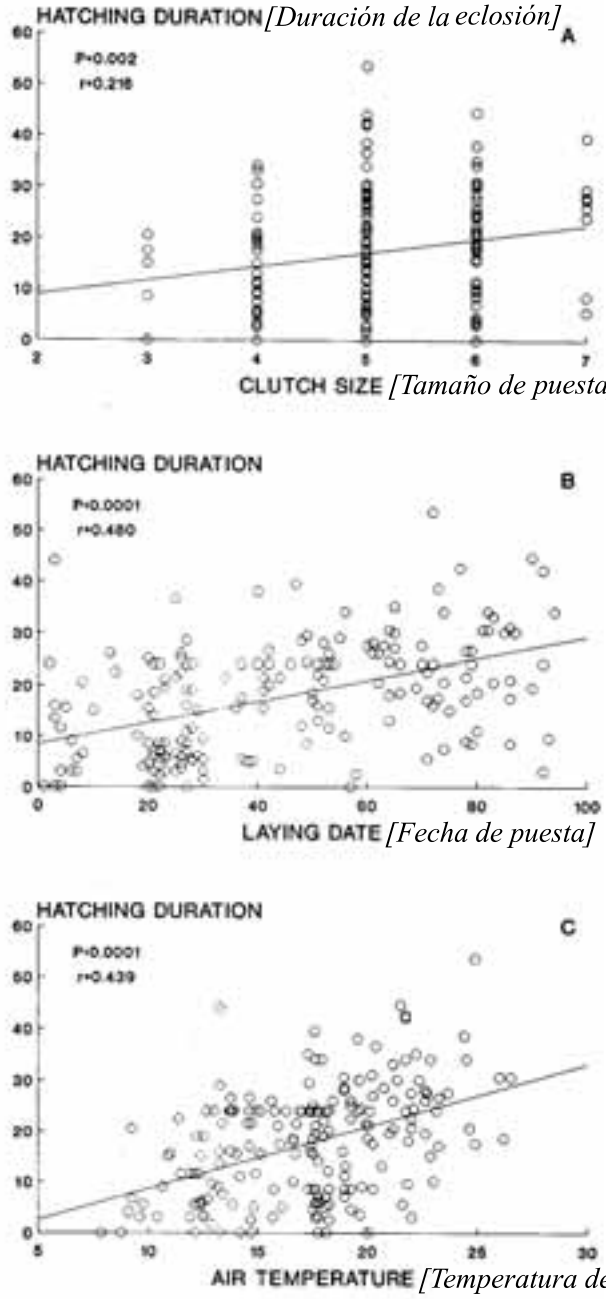

FIG. 4.—Linear relations between brood hatching durations (hours) as a measure of hatching asynchrony and three independent variables for 194 non-experimental House Sparrow *Passer domesticus* nests during 1985-1989. Day 1 for laying date was the earliest laying date recorded (Reprinted from Veiga & Viñuela (1993) *Ornis Scandinavica*, 136: 17-27, with permission from the Managing Editor of the Journal).
[Relaciones lineales entre la duración de la eclosión de la nidada (horas) como medida de asincronía de eclosión y tres variables independientes para 194 nidos de Gorrión Común Passer domesticus *durante 1985-1989 (Reproducido de Veiga & Viñuela (1993) con permiso).]*

diterranean can have dramatic effects on nestling growth, energy expenditure, haematocrit and survival (Møller *et al*., 1994; Merino & Potti, 1995b; Moreno *et al*. 1999; Potti *et al*., 1999; Fig. 5) as well as affect parental effort and well-being (Merino *et al*., 1998; Potti *et al*., 1999). Hematozoan infections also reduce breeding success (Sanz *et al*., 2001a) and may affect the productivity of second broods if parasites increase seasonally (De Lope & Møller, 1993). High hemoparasite prevalence may be the cause of increased female primary reproductive output in old females (Sanz *et al*., 2001b). Field experiments in Spain have also revealed that ectoparasites (Christe *et al*., 2002) and blood parasites (Merino *et al*., 2000) can exert detectable effects on parental fitness. These experiments suggest that absence of effects cannot be deduced from observational studies without manipulating parasite levels (e.g. Tella *et al*., 1996). These results strongly suggest that parasitism is not a secondary determinant of avian survival and reproduction in the Mediterranean but a main fitness factor in its own right. However, more studies on a broader range of species and habitats are needed to support this geographic effect.

Sexual selection and mating systems

Sexual selection through partner choice (Darwin, 1871) was unjustly neglected until the simultaneous revival of the ideas of Fisher (1930) and the proposal of the provocative handicap model (Zahavi, 1975). Beginning in the 1970's, the possibility that many attributes of birds could be explained by sexual selection became a hot topic in evolutionary and behavioural ecology (Andersson, 1994). Several models for the functioning of sexual selection have been proposed, from those based on direct

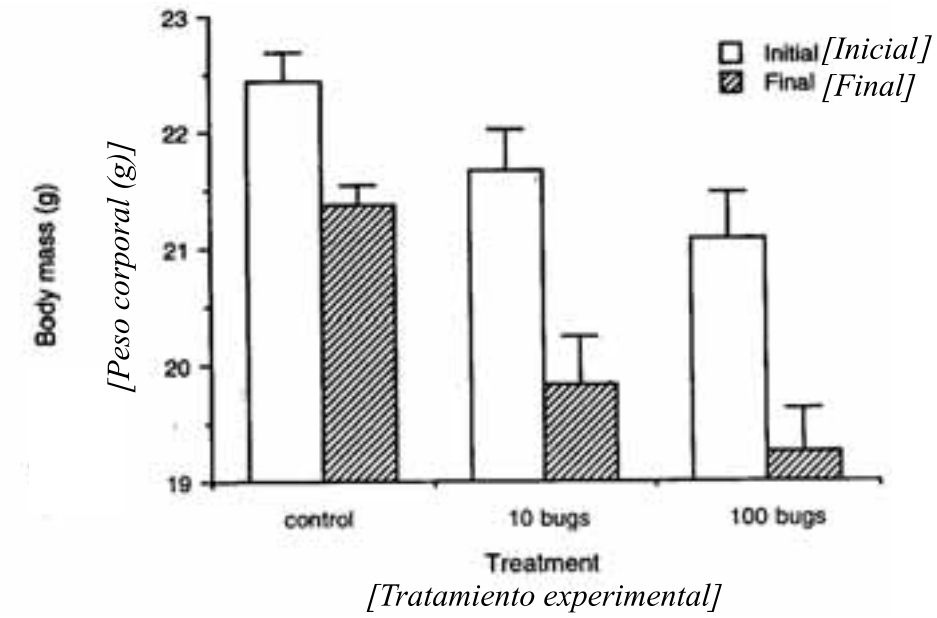

FIG. 5-.—Body mass of House Martin *Delichon urbica* chicks in relation with experimental inoculation with house martin bugs *Oeciacus hirundinis*. Initial and final values refer to before and after measurements of metabolic rate made at 15-16 days of age (Reprinted from Møller *et al*. (1994) *Oecologia*, 98: 263-268, with permission from Springer-Verlag).
[Pesos de pollos de Avión Común Delichon urbica *en relación con un experimento de infestación experimental con 10 o 100 chinches parásitos* Oeciacus hirundinis. *Los valores inicial y final se refieren a antes y después de mediciones de metabolismo realizados a los 15-16 días de vida (Reproducido de Møller* et al. *(1994) con permiso).]*

benefits for the choosing individual to models based on genetic benefits and those suggesting an arbitrary association between mate choice preferences and selected traits. Hamilton & Zuk (1982) gave a further push to the field by proposing a realistic model for the continuous operation of sexual selection through the arms-race between parasites and their avian hosts. Recently, the operation of female choice on honest signals of genetic quality by males has focussed on physiological trade-offs between immunity and the development of ornaments (Folstad & Karter, 1992). The focus on a few model species in North temperate habitats has restricted until recently the scope of selection criteria emphasised in the literature on mate choice. Most studies have dealt with plumage ornaments or song (Andersson, 1994). Studies on Iberian populations have revealed complex behaviours that may be used as cues by females as well as detected ornamental characters that are differentially selected across European populations.

Consumption of ungulate droppings to acquire the carotenoids necessary for maintenance of ornamental facial skin coloration has recently been found in Egyptian Vultures *Neophron percnopterus* in Spain (Negro *et al*., 2002). The consumption of faecal material could be a risky handicap due to the infection hazards involved. Also, the use of antioxidants like carotenoids for ornamental purposes could indicate a strong antioxidant capacity (Lozano, 1994). Negro *et al*. (1999) also interpreted the deliberate rusty staining of body feathers in the Bearded Vulture *Gypaetus barbatus* as a signal used in mate choice, although this interpretation has been questioned (Arlettaz *et al*., 2002). Conspicuous weight lifting by birds had not been revealed in the study of sexual selection until the characteristic nest building behaviour of Black Wheatears *Oenanthe leucura* described by Richardson (1965) was reinterpreted as a post-mating sexual advertisement by males of their condition or their disposition for nestling feeding (Moreno *et al*., 1994; Soler, M. *et al*., 1999a). Manipulating the expression of the display led to changes in female investment in reproduction (Soler *et al*., 1996; Fig. 6). Nest construction had been traditionally considered as an activity directly related to the adaptive function of nests for incubation and nestling rearing. However, elaborate nest building may be a reliable cue of male parental quality in different species (Soler, J. J. *et al*., 1998a, 1998b; Palomino *et al*., 1998) and may lead to female decisions about clutch size being based on male nest construction behaviour (Soler, J. J. *et al*., 2001; De Neve & Soler, 2002). The reinterpretation of well-known behaviours in the light of sexual selection theory by Spanish researchers has just begun, so we can hope for more fascinating discoveries.

Some well-studied plumage ornaments like the Barn Swallow's tail or the white forehead patch of *Ficedula* flycatchers have received their fair share of attention in Spain. While sexual selection operates similarly on the first across Europe, it varies in its association with the second. Thus, the white forehead patch is a sexually selected trait in the Collared Flycatcher *Ficedula albicollis* (Gustafsson *et al*., 1995), but apparently does not function as such in north and central European populations of the Pied Flycatcher (Dale *et al*., 1999). However, it operates as an ornament selected by females in Spanish Pied Flycatchers (Potti & Montalvo, 1991; Potti 1993). It is also present in old females in the Spanish population (Potti & Merino, 1996), who have argued that it may be an ornament in females expressing resistance to trypanosome infection. However, Tella *et al*. (1997) argue that the expression of male characters in female Lesser Kestrels *Falco naumanni* is the outcome of hormonal changes in females related to age. The female angle on sexual selection has also been stressed in a recent suggestion that bright egg colours in birds may express the laying females' genetic quality (Moreno & Osorno, 2003). The long outer tail feathers of male Barn Swallows operate as a sexually selected trait in populations across Europe (Møller, 1994; Møller & De Lope, 1995). However, sexual dimorphism in this trait is less marked in Spanish than in Scandinavian populations (De Lope, 1985; Møller, 1994), presumably due to the higher costs of maintaining extravagantly long tails when foraging efficiency is most constrained. Insects may increase flight velocity at higher temperatures and be more difficult to capture. Møller *et al*. (1995) have shown that tail elongation experiments have a larger proportional effect on prey size in Spain than in Denmark, which shows that male tail length is shorter in the area where a long tail is a larger handicap in terms of foraging

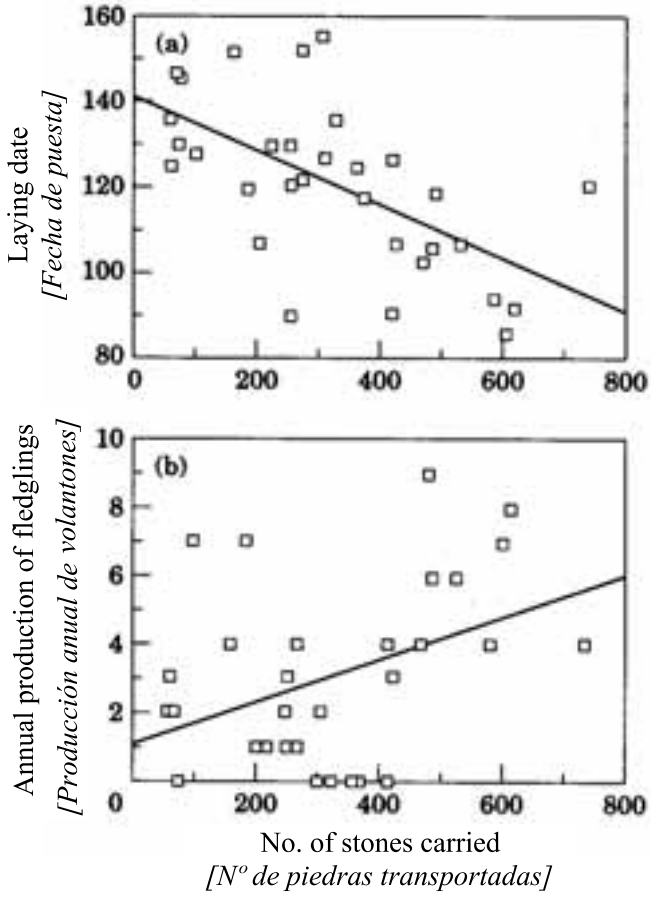

FIG. 6.—The relationship between stone carrying by male Black Wheatears *Oenathe leucura* and (a) laying date (1 = 1 January) and (b) annual production of fledglings. The lines are significant regressions. Females advance laying and raise more fledglings when paired with intensively displaying males (Reprinted from Soler, M. *et al*. (1996) *Animal Behaviour*, 51: 247-254, with permission from Elsevier).
[La relación entre piedras transportadas por machos de Collalba Negra Oenanthe leucura *y (a) fecha de puesta (1 = 1 Enero) y (b) producción anual de volantones. Las lineas representan regresiones significativas. Las hembras ponen antes y sacan adelante más pollos si están emparejadas con machos que exhiben más vigor (Reproducido de Soler, M.* et al. *(1996) con permiso).]*

ability (Fig. 7). A study on the carotenoid-based yellow coloration of breast feathers in the Blue Tit (Senar *et al*., 2002) has revealed the operation of the «good parent» (Hoelzer, 1989) process of sexual selection in a species where the emphasis had been on «good-genes» models of sexual selection based on blue head feathers (Sheldon *et al*., 1999). The fact that Blue Tits are also yellow tits supports the idea that different kinds of ornamental coloration within an individual may provide different types of information to prospective females. A similar argument can be proposed for tail feathers and carotenoid-based coloration in Barn Swallows (Ninni *et al*., 2004). If parasites have stronger effects on fitness in the Mediterranean, we could expect more selection on traits signalling anti-parasite resistance in southern populations than farther north. This possibility and the underlying assumption remain to be tested.

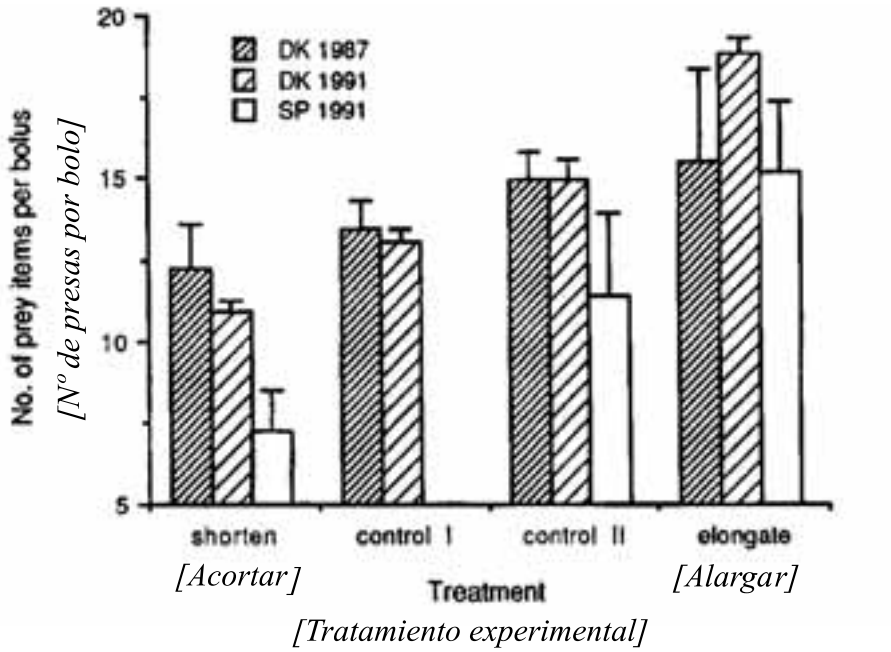

FIG. 7.—The relationship between mean (± SE) number of prey items per bolus fed by male Barn Swallows *Hirundo rustica* to their first brood offspring aged 8-12 days in relation to tail size manipulation in Denmark (DK) and Spain (SP). Elongated tails reduce manoeuvrability in flight and impair capture of large fast flying insects (Reprinted from Møller *et al*. (1995) *Behavioural Ecology and Sociobiology*, 37: 289-295, with permission from Springer-Verlag).
[Número promedio (± error estándar) de presas por bolo cebado a primeras nidadas de 8-12 días por machos de Golondrina Común Hirundo rustica *sometidos a distintos tratamientos de manipulación de la longitud de cola en Dinamarca (DK) y España (SP) (Reproducido de Møller* et al. *(1995) con permiso).]*

A new paradigm in the study of brood parasitism

The literature on interspecific avian brood parasitism has until recently been dominated by the study of just two species which not coincidentally are the only brood parasites breeding in temperate and northern Europe and North America, the European Cuckoo *Cuculus canorus* and the Brown-headed Cowbird *Molothrus ater* (Davies, 2000). In this limited scenario, coevolutionary arms races between brood parasites and host species have been predicated as driving patterns of egg rejection by hosts and host selection by parasites. During recent years, a new model species for the study of brood parasitism has emerged in Spain, namely the Great Spotted Cuckoo *Clamator glandarius* a specialist parasite on corvids, especially the Magpie *Pica pica*. The natural history of brood parasitism by the Great Spotted Cuckoo had been previously explored by several Spanish researchers, including the great naturalist J. A. Valverde (Alvarez & Arias-de-Reyna, 1974; Alvarez et al., 1976; Valverde, 1953, 1971). Based on these and later studies (Arias-de-Reyna & Hidalgo, 1982; Arias-de-Reyna *et al*., 1982, 1987), M. Soler and his research group started a series of ground-breaking studies in the 1990's. The behavioural complexity and the refinement in the parasite-host interactions revealed in this system have widely surpassed those detected in other systems. Great Spotted Cuckoos perform a special type of parental care by following the fate of parasitic eggs in host nests and by punishing egg ejecting magpies with egg or nestling destruction (Soler, M. *et al*., 1995b). After relaying, hosts respond to

this «mafia» activity by accepting parasite eggs (Soler, J. J. *et al*., 1999b; Fig. 8). Parent cuckoos keep contact with their offspring in host nests and defend those nests from predators (Soler, M. *et al*., 1999b). They use host nest size and elaborateness as indicators of Magpie parental quality in order to select the best growth conditions for their offspring (Soler, J. J. *et al*., 1995). Hosts respond by making smaller nests in areas with many parasites to escape parasite preferences (Soler, J. J. *et al*., 1999c). In the European Cuckoo model system, Alvarez (2000) has also detected individual selection of hosts based on traits presumably related to parental quality. When parasite egg ejection becomes too widespread for «mafia» tactics to succeed, cuckoos apparently move to areas with naive hosts and few parasites (Soler, M. *et al*., 1998). The cycle then starts again, as hosts begin to develop discrimination. Discrimination ability appears to be costly in terms of neural capacity, as hosts soon lose it after parasitism rates decline to some low threshold. Also, Magpies apparently lose their territorial behaviour and breed semicolonially and very synchronically after suffering heavy parasitization. These behavioural adjustments reduce the impact of brood parasitism, forcing Cuckoos to move on (Martínez *et al*., 1996). The studies on the Great Spotted Cuckoo have considerably broadened our view about tactics and countertactics in the protracted arms races between brood parasites and hosts. They have shown that brood parasites care to some degree for their offspring and that hosts may develop other ways than egg discrimination to avoid being

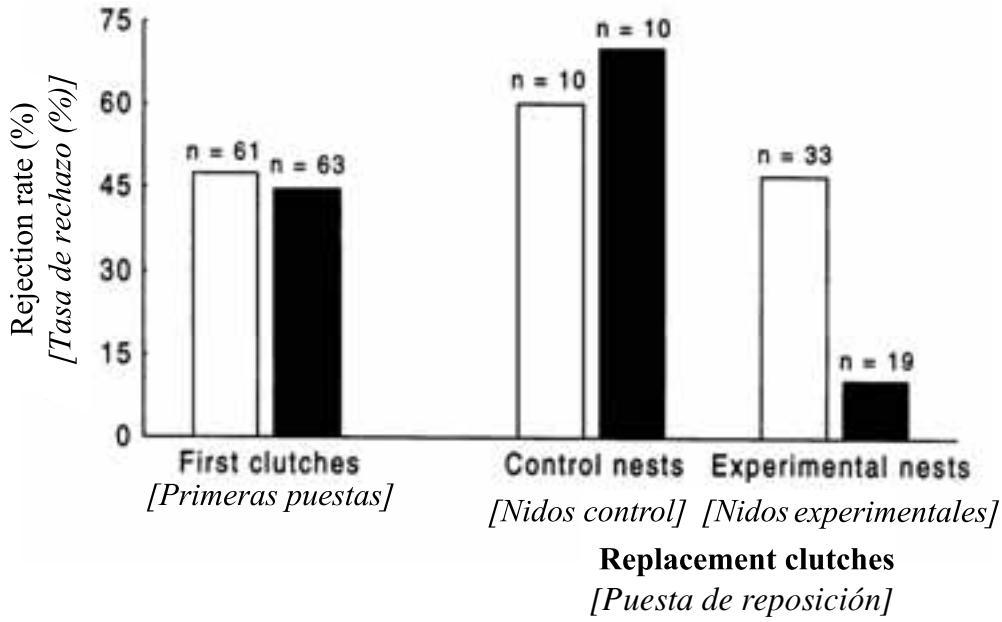

FIG. 8.—Rejection rate of first and replacement Magpie *Pica pica* clutches in relation to the following experimental treatments: control nests where no model Great Spotted Cuckoo *Clamator glandarius* egg was introduced before experimental predation; experimental nests where a model cuckoo egg was introduced before experimental predation in study plots with a low (open bars) and a high parasitism rate (shaded bars) (Reprinted from Soler, J. J. *et al*. (1999b) *Behavioral Ecology*, 10: 275-280, with permission from Oxford University Press).

[Tasa de rechazo de primeras puestas y reposiciones de Urraca Pica pica *en relación con los siguientes tratamientos experimentales: nidos control donde no se introdujo ningún modelo de huevo de Críalo* Clamator glandarius *antes de la depredación experimental; nidos experimentales donde se introdujo un modelo de huevo de críalo antes de la depredación experimental en parcelas de estudio con bajas (barras blancas) o altas (barras negras) tasas de parasitismo de puesta (Reproducido de Soler, J. J.* et al. *(1999b) con permiso).]*

parasitized. Arms races are going on at the regional and local scales and in «ecological time», allowing the changing battlefronts to be followed here and now.

General Discussion

The brief review presented above gives just a glimpse of the fascinating discoveries of Spanish ornithologists studying avian breeding adaptations. Although most contributions are recent, they show an upsurge of interest in the study of breeding biology based on hypotheses and models (Potti & Moreno, 1996). Although a strong effort has led to an increasing number of detailed observational and experimental studies, there are still many important gaps in our knowledge about avian reproductive biology in the Mediterranean. Here, I will try to generalise from the information available and point out the weak points in our understanding of avian breeding adaptations in Mediterranean Europe.

One of the main topics of interest in avian life histories has traditionally been the geographic comparison between north temperate and tropical populations. The contrast is so marked (Stutchbury & Morton, 2001) that it appears as a discontinuity rather than as extremes of a geographic gradient. This life history gap may be bridged by studies of Mediterranean populations breeding in less temperate areas and faced with predator and parasite faunas more similar to those of tropical habitats. Birds breeding in Mediterranean habitats may be to a greater degree multi-brooded when faced with long breeding seasons and intense nest predation. However, no comparative study has yet quantified latitudinal trends in multibroodedness across Europe and the evidence for more broods farther south is mixed at best. Confirmation of multi-broodedness requires intensive population studies on marked individuals, something until fairly recently uncommon in Spanish ornithology. Laying several clutches during a breeding season is linked to small clutches and broods, enabling rapid relaying (Milonoff, 1989). However, clutches tend to be smaller than farther north also for single-brooded species. There are two possible explanations for this difference with other European populations. Either reduced adult extrinsic mortality induces a lower fecundity (Martin, 2002), or fecundity is low due to nest predation or food limitation due to daylight constraints (Lack, 1954). In both cases we expect increased adult survival and reduced annual fecundity in Mediterranean as compared to northern populations. There is some evidence from geographic comparisons of higher adult survival in the south, although this conclusion is tentative due to the low number of studies and species involved. Mild winters for resident species and short migration routes for tropical migrants may imply lower extrinsic mortalities outside of the breeding season. The possibility that birds senesce at a slower rate in the Mediterranean as a response to lower extrinsic mortalities has been proposed based on a single study (Sanz & Moreno, 2000), and should be confirmed in further populations. Higher breeding densities could explain the smaller clutches, mediated by competition for food. Breeding densities in relation to available resources may be higher, although a recent geographic comparison of breeding densities across Europe did not include the Iberian Peninsula (Forsman & Mönkkönen, 2003). The problem with inferring food limitation from geographic comparisons of densities is that resource distributions should be kept constant to make information from different areas comparable. However, nest predation could also be higher than farther north given the importance of snakes and lizards as nest predators in the Mediterranean (*e.g.* Belda *et al.*, 1995). Food appears to be scarce for insectivorous birds in sclerophyllous habitats typical of the Mediterranean region (Blondel *et al.*, 1991; Banbura *et al.*, 1994). However, this does not explain the low clutches of birds in deciduous habitats (Sanz, 1997, 1998). A much stronger effort devoted to demographic studies of Mediterranean populations is needed before we can conclude that they bridge the life history gap between tropical and north temperate life histories.

Heat may be more of a problem for breeding birds in the Mediterranean than exposure. Embryos may start developing too soon and force parents to incubate early in the laying sequence. Hatchability may decline in the warmest areas or seasons. Although, the evidence for viability losses in some studies is tantalizing, more experimental studies on embryo

survival in hot climates are needed to confirm the association between incubation and hatching patterns and thermal regimes. Heat loads and water loss may select against large broods in the Mediterranean. The duration of the breeding season may be constrained by hot and dry summers, limiting the number of broods that can be squeezed into a single season. The thermal constraints experienced by populations in the Mediterranean may be further reinforced by presumable effects of climate change. Sanz *et al*. (2003) have shown that Spanish Pied Flycatchers are experiencing in the last decades a gradual lack of synchrony with their main prey in deciduous woodlands, with corresponding reductions in parental effort and reproductive success. Peñuelas *et al*. (2002) have shown that some migrants are delaying their arrival from their African breeding grounds in response to global change and are thus potentially confronting higher temperatures in their breeding territories. The thermal physiology of reproduction in hot climates and the adjustment between birds and resources necessary for breeding may become two 'hot' topics for future ornithological research in Spain.

Parasites may exert a considerable selective pressure in the Mediterranean according to some published studies. Benign climatic conditions may favour the development of parasites or their vectors. Some ectoparasites may function more like predators by destroying whole broods and appearing unpredictably in space and time. Parental desertion is a frequent outcome of ectoparasite infestations in hole-nesting Spanish birds (J. Potti & F. De Lope, *pers. obs*.), although no study has yet compared desertion rates due to this cause in the Mediterranean and farther north. The stress induced by parasites on adults may constrain reproductive success but could also select for higher reproductive efforts (Forbes, 1993; Sanz *et al*., 2001b). Thus, parasites could be involved in intra-population variance in reproductive effort and success. If parasites have a stronger impact on hosts in the Mediterranean than in more temperate areas, we could expect more displays and ornaments indicating genes for resistance in studies conducted in southern Europe as compared to areas farther north. There is no such evidence yet, although Spanish researchers have studied among the most elaborate behavioural displays of condition or performance found in European birds. Studies in Spain have also revealed marked geographic variation in the development and significance of ornamental traits across Europe, possibly associated to the shifting importance of signals of anti-parasite resistance. More studies are needed to confirm if parasitism has stronger impacts on Mediterranean birds. Some initial analyses have suggested that parasites exert a stronger selection on the immune system in tropical birds (Møller, 1998). A similar comparison between Mediterranean and north temperate populations would be worthwhile. Finally, parasites and their vectors may increase in the Mediterranean due to climate change, although the evidence in favour of this possibility is not convincing (Kovats *et al*., 2001). However, the need to monitor possible changes in prevalence must be stressed in the face of potential impacts of avian health on conservation. The study of brood parasitism and coevolution in the Great Spotted Cuckoo-Magpie system is still active and may reveal more surprises in the future. It may offer a better window into the evolutionary origin of brood parasitism than other systems due to the behavioural flexibility and complexity shown by its participants.

To conclude, Spanish researchers have started to unravel the breeding adaptations of Mediterranean bird populations during the last decades. There has been no historical background on which to find support, so researchers have incorporated ideas and models based on studies from North temperate areas. They have confirmed latitudinal trends in demography and detected geographic variation in selective pressures. Studies in the Mediterranean may bridge the gap between the tropics and North temperate areas and offer a unified view of avian life histories and mating systems, but much work still remains to be done.

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