



Mate guarding and male body condition shape male fertilization success and female mating system in the common quail

Ines Sanchez-Donoso ^{a,*}, Carles Vilà ^a, Manel Puigcerver ^b,
José Domingo Rodríguez-Teijeiro ^c

^a Conservation and Evolutionary Genetics Group, Doñana Biological Station (EBD-CSIC), Spanish National Research Council, Seville, Spain

^b Experimental Sciences and Mathematics Didactics Department, University of Barcelona, Barcelona, Spain

^c Evolutionary Biology, Ecology and Environmental Sciences Department, University of Barcelona, Barcelona, Spain

ARTICLE INFO

Article history:

Received 20 April 2017

Initial acceptance 9 June 2017

Final acceptance 14 November 2017

MS. number: 17-00343R

Keywords:

Coturnix coturnix
mating system
microsatellites
pair bond
paternity analysis
radiotelemetry
sperm loading hypothesis
sperm precedence

In species with female polygamy, pair bonds are frequently established since mate guarding can determine male fertilization success. However, extending the duration of pair bonds also implies reducing the chances of finding new mates. Males face a trade-off between mate guarding and looking for new mates, which can be shaped by their body condition. Here, we investigated the effect of male body condition and mate guarding over the female mating system (genetic monogamy or polygamy) and the male fertilization success in the common quail, *Coturnix coturnix*, a species with sperm storage and thus the potential for postcopulatory selection, and without paternal care. We monitored 20 females and 32 males. We genotyped them, the 21 clutches laid by these females and a large proportion of the males present in the population, which could have sired the clutches, to perform paternity analyses. We tested whether it is the pairing order or the duration of the pair bond that determines the fertilization outcome in clutches with multiple fathers. We hypothesized that males with better body condition might be able to find a mate faster, reducing the cost of mate switching and increasing fertilization success by spending less time in a pair bond. We observed socially monogamous and polygamous females, and our genetic analyses revealed that broods could be sired by one and by multiple fathers. Female genetic polygamy was more frequent when first matings were with males in good body condition. We detected two or three different fathers in multiple paternity broods. The male that mate guarded for longest was the one that sired most of the clutch. Although males in better body condition seemed to establish shorter pair bonds, further data are needed to confirm this trend.

© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Female polygamy is widespread in nature (Parker & Birkhead, 2013; Shuster & Wade, 2003). Despite the costs that it entails, such as increased risk of disease, predation or loss of paternal care for offspring (Reynolds, 1996), female polygamy offers direct and indirect benefits, which have made it an evolutionarily successful mating strategy for multiple taxa (Hosken & Stockley, 2003, pp. 173–194; Slatyer, Mautz, Backwell, & Jennions, 2012). Direct benefits include, for example, reduction of conspecific harassment, access to more food or territory, or increased fertility (Arnqvist & Nilsson, 2000; Reding, 2015). In cases where males do not provide paternal care, the benefits of female polygamy are mainly indirect and have a genetic basis, for example increasing the chances

of obtaining good genes and genetically diverse offspring (reviewed by Jennions & Petrie, 2000; Kempenaers, 2007; Zeh & Zeh, 2001). This polygamy often implies an assessment of male quality by the female. In birds, females assess male quality using several proxies, such as song, courtship, male–male competition, secondary sexual characters or body condition (Byers, Akresh, & King, 2016; Hagelin, 2002; Hasselquist, Bensch, & vonSchantz, 1996; Kempenaers, Verheyen, & Dhondt, 1997; Morales, Alonso, Martín, Martín, & Alonso, 2003). Body condition correlates with fitness in several bird species, in terms of both survival and reproduction (Chastel, Weimerskirch, & Jouventin, 1995; Forstmeier, 2002; reviewed in; Labocha & Hayes, 2012).

The mechanisms of mate choice are not the same across species and are modulated not only by behaviour, but also by anatomical and physiological constraints that contribute to postcopulatory sexual selection. Avian females possess sperm storage tubules in their oviduct where sperm from several males accumulate, allowing

* Correspondence: I. Sanchez-Donoso, Conservation and Evolutionary Genetics Group, Doñana Biological Station (CSIC-EBD), Avenida Américo Vespucio, 26, 41092, Seville, Spain.

E-mail address: ines.sanchezdonoso@gmail.com (I. Sanchez-Donoso).

the fertilization of ova long after copulation (Birkhead & Møller, 1993). Fertilization by sperm from one male or another can be biased as a result of postcopulatory sexual selection as determined by a combination of sperm competition, potential cryptic female choice and physical factors (Birkhead, 1998; Birkhead & Biggins, 1998; Birkhead & Pizzari, 2002; Dean, Nakagawa, & Pizzari, 2011; Eberhard, 2009). For several species, mating order or timing in relation to the female's fertile period are important for male fertilization success. In these species, the last male to copulate with a female sires most of the clutch ('last-male sperm precedence'; Briskie, 1996; Birkhead & Parker, 1997, pp. 121–145). In most cases, though, fertilization success is determined by the relative volume and quality of the ejaculates of the rival males (reviewed in Snook, 2005). Thus, some studies have reported that, at least in insects, males that copulate more frequently or for longer durations have higher fertilization success ('sperm loading'; Dickinson, 1986; Parker & Simmons, 1991; Simmons & Parker, 1992). Mate guarding could favour repeated inseminations and prevent cuckolding and harassment by other potential mates by chasing away rival males, increasing fertilization rates of the guarding male (Birkhead & Møller, 1992; Danchin, Giraldeau, & Cézilly, 2008, pp. 343–354).

Mate guarding also implies risks, entailing a trade-off for both males and females (Cézilly, Prévault, Dubois, Favre, & Patris, 2000). Being in a pair bond increases predation risk, injuries caused by the mate, risk of infection and parasite transmission, etc. (Birkhead & Møller, 1992; Cooper & Vitt, 2002; Le Boeuf & Mesnick, 1991; Mougeot & Bretagnolle, 2000; Sheldon, 1994). In species with no paternal care, males face a trade-off between guarding a female and looking for new mates (Birkhead & Møller, 1992; Dickinson, 1995; Fryer, Cannings, & Vickers, 1999). Male attractiveness can shape this trade-off, since the pressure to guard a female could be less strong for sexually attractive males, which would also have higher chances of getting a new partner.

The common quail, *Coturnix coturnix*, is a migratory galliform that breeds in Palaearctic grasslands and croplands (Gallego, Puigcerver, & Rodríguez-Teijeiro, 1997; Guyomarc'h, Combreau, Puigcerver, Fontoura, & Aebischer, 1998). This species is an interesting study system to analyse mate choice when only indirect benefits are obtained, as well as the effect of mate guarding on male fertilization success when postcopulatory selection exists (see Methods). Both the common quail and the Japanese quail, *Coturnix japonica*, its sister species, have been widely used for laboratory and field research on behaviour, including reproductive behaviour and learning (Adkins-Regan, 2015; Birkhead & Fletcher, 1994; Cornil & Ball, 2010; Correa, Horan, Johnson, & Adkins-Regan, 2011; Domjan, Mahometa, & Mills, 2003; Persaud & Galef, 2005a; Rodrigo-Rueda, Rodríguez-Teijeiro, Puigcerver, & Gallego, 1997; Rodríguez-Teijeiro, Puigcerver, Gallego, Cordero, & Parkin, 2003; Sanchez-Donoso et al., 2016). Yet, their behaviour and social systems in the wild are poorly known.

In this study, we investigated female mate choice and male fertilization success in the common quail by monitoring adult quails and assigning genetic paternity of their offspring. First, we examined the female mating system and the factors associated with it. Second, we studied the relationship between male fertilization success and pair bond order, pair bond duration and male body condition. Finally, we explored whether male body condition shapes the male's trade-off between mate guarding and looking for new mates.

METHODS

Study Species

The common quail exhibits several characteristics that make it a good candidate to study female mate choice and the effect of mate

guarding and male body condition on male fertilization success. (1) Males do not provide paternal care (Glütz Von Blotzheim, Bauer, & Bezzel, 1973). While females incubate, males look for new partners in the same location or elsewhere (Rodríguez-Teijeiro, Barroso, Gallego, Puigcerver, & Vinyoles, 2006; Rodríguez-Teijeiro et al., 2009). (2) Postcopulatory sexual selection exists in this species. Females have sperm storage tubules where sperm from more than one male can be stored and can fertilize eggs up to 6 days after copulation (Sanchez-Donoso et al., 2016). (3) Mate guarding occurs, probably preventing extrapair copulations (Rodrigo-Rueda et al., 1997; Rodríguez-Teijeiro et al., 2003) or forced copulations (as observed in Japanese quail; Persaud & Galef, 2005a) and/ or increasing the sperm load in the female's oviduct by repeated copulations. (4) Male body condition index (BCI, calculated as a relationship between mass and wing length) is an individual intrinsic property; it does not change during the breeding season and is not influenced by the physiological status of the bird (Sardà-Palomera, Puigcerver, Vinyoles, & Rodríguez-Teijeiro, 2011), so it can be used as a proxy of male quality. (5) Body condition can be associated with male fertilization success. Males in better body condition tend to aggregate with other males and engage in calling competitions to attract females and establish temporary pair bonds (Guyomarc'h et al., 1998; Sardà-Palomera et al., 2011). Females are attracted by these aggregations, which are mainly composed of high BCI males (Sardà-Palomera et al., 2011). In addition, male–male confrontations occur and are resolved in favour of the male with the best body condition (Rodrigo-Rueda et al., 1997). In Japanese quail, females tend to be fertilized by the male that they prefer (Adkins-Regan, 1995; Domjan et al., 2003; Persaud & Galef, 2005b) and males in relatively poor condition have lower fertilization success, probably because females find them less attractive and avoid inseminations (Correa et al., 2011).

Sampling and Monitoring

The field study was carried out in an area of about 1 km² in northeast Spain (Mas Esplugues, Tarragona province, Spain, 41°25'N, 1°23'E, 628 m above sea level), in a short and narrow valley with winter cereal crops (mainly barley and wheat), which constitute a suitable breeding habitat for quail (Glütz Von Blotzheim et al., 1973). This area holds an open quail population in which individuals continually arrive during the breeding season, spend some time and leave in search of other suitable habitat patches and mates (Rodríguez-Teijeiro, Puigcerver, & Gallego, 1992). The field data used for this study are from surveys conducted during the breeding seasons of 1996, 1997, 1999, 2000 and 2001 (from mid-April, coinciding with the arrival of the first migrants, to the beginning of August, when the breeding season ends).

Since quail breed inside dense cereal crops, direct behavioural observations are practically impossible. For that reason, we monitored pairs using radiotelemetry (Rodríguez-Teijeiro et al., 2003). We used nine walk-in funnel traps (144 x 67 cm and 87 cm high) to capture males. Traps were evenly spaced along the edge of the cereal plots facing the cereal. Inside these traps we put a smaller cage containing an adult female that acted as a sexual decoy (following Puigcerver et al., 2014; Rodríguez-Teijeiro et al., 2003; Sardà-Palomera et al., 2011). The females used as sexual baits were 1 or 2 years old. They were obtained from eggs hatched in the laboratory that were taken from wild nests during previous breeding seasons, and were kept for up to a year with minimal human interference in semicaptivity in a large pen (see below). Traps were checked every 2–3 days to keep disturbance by researchers to a minimum. Trap and cage roofs were covered with foam to prevent quail injuring their heads when jumping; the roofs also protected them from direct sunlight and rainfall. Water (from

an 8-litre tank) and food (vitamin-supplemented wheat) were supplied ad libitum both to decoys and to trapped individuals. Food and water supplies were checked at every visit and refilled if necessary. Cages had double wire to protect the quails against predators, and traps were sprayed at every visit with a mammal repellent. These field protocols were designed, after a pilot study, to minimize stress and improve welfare conditions for the birds, as recommended by Cuthill (1991) and the ASAB/ABS Guidelines for the treatment of animals. When a free-ranging male entered a funnel trap, we took morphometric measures (weight and wing length), determined age by the presence (adults) or absence (yearlings) of an 'anchor' pattern in its throat feathers (see Cramp & Simmons, 1980; Puigcerver, 1990), ringed it and the decoy female and took blood samples of both for genetic analyses (100 µl of blood from the jugular vein). We attached backpack radio transmitters (PIP-3 Biotrack button cell tags that weighed <5% of their body weight, to avoid disturbing their normal behaviour; Kenward, 1987) and then released them. Another female was put in the cage to replace the released one and to continue trapping males. Released individuals were monitored every 2–3 days with a telemetry receiver (R1000, 148–174 MHz; Communications Specialists, Inc., Orange, CA, U.S.A.) and a three-element Yagi antenna to locate them and to check whether they had established a pair bond or nested (Rodríguez-Teijeiro et al., 2003), until they disappeared from the study area or were found killed by predators. We considered that an individual had left the area when we did not detect its radiosignal again during the remaining breeding season. For another experiment (see Sardà-Palomera et al., 2011), we also set three additional traps using wild-caught males as baits to attract other males (unpaired males tend to aggregate; Sardà-Palomera et al., 2011). In one case, a female was attracted to one of these traps and this pair was also included in the current study.

To assess whether a male and a female released together formed a pair bond (sensu Hinde, 1964), at the next visit we approached the pair to separate them (Rodríguez-Teijeiro et al., 2003). When we observed searching behaviour between the separated individuals (calls and putative search movements, Rodríguez-Teijeiro et al., 2003) and later telemetric fixes indicated that they were again within 5 m of each other, we assumed that a pair bond existed between them. They were categorized as unpaired if they flew off alone and showed no signs of searching behaviour in the next 30 min. When a female was apparently unpaired but we detected searching behaviour towards an untagged male, we tried to capture this new male (by using a net and female decoy call, see Gallego, Puigcerver, Rodríguez-Teijeiro, Rodrigo-Rueda, & Roldán, 1993) and, if successful, we took morphometric measures, ringed, sampled and radiotagged the new partner and assumed that a mate switch had occurred. When individuals showed the same status on two or more consecutive visits, we assumed that they had maintained that status in the intervening time. Occasionally, the mating status could not be assessed due to difficulties in field work.

We located the nests of the radiotagged females. Between 2 and 5 days after the female was observed incubating for the first time, the clutch was collected and incubated in the laboratory, except for three broods (B8, B9 and B13) that were collected before the female started incubation due to technical problems with the radio transmitters. Since female common quail naturally lay several clutches during a breeding season (Puigcerver, Rodrigo-Rueda, Rodríguez-Teijeiro, & Gallego, 1997), we expected that removal of a clutch would not affect the subsequent natural reproductive behaviour of the females. Hatched chicks were reared in a laboratory facility in the University of Barcelona. Several weeks after they hatched, we took a blood sample from each of them (20 µl, from the brachial vein) and moved them to a large pen (12 x 8 m and 5 m high, with approximately 1 m² per individual when the highest

densities were reached), which was cultivated with lucerne, *Medicago sativa*, built with wire mesh and covered with netting. They lived there in semicaptivity (with space for moving, grooming and interacting socially, food and water ad libitum and infrequent human disturbance) until the next breeding season, when they were used as sexual decoys or in other studies. Since these birds had already been genotyped as chicks, we did not take new blood samples. Eggs that did not hatch after 20 days of incubation in the laboratory were opened and a tissue sample was taken from the dead embryo if there was one.

To identify other individuals in the area that could potentially mate with the released females, we also captured single males by attracting them with a recorded female call used as a decoy (Gallego et al., 1993). These males were ringed, measured, blood was drawn for paternity analyses and they were released in the same place. Of these, we genotyped those that were captured from 15 days before the beginning of the fertile period (see below) of the first released female to 15 days after the beginning of the incubation of the last laying female studied. This period was chosen because the male population in the study area turns over almost completely every 15 days, approximately (Rodríguez-Teijeiro et al., 1992) and these males could have been present in the area during the females' fertile periods.

Following this methodology, we closely monitored 20 females randomly chosen from all the females that acted as decoys and the 32 males that associated with them. We located 21 nests as soon as the females started incubating (one of the 20 females laid a replacement clutch). Nine broods were studied in 1996, four in 1997, three in 1999, two in 2000 and three in 2001 (Table 1 and Fig. S1 in the Supplementary Material). In total, we genotyped the 20 radiotagged females, 170 wild males (those detected in the area when the radiotagged females were in their fertile period: 40 from 1996, 55 from 1997, 29 from 1999, 31 from 2000 and 15 from 2001, including the 32 that were radiotagged), and 183 chicks and embryos from the clutches.

Ethical Note

On rare occasions we had to treat minor injuries on the head of trapped individuals because they jumped and hit the trap ceiling (covered with foam to minimize potential damage) or because of pecking when two males entered the same trap (this happened on 10 occasions; we did not include these males in this study). Injuries were superficial in all cases and could be treated in the field. Individuals were released after verifying they were in good condition. We confirmed that these quail recovered completely from their injuries when we recaptured them in the same or other traps ($N = 6$ recaptures), which also indicated no aversion to the traps. Moreover, all showed normal social and reproductive behaviour. If a caged individual was in poor condition due to stress or disease, we removed it from the experiment and brought it to the semicaptive facilities. Individuals that did not attract feral quail after a few days of being put in the cages as decoys were removed to the large pen, since this could be a symptom of stress.

Removal of the clutches did not affect the studied individuals or the natural common quail population. We observed that the monitored males behaved naturally, establishing new pair bonds after mating; a radiotagged male that stayed in the area continued pairing and several of the females laid another clutch. These observations suggest that the experiment did not disturb the animals' behaviour.

All work was conducted according to the guidelines of the Federation of European Laboratory Animal Science Associations (FELASA). The work fulfils the ethic recommendations of the European Union and the Spanish legislation (Spanish Law 5/1995 and

Table 1
Details of the broods analysed

Brood	Year	No. of eggs (fertilized)	F	M1	M2	M3	M4	Genotyped offspring (%)	FFP monitored (%)
B1	1996	11	11	11	.	.	.	100	100
B2	1996	10 (9)	9	9 ³	.	.	.	100	100
B3	1996	12 (11)	11	11 ³	.	.	.	100	<60
B4	1996	7	7	7	.	.	.	100	100
B5	1996	13	13	12 ⁵	1 ⁶	.	.	100	60–80
B6	1996	14	13	1	12 ⁵	.	.	93	60–80
B7	1996	10 (9)	8	8 ⁶	.	.	.	89	<60
B8*	1996	9	8	0	4	2	2	89	≥80
B9*	1996	9 (8)	7	7	.	.	.	88	0
B10	1997	8	8	1	7 ¹²	.	.	100	100
B11	1997	11	11	9	2 ¹²	.	.	100	≥80
B12	1997	10	10	9	1	.	.	100	≥80
B13*	1997	6	6	6	.	.	.	100	0
B14	1999	11	11	10	1	.	.	100	100
B15	1999	8 (6)	4	0	1	3	.	67	100
B16	1999	11	5	3	2	.	.	46	≥80
B17	2000	8	7	4 ²⁶	3	.	.	88	100
B18	2000	13	10	6 ²⁶	2	2	.	77	≥80
B19	2001	11 (10)	9	9 ^{G4}	.	.	.	90	100
B20	2001	11 (9)	6	4	2 ^{G4}	.	.	67	≥80
B21	2001	10 (8)	5	5	.	.	.	63	100

Broods marked with an asterisk were collected before the female started incubation, so the clutch was probably incomplete. Broods B3 and B4 were laid by the same female. No. of eggs (fertilized): number of eggs known to be laid; in parentheses, maximum possible number of eggs fertilized (assessed by the number of chicks and the presence of embryos), no number in parentheses means that all the eggs were fertilized. Some eggs were lost (mainly due to predation) or genotyping failed. Lost eggs were assumed to have been fertilized. F: number of offspring genotyped and laid by the monitored female (assessed by paternity analyses). Differences between this number and the number of fertilized eggs are due to failure in genotyping or unknown fertilization status (eggs eaten by predators). M1, M2, M3 and M4: number of eggs fertilized by the different mates of the female (detected by observation of the social behaviour or by genetic analyses). The males are ordered according to pairing order and assuming no extrapair copulations occurred. Underlined numbers: pairing order unknown. Superscripts: identification code of fathers involved in more than one brood; codes correspond to those in Fig. S1 in the Supplementary Material. Genotyped offspring (%): percentage of the brood that was genotyped (assuming all lost eggs were fertilized). FFP monitored (%): percentage of the female fertile period (FFP) that was monitored.

Decree 214/1997) and has been approved by the Ethics Committee on Animal Experimentation from the University of Barcelona. All our experimental work was carried out in accordance with the ASAB/ABS Guidelines for the treatment of animals. All personnel involved in animal care were properly certified for animal handling and experimentation by the Regional Government ('Generalitat de Catalunya, Direcció General del Medi Natural') and had broad expertise in husbandry of chicks and adult quail. All fieldworkers were trained, competent and certified to handle and ring quail, take blood samples and attach transmitters. The field work team comprised five or six people, which was sufficient to ensure that all the traps were visited with the regularity needed to safeguard the welfare of the caged individuals.

Typing of Microsatellite Loci and Parentage Analyses

Genetic paternity analyses were carried out to identify the father and mother of each chick and embryo. Blood and tissue samples were stored at -20°C in 95% ethanol until DNA was extracted using a DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia, CA, U.S.A.) following the manufacturer's protocols. Individuals were genotyped for nine unlinked autosomal microsatellite loci originally developed for Japanese quail (Koyang et al., 2000; 2002): GUJ0001, GUJ0039, GUJ0044, GUJ0057, GUJ0065, GUJ0074, GUJ0085, GUJ0093 and GUJ0097. These markers are highly polymorphic and had previously been used for hybrid identification in common quail

(Sanchez-Donoso et al., 2012; 2014). Loci were amplified by polymerase chain reaction (PCR).

PCR amplifications for all loci except GUJ0057 were conducted in a Multiplex with the Type-it Microsatellite PCR Kit (Qiagen) in a final volume of 5 μl , containing 2.5 μl Type-it Multiplex PCR Master Mix, 0.5 μl 5x Q-Solution, 0.5 μl MgCl₂ 25 mM, 0.25 μl Primer Mix, 0.25 μl miliQ H₂O and 1 μl DNA. The primer MIX contained primers of loci GUJ0065, GUJ0074, GUJ0085, GUJ0093 and GUJ0097 at 1 μM , and primers of loci GUJ0001, GUJ0039 and GUJ0044 at 0.5 μM (see Table S1 in the Supplementary Material). Amplifications were performed with the following cycling conditions: 15 min at 95 $^{\circ}\text{C}$; 40 cycles of 30 s at 95 $^{\circ}\text{C}$, 90 s at 59.5 $^{\circ}\text{C}$, 60 s at 72 $^{\circ}\text{C}$; 30 s at 60 $^{\circ}\text{C}$; keep at 4 $^{\circ}\text{C}$.

PCR amplifications for locus GUJ0057 were conducted with the HotStarTaq DNA Polymerase kit (Qiagen) in a final volume of 5.5 μl , containing 0.5 μl 10x PCR buffer, 1 μl 5x Q-Solution, 0.8 μl MgCl₂ 25 mM, 0.06 μl dNTPs 20 mM, 0.2 μl each primer at 10 μM , 0.025 μl HotStarTaq, 1.715 μl miliQ H₂O and 1 μl DNA. Amplifications were performed in a touch-down PCR with the following cycling conditions: 15 min at 95 $^{\circ}\text{C}$; 40 cycles of 30 s at 95 $^{\circ}\text{C}$, 30 s at 59.5 $^{\circ}\text{C}$ dropping 0.2 $^{\circ}\text{C}$ per cycle, 30 s at 72 $^{\circ}\text{C}$; 10 s at 72 $^{\circ}\text{C}$; keep at 4 $^{\circ}\text{C}$.

All PCR products were separated by electrophoresis on an ABI 3730 sequencer (Applied Biosystems, Inc., Foster City, CA, U.S.A.) following the manufacturer's protocols. Alleles were sized and scored using the software GeneMapper v3.5 (Applied Biosystems). The genotype data set is available at <http://hdl.handle.net/10261/157217> and at <http://www.consevol.org/resources.html>.

To assess marker informativeness, we used all male genotypes (170 putatively unrelated individuals) to calculate the number of alleles per locus, observed (H_o) and expected (gene diversity, H_e) heterozygosity (Nei, 1987), and the polymorphic information content of each marker (PIC; Botstein, White, Skolnick, & Davis, 1980). These indexes were calculated using CERVUS 3.0.3 (Kalinowski, Taper, & Marshall, 2007).

The paternity of embryos and chicks was assigned by using the maximum likelihood method implemented in CERVUS 3.0.3 (Kalinowski et al., 2007). This software assigns parentage based on a pairwise likelihood comparison. Simulations based on allele frequencies allowed an estimation of the significance of paternity assignments (Kalinowski et al., 2007). Simulations of parentage were run for 1 000 000 offspring. We set a minimum probability of 99% for parentage assignments. The minimum number of typed loci required for analyses was five. We used the parent pair analysis implemented in the software, which assigns offspring to the potential parent pair with the highest log-likelihood ratio. Paternities were confirmed using COLONY 2.0.2.3 (Jones & Wang, 2009) in all cases, showing that this reduced number of highly polymorphic markers allows a robust identification of parent pairs. This software implements a maximum likelihood method to infer sibship and parentage jointly. We used it also to infer the genotypes of possible nonsampled fathers. In both approaches, analyses were done including only the individuals sampled during the same breeding season.

Statistical Analyses

We analysed the effect of several traits on the female mating system deduced from the paternity analysis of the offspring (from now on, genetic mating system to differentiate it from inferences on reproductive behaviour based on observations) and male fertilization success (dependent variables). Female genetic mating system was a categorical variable with two levels: genetic monogamy and genetic polygamy. Male fertilization success was inferred as the minimum proportion of embryos sired by a male in a brood in relation to the maximum number of embryos possible in

that brood. The exact number was not always known because in some cases not enough markers were successfully genotyped (see above) or because some eggs were lost (mainly due to predation). Since we could not know whether lost eggs were fertilized or not, we assumed that all lost eggs were fertilized. This prevented an inflated estimate of the proportion of offspring assigned to a given father. When the maximum number of embryos was unknown, we calculated the proportion of embryos sired in relation to the number of eggs of the brood, minimizing fertilization success. We used a proportion instead of the absolute number of sired embryos to correct for the size of the clutch. This was calculated with the `cbind()` function in R 3.3.3 (R Core Team, 2017).

We analysed the effect of the following variables: female and male identity, pair bond duration, day in the female fertile period (FFP) when the pair bond was established (starting day), order of the pair bond in the FFP and male body condition. We also tested relationships among these variables. We defined the female fertile period (FFP) as the period of time when sperm could fertilize an egg. We assumed that it comprised from 7 days before the first egg was laid until the day before the last egg was laid. Common quail lay one egg per day, which is fertilized the day before. Since we did not have precise data on the day when the eggs were laid, we estimated this date by assuming an 18-day incubation period based on previous direct observations and on the literature (Verheyen, 1950). Since the fertile period of the closely related Japanese quail was estimated to start 7–11 days before the onset of laying (Birkhead & Fletcher, 1994; Higaki, Yoshimura, Tamura, & Okamoto, 1995; Sittmann & Abplanalp, 1965), we assumed 7 days for common quail (the most conservative approach to study female polygamy). Pair bond duration was calculated as the proportion of time the pair bond lasted over the total FFP. The minimum duration of the pair bond was taken as the length of time that the pair was recorded together. Since the birds were not monitored every day, we calculated the midpoint between the minimum and the possible maximum duration of the pair bond. This value was rounded down to an integer. We transformed the number of days into a proportion of the FFP duration to control for the different lengths of the fertile period for different females (proportion calculated with the `cbind()` function). We recorded the day when the pair bond was detected for the first time in relation to the FFP (count variable). For broods of genetically polygamous females, we also recorded the order of each pair bond in the FFP. The BCI was calculated for each male as the residuals of an ordinary least squares linear regression of mass against wing length. We used wing length to calculate BCI because it was the morphological variable that best correlated with body mass, as suggested by Lormée, Jouventin, Trouve, and Chastel (2003) for calculating a body condition index (Jakob, Marshall, & Uetz, 1996). Since BCI is known to show significant variation across years (Sardà-Palomera et al., 2011), we estimated BCI of a male by calculating a linear regression per year with data from all males captured that year (not only with the monitored males).

Statistical analyses were conducted in R 3.3.3 (R Core Team, 2017). Generalized linear models (GLMs) were fitted using the `glm()` function and constructed assuming a binomial error distribution with a logit link function or a Poisson error distribution with a log link function, depending on the nature of the response variable analysed. Models were tested for the presence of outliers, homoscedasticity, normality and overdispersion. Overdispersed models were recalculated assuming a quasibinomial or a quasi-Poisson error distribution. The significance of the factors studied was evaluated by an analysis of deviance with the function `Anova()` available in the package `car` (Fox & Weisberg, 2011). The test used for the analysis of deviance in non overdispersed models was a likelihood ratio test (chi-square test), while an *F* test was used in overdispersed

models. Since age has a significant effect on BCI in common quail (Sardà-Palomera et al., 2011), it was initially considered in all GLMs involving BCI. However, it did not have a significant effect in any of the models, so was discarded. We initially added brood too, as a factor to control for nonindependence of data in GLMs where males involved in the same brood were analysed. Since it did not have a significant effect, we removed it from the final models. For these reasons, coefficients given in the text are from models without age and brood as explanatory variables. Notation of the final models and their output can be found in the Supplementary Material.

Owing to different success in FFP monitoring and offspring genotyping, which broods were used in the analyses depended on the variables considered. Two broods (B9 and B13) were not included in the analyses involving monitoring since their radio transmitters did not work properly (analyses with starting day of the pair bond and pair bond duration as variables). As a quality measure, the male from brood B7 was excluded from analyses involving pair bond duration because the estimated time that he could have been paired had an exceedingly wide range (from 1 to 11 days, see Fig. S1 in the Supplementary Material). Brood B4 was excluded from analyses of the female mating system since it was a replacement clutch in which the male was paired with the female since long before the FFP started (8 days before at least), and we suspect that other factors related to the loss of the first clutch and not recorded in this study could be affecting this bond. Broods with less than 85% of embryos successfully genotyped were not included in analyses involving male fertilization success (broods B15, B16, B18, B20 and B21).

RESULTS

All 20 monitored females nested and laid eggs after their release (Table 1, Fig. S1 in the Supplementary Material). One of them laid a replacement brood that we also studied (B4) 22 days after the first one had been removed (B3). We could determine that in nine cases the released male and female established a pair bond for some days, while they did not in seven cases (unknown in the other four cases). Seven of these nine pairs produced offspring. The maximum number of eggs per brood was 13. The average number of eggs was 10.7 for the 17 complete first clutches (collected after the female had stopped laying eggs and incubation started) and excluding the replacement clutch. The percentage of fertilized eggs in the completely analysed broods (eight of these 17 clutches) was 97%.

All loci were confirmed to be very polymorphic, as expected. A total of 213 alleles were found. The number of alleles per marker ranged between 12 and 39 (mean + SE = 23.7 + 7.2) and the mean PIC was 0.89 (SE = 0.06). Expected heterozygosity (H_e) values ranged from 0.73 to 0.95 (mean + SE = 0.89 + 0.07), and observed heterozygosity (H_o) was practically identical (mean + SE = 0.89 + 0.06). About 91% of the 373 individuals studied were successfully genotyped for seven or more of the nine markers. Genotypes of four offspring were of low quality (fewer than five loci successfully genotyped) and were consequently discarded from the analyses. Genetic analyses confirmed that all females were mothers of their clutches (Table 1). Twenty-five males were identified as fathers. COLONY inferred the existence of four additional fathers that had not been trapped, adding to a total of 29 different fathers (sampled fathers + nonsampled fathers inferred by COLONY, per year: 9 + 1 in 1996, 6 + 0 in 1997, 5 + 1 in 1999, 3 + 1 in 2000 and 2 + 1 in 2001). Six males sired offspring in more than one brood (see Table 1).

Female Reproductive Behaviour and Genetic Mating System

We observed 21 pair bonds (Fig. S1 in the Supplementary Material). Although we failed to identify any pair bond with certainty

for one female, we observed between one and three for all the others. The duration of the pair bonds ranged from 1 to 10 days (mean + SE = 6.9 + 3.5, $N = 18$), although the maximum duration could be longer (up to 13 days) due to the time between monitoring attempts. In the case of the replacement brood, the male and female established a pair bond that lasted between 17 and 22 days, from the loss of the first brood until laying the first egg of the second brood. Pair bonds were observed to occur at any time during the FFP until about 4 days before incubation started (from 1 to 6 days, $N = 13$ females that were monitored during the days before incubation started), and represented between 5 and 46% of their fertile period (25% on average). In two cases (B6 and B10), the female remained unpaired at least 1 day between two successive pair bonds. The same could have happened in three other cases (B5, B18 and B19), while in two (B8 and B15) mate switching could have happened immediately after the first male left (monitoring limitations did not allow the detection of any period of time unpaired). When all eggs were laid, incubation started, and females remained unpaired. For the nine females that could be monitored during their entire fertile period (see Table 1), we inferred social monogamy (the female was observed paired with only one male) in seven cases and sequential social polygamy (the female was observed paired with several males in successive pair bonds) in two cases. All males that were observed in a pair bond sired offspring in the clutch, except for two males (first mates in broods B8 and B15) that paired but did not sire any offspring. That could be because not all the eggs of these two clutches could be genotyped.

Female genetic monogamy and polygamy were detected as well (one or several males genetically identified as fathers of the clutch). However, genetic results unveiled a larger proportion of genetically polygamous females than expected by social monitoring; two of the socially monogamous females monitored during their entire fertile period were genetically polygamous, and at least 12 of the 21 broods had more than one father. Still, this could be an underestimate because not all clutches could be completely genotyped (Table 1). Number of eggs and number and proportion of eggs fertilized did not differ between broods from genetically monogamous and polygamous females (number of eggs: chi-square test: $\chi^2_1 = 0.140$, $P = 0.709$; number of eggs fertilized: chi-square test: $\chi^2_1 = 0.504$, $P = 0.478$; proportion of eggs fertilized: F test: $F_{1,16} = 1.657$, $P = 0.261$; excluding clutches collected before the female started incubation).

We found that two or three siring males participated in multiple paternity broods. Two fathers were detected in 10 broods and three in two broods. We detected three different classes of fathers regarding their fertilization success per brood: low-siring fathers, with a minimum proportion of sired embryos ranging up to 22% (mean + SE = 12 + 8%, $N = 9$); medium-siring fathers, with 38–50% ($44 \pm 6\%$, $N = 3$) of the offspring sired by them; and high-siring fathers, with at least 82% (mean + SE = 93 + 6%, $N = 14$) of the brood sired.

The contribution of the fathers involved in the same multiple paternity brood was very unequal: one sired most of the clutch (main father). The main fathers sired 70% of the offspring in the broods with two fathers (on average, SE = 24, $N = 10$), reaching 83% in the clutches with more than 85% of the offspring genotyped (on average, SE = 15, $N = 7$). In the three fathered broods ($N = 2$), the main father sired 45% of the embryos.

Factors Associated with Female Genetic Monogamy or Polygamy

We expected that if the first pair bond was established late in the FFP, the female would have less time for mating afterwards and the chances of being genetically monogamous would be higher. However, our results were not conclusive: the first pair bond was

formed later in genetically monogamous than in polygamous females, but the difference was not significant (day-2 and -5 of the FFP, respectively; chi-square test: $\chi^2_1 = 3.268$, $P = 0.071$; Model 1 Supplementary Material). More data are needed to properly assess this hypothesis. Timing in relation to the FFP did not affect duration of the first pair bond ($\beta = 0.187$, SE = 0.175, $P = 0.313$; Model 2 Supplementary Material). Duration of the first pair bond was not significantly different between genetically monogamous and polygamous females (6.6 days; F test: $F_{1,10} = 0.441$, $P = 0.522$; Model 3 Supplementary Material). This suggests that the first partner did not reduce the probability that a female mated with other males by maximizing the duration of his pair bond. Interestingly, we found that first male partners of genetically polygamous females had significantly higher BCIs than those of genetically monogamous females (F test: $F_{1,9} = 12.836$, $P = 0.006$; Model 4 Supplementary Material, Fig. 1). This could imply that male partners with high BCI spend less time paired with the females, but we did not find a significant relationship between BCI of the first male partner and time paired with him ($\beta = -0.086$, SE = 0.073, $P = 0.272$; Model 5 Supplementary Material). Further research is needed to fully understand this relationship (see Discussion).

Contribution of the Different Fathers in Multiple Paternity Broods

Male identity seemed not to be linked to the proportion of the clutch that he sired. We detected that six males were fathers in more than one brood. One of them was the only father of the clutch twice (Table 1, male 3 in broods B2 and B3), two were the main father twice (male 5 in broods B5 and B6, and male 26 in broods B17 and B18), while three were main fathers in one of the broods but minority fathers in the other one (males 6, 12 and G4, in broods B5 and B7, B10 and B11, and B19 and B20, respectively). Of the latter, in two cases the father sired first a large number of offspring in one clutch and a smaller number in a later one, while the situation was the reverse for the other male. This suggests that participation in single or multiple paternity broods may be context dependent, not individually fixed.

Although it was not always possible to determine which male was paired first or last with a female, the main father of a brood was not necessarily either the first mate (it was in three cases but not in the other four) or the last (it was in four cases but probably not in two other cases). So, being either the first or the last that copulated with a female would not guarantee siring most of the clutch.

Since fertilization success did not seem to depend on mating order, we investigated whether it was related to the duration of the

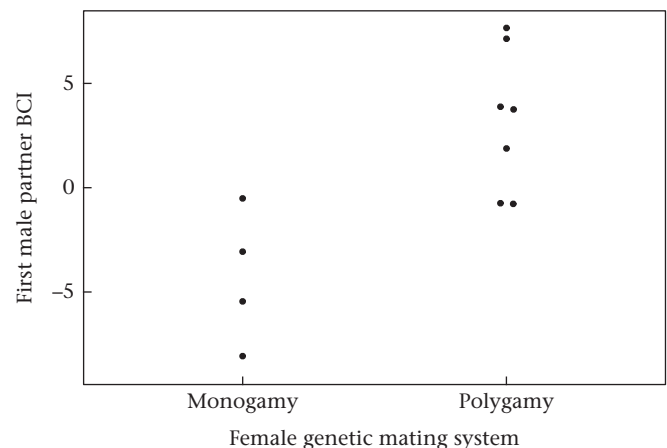


Figure 1. Body condition index (BCI) of first male partners for genetically monogamous females (only one male sired their broods) and for genetically polygamous females (several males sired their broods).

pair bond. Pair bond duration did not have an overall significant effect on male fertilization success when we analysed all the data together ($\beta = 4.005$, $SE = 2.372$, $P = 0.117$; Model 6 [Supplementary Material, Fig. 2a](#)). Short pair bonds could result in both high and low siring proportions, but low-siring fathers guarded the female for a short time, between 10.5 and 20% of the FFP (mean + SE = 14.9% + 4.8, $N = 3$). This was significantly shorter than the duration for medium-siring fathers (mean + SE = 69 + 22.6%, $N = 2$; $\beta = 2.515$, $SE = 1.020$, $P = 0.031$; Model 7 [Supplementary Material](#)). Pair bond duration for high-siring fathers was more variable, from 14 to 100% of the FFP (mean + SE = 50 + 27%, $N = 9$). Importantly, when

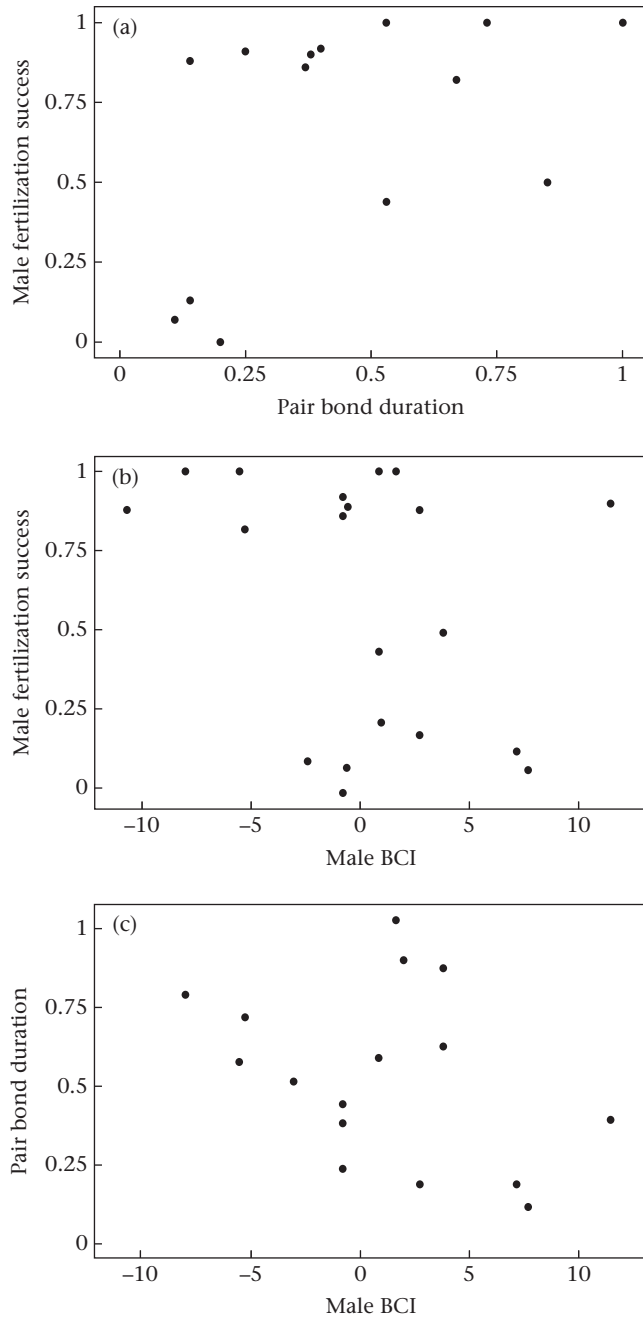


Figure 2. (a) Male fertilization success (minimum proportion of fertilized embryos) in relation to pair bond duration (proportion of the female fertilization period, FFP, they were paired with the female). (b) Male fertilization success (minimum proportion of fertilized embryos) in relation to the male's body condition index (BCI). (c) Pair bond duration (proportion of the FFP paired with the female) in relation to male BCI.

comparing fathers involved in the same brood, in all cases the male that sired more offspring was the one that established the longer pair bond with the female ($N = 9$ multiple paternity broods). These results suggest that fertilization success would not depend on how long the male guarded the female, but on the relative time the different males were paired with her. Comparing males involved in the same brood, the male that established the longest pair bond was not always the first partner; it was in three cases but not in two others (we could not determine it for seven broods).

Male BCI did not show a significant effect on male fertilization success ($\beta = -0.133$, $SE = 0.080$, $P = 0.112$; Model 8 [Supplementary Material, Fig. 2b](#)). To the contrary, when comparing fathers of the same brood, the main father was the one with the lowest BCI in most cases (five of six broods). BCI did not show a significant effect on the duration of the pair bond when analysing all data together ($\beta = -0.076$, $SE = 0.055$, $P = 0.188$; Model 9 [Supplementary Material, Fig. 2c](#)), but when comparing males involved in the same brood, the highest BCI male was the one that spent the shortest time paired with the female in four of five cases. However, the small sample size urges caution when interpreting this result. In addition, the highest BCI male could be the first or the last one paired with the female ($N = 2$ and 3, respectively; it could not be determined for two broods). Our data set is too small to infer whether females did establish sequential pair bonds based on male BCI or not.

DISCUSSION

Avian mating systems can range from strictest monogamy to extensive polygamy ([Birkhead & Møller, 1992](#)). In species with sperm storage capacity, sequential polygamy can be beneficial from an evolutionary point of view, since it can increase fertilization success and offspring genetic variability ([Adkins-Regan, 2015](#)). In the case of female common quail, we observed cases of social and genetic monogamy and cases of social and genetic sequential polygamy during one breeding attempt. Genetic polygamy was very frequent among females (even more than social polygamy detected by means of behavioural monitoring), which sequentially established temporary pair bonds and mated with multiple males (usually two) during one breeding attempt. Even though our monitoring efforts were not aimed at this, we also detected social and genetic sequential polygamy among males.

Female Mating System

Body condition (BCI) of the first partner affected the female mating system. Females that established their first pair bond and mated with high BCI males tended to mate later with other males during the same breeding attempt. We explored whether this was because higher BCI males spent less time in the pair bond and so females would have more time to look for other partners while still fertile, but our data were too limited to properly evaluate this hypothesis.

Duration of first pair bonds did not differ between genetically monogamous and polygamous females. Thus, long first pair bonds did not prevent females from mating again. We did not find conclusive differences in the timing of the first pair bond in relation to the FFP between genetically monogamous and polygamous females. More data are needed to disentangle whether early first pair bonds favour females mating with other males.

The female mating system can depend also on external factors not studied here, such as the sex ratio of the reproductive population. An adult sex ratio biased towards males favours female genetic polygamy, since males may compete for a smaller number of females ([Birkhead & Møller, 1992](#); [Harts & Kokko, 2013](#); [Richardson](#)

& Burke, 2001). In common quail, the sex ratio tends to be biased towards males at higher latitudes. Males move sooner to higher latitude breeding grounds, looking for new mates, while females stay longer in the same location where mating occurred, incubating and taking care of the offspring. Therefore, we could expect more genetically polygamous females in northern than in southern latitudes.

Male Fertilization Success

Sperm storage and postcopulatory sexual selection have previously been detected in quail (Adkins-Regan, 1995; Birkhead & Fletcher, 1994; Sanchez-Donoso et al., 2016; Sittmann & Abplanalp, 1965). In Japanese quail, fertilization success from a single copulation is low and multiple successful inseminations are required to guarantee fertilization of an entire clutch (Adkins-Regan, 2015). Previous findings showed that common quail sperm could be kept viable in the female sexual tract for about 6 days (Sanchez-Donoso et al., 2016). This may not be long enough to fertilize entire clutches of an average size of 10–11 eggs (Gallego et al., 1993, and this study). Thus, several copulations may be necessary to reach high rates of fertilization. Since pair bonds could foster more opportunities for copulation, pair bonds lasting for several days are likely to favour the successful fertilization of a high proportion of the clutch. The timing of the end of mate guarding varies between bird species; in some species it ends when egg laying starts (Arvidsson, 1992) while in others it continues during the egg-laying period (Birkhead, 1982). In species with no paternal care of the offspring, like the common quail, the costs of mate guarding may exceed the benefits when fertilization of the entire clutch is ensured. In our population, pair bonds lasted until some days before the last egg was laid (4 days, on average), suggesting that at that point females had enough sperm for fertilizing all the remaining ova (egg fertilization was observed before and during clutch laying, as in the Japanese quail; Adkins-Regan, 1995).

Our results indicate that male fertilization success is not an individual trait, but it is context dependent, since the same male could sire most of the brood in one clutch but a small proportion in another. Male fertilization success was determined by the duration of the pair bond in relation to the other mates' pair bond duration. Pair bond order did not affect fertilization success. This is consistent with previous findings in captivity that suggested that last-male sperm precedence does not occur in this species (Sanchez-Donoso et al., 2016). Instead, the 'sperm loading' hypothesis (Dickinson, 1986; Parker & Simmons, 1991; Simmons & Parker, 1992) is supported by our results. We hypothesize that mate guarding facilitates copulation in the common quail, increasing the amount of sperm stored in the female's oviduct. When a second male mates with the same female, the sperm of the new partner starts increasing in the sperm storage tubules in relation to the first male's sperm. Thus, the first male's fertilization success declines, probably due to passive sperm loss (Birkhead & Biggins, 1998; Birkhead & Fletcher, 1994; Lessells & Birkhead, 1990), decrease in sperm viability and competition with the overrepresented sperm from the second male (Birkhead & Pizzari, 2002). Males from several taxa can assess female fertility or mating status and the level of sperm competition they face, and adjust their reproductive behaviour accordingly, for example courtship and mate guarding, copulation duration, quantity of sperm transferred (reviewed in Wedell, Gage, & Parker, 2002). Further research is needed to disentangle whether quail males could discriminate the female's mating history and adjust their pairing and mating behaviour accordingly, to maximize their fertilization success while minimizing the time paired.

Fertilization success could also be increased by protecting the female against copulations with other males through mate guarding, but several aspects of common quail biology indicate that the 'rival chasing' hypothesis cannot explain fertilization success as efficiently as the 'sperm loading' hypothesis. (1) As indicated before, several ejaculates are most probably needed to ensure the fertilization of the entire clutch, as in the Japanese quail (Adkins-Regan, 2015). A male could increase the number of copulations if he keeps close to the female in a pair bond relationship. (2) Being paired could foster fertility through hormonal responses. Testosterone levels (related to sperm production) in Japanese quail males increase when they spend a prolonged time near a female (Delville, Sulon, Hendrick, & Balthazart, 1984). (3) Frequent copulation is often the only putative paternity protection in bird species where males are unable to guard their mates (Møller & Birkhead, 1991). In common quail, pair bonds are temporary and do not last for the whole FFP, so the male partner does not guard his paternity for all that time. The paired males' strategy is probably based on loading as much sperm as possible while still paired. (4) Females are very cryptic and hardly detectable by males if they do not actively approach the males and produce subtle calls in answer to the loud and frequent male calls. The reduced visibility inside cereal crops makes calling the main form of detection among individuals. Thus, encounters between single males and paired females could hardly happen if females do not want to be detected. Owing to the costs that pairing entails, we expect that a paired female would look for another partner probably only if the calling male seems better than the partner (calling is a proxy of male condition; Puigserver, Rodríguez-Teijeiro, Zijlstra, Bonet, & Gallego, 1999) and with the aim of having an extrapair copulation or switching mates. In this case, the partner may be unable to defend his pair bond against the intruder because male–male encounters tend to be resolved in favour of the best BCI male (Rodrigo-Rueda et al., 1997) and females tend to be more receptive to inseminations from the male that they prefer (Persaud & Galef, 2005b). In summary, chasing rivals does not seem to be the reason for mate guarding when the rivals are in better body condition and females prefer to interact with high BCI males.

Although previous studies pointed to the importance of body condition for reproductive performance (e.g. Chastel et al., 1995), we did not find a relationship between male BCI and fertilization success nor an obvious effect of BCI on pair bond duration. However, when comparing partners of the same female, our results seemed to indicate that the highest BCI partner was the one that spent less time paired (four of five cases) and sired fewer offspring (five of six cases). Although this relationship must be considered with caution due to the small sample size, it suggests that BCI would have an indirect negative effect on male fertilization success through a minimized pair bond duration. Even though that could seem an evolutionary paradox, it is not necessarily so. First, BCI should not be interpreted as an absolute male feature but as a relative measure of attractiveness compared to the rest of the male population. Although we might rank the males present in an area at a given time based on their BCI, the rank of a male can be highly dynamic during the breeding season due to the continual changes in the composition of the male population. This can translate into changes in a male's relative attractiveness to females. This could explain why the comparison of BCI values of all the males monitored during several breeding seasons did not reflect a relationship with either fertilization success or pair bond duration, while comparing the BCI of the males that participated in siring the same brood has more sense from a biological point of view. Second, and perhaps more important, fertilization success in one clutch is not the same as the lifetime reproductive success (fitness) of a male, which could include other clutches in the same or in other breeding

grounds, during one or multiple breeding seasons (Rodríguez-Teijeiro et al., 1992). A meta-analysis performed by Harts, Booksmythe, and Jennions (2016) showed that high-quality avian males (assessed by various measures of male quality) were under selection to use a less protective strategy, since they spent significantly less time guarding their mates but copulated more frequently. These authors also hypothesized that while low-quality males might mate-guard intensively because they are unlikely to gain paternity elsewhere (Kempnaers, Verheyen, & Dhondt, 1995), high-quality males would engage in more matings and might lose paternity in a clutch, but still have a higher total offspring count by siring offspring in other clutches (Balenger, Johnson, & Masters, 2009; Cleasby & Nakagawa, 2012; Webster, Pruett-Jones, Westneat, & Arnold, 1995). Our results do not allow us to determine whether higher BCI males have more opportunities to father other clutches, but we hypothesize that this could be the case. High BCI males are more attractive to females (females are attracted by groups of males, where high BCI males aggregate; Sardà-Palomer et al., 2011). Thus, we expect that these males could establish more pair bonds and mate more times during the breeding season than low BCI males. In this scenario, high BCI males would spread their offspring across different nests, reducing the risk of losing all offspring if the nest is lost (e.g. by predation of the nest or the female, loss of the nest or habitat during harvesting, adverse meteorological conditions, etc.). In addition, mating with multiple females enhances the genetic diversity of the progeny, potentially increasing the overall fitness of high BCI males. Monitoring of the reproductive behaviour of males during their entire life would be necessary to understand the role of BCI from an evolutionary point of view.

Conclusions

The common quail mating system is flexible, with short-term pair bonds and mate switching. This is very different from the mating system of most songbirds and of other galliforms (Bennett & Owens, 2002). Our results showed that both genetic and social monogamy and polygamy occur among female common quail during a single breeding attempt. Social and genetic polygamy occur also among males. Female genetic polygamy was more frequent in females that first paired with males in good body condition. The relative pair bond duration in comparison to the duration of the pair bonds of the other partners of the same female was the main factor determining male fertilization success. This study can help to interpret the results from experimental studies on reproductive behaviour and learning of the common and Japanese quails and also adds to our understanding of the diversity of avian mating systems.

Acknowledgments

We are most grateful to the Pons family for kindly allowing us to do research on their property; S. Gallego, E. Pérez-Masdeu, F.J. Rodrigo-Rueda, I. Hernández, V. Bonet-Arbolí and A. Barroso for technical assistance in the field; J. Echegaray, J.A. Leonard and V. Muñoz-Fuentes for support during the laboratory work; J.A. Leonard also for reviewing the English text; the members of the Conservation and Evolutionary Genetics group at the Doñana Biological Station, three referees and the Editor for comments and suggestions that improved the manuscript. The Spanish Government ('Secretaría de Estado de Universidades e Investigación') provided financial support (PB93-0810, BOS2000-0564-CO2-01). The Catalan Government ('Generalitat de Catalunya') also provided financial support in 2000 and supported the research team (1995SGR-0019, 1997SGR00158, 1999SGR00019 and 2001SGR00091).

Supplementary Material

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.anbehav.2017.12.012>.

References

- Adkins-Regan, E. (1995). Predictors of fertilization in the Japanese quail, *Coturnix japonica*. *Animal Behaviour*, 50(5), 1405–1415.
- Adkins-Regan, E. (2015). Hit or miss: Fertilization outcomes of natural inseminations by Japanese quail. *PLoS One*, 10(7), e0131786. <https://doi.org/10.1371/journal.pone.0131786>.
- Arnqvist, G., & Nilsson, T. (2000). The evolution of polyandry: Multiple mating and female fitness in insects. *Animal Behaviour*, 60(2), 145–164. <https://doi.org/10.1006/anbe.2000.1446>.
- Arvidsson, B. L. (1992). Copulation and mate guarding in the willow warbler. *Animal Behaviour*, 43(3), 501–509. [https://doi.org/10.1016/S0003-3472\(05\)80108-3](https://doi.org/10.1016/S0003-3472(05)80108-3).
- Balenger, S. L., Johnson, L. S., & Masters, B. S. (2009). Sexual selection in a socially monogamous bird: Male color predicts paternity success in the mountain bluebird, *Sialia currucoides*. *Behavioral Ecology and Sociobiology*, 63, 403–411. <https://doi.org/10.1007/s00265-008-0674-5>.
- Bennett, P. M., & Owens, I. P. F. (2002). *Evolutionary ecology of birds: Life histories, mating systems, and extinction*. Oxford, U.K.: Oxford University Press.
- Birkhead, T. R., & Pizzari, T. (2002). Postcopulatory sexual selection. *Nature Reviews Genetics*, 3, 262–273. <https://doi.org/10.1038/nrg774>.
- Birkhead, T. R. (1982). Timing and duration of mate guarding in magpies, *Pica pica*. *Animal Behaviour*, 30(1), 277–283. [https://doi.org/10.1016/S0003-3472\(82\)80264-9](https://doi.org/10.1016/S0003-3472(82)80264-9).
- Birkhead, T. R. (1998). Cryptic female choice: Criteria for establishing female sperm choice. *Evolution*, 52(4), 1212–1218. <https://doi.org/10.2307/2411251>.
- Birkhead, T. R., & Biggins, J. D. (1998). Sperm competition mechanisms in birds: Models and data. *Behavioral Ecology*, 9(3), 253–260. <https://doi.org/10.1093/beheco/9.3.253>.
- Birkhead, T. R., & Fletcher, F. (1994). Sperm storage and the release of sperm from the sperm storage tubules in Japanese Quail *Coturnix japonica*. *Ibis*, 136(1), 101–105. <https://doi.org/10.1111/j.1474-919X.1994.tb08137.x>.
- Birkhead, T. R., & Møller, A. P. (1992). *Sperm Competition in Birds. Evolutionary Causes and Consequences*. New York, NY: Academic Press.
- Birkhead, T. R., & Møller, A. P. (1993). Sexual selection and the temporal separation of reproductive events: Sperm storage data from reptiles, birds and mammals. *Biological Journal of the Linnean Society*, 50(4), 295–311. <https://doi.org/10.1111/j.1095-8312.1993.tb00933.x>.
- Birkhead, T. R., & Parker, G. A. (1997). Sperm competition and mating systems. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural Ecology: An Evolutionary Approach*. U.K.: Blackwell: Oxford.
- Le Boeuf, B. J., & Mesnick, S. L. (1991). Social behavior of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour*, 116(1), 143–162. <https://doi.org/10.1163/156853990X00400>.
- Botstein, D., White, R. L., Skolnick, M., & Davis, R. W. (1980). Construction of a genetic linkage map in man using restriction fragment length polymorphisms. *American Journal of Human Genetics*, 32(3), 314–331. Retrieved from: <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1686077/>.
- Briskie, J. V. (1996). Spatiotemporal patterns of sperm storage and last-male sperm precedence in birds. *Functional Ecology*, 10(3), 375–383. <https://doi.org/10.2307/2390286>.
- Byers, B. E., Akresh, M. E., & King, D. I. (2016). Song and male quality in prairie warblers. *Ethology*, 122(8), 660–670. <https://doi.org/10.1111/eth.12513>.
- Cézilly, F., Préalut, M., Dubois, F., Faivre, B., & Patris, B. (2000). Pair-bonding in birds and the active role of females: A critical review of the empirical evidence. *Behavioural Processes*, 51(1–3), 83–92. [https://doi.org/10.1016/S0376-6357\(00\)00120-0](https://doi.org/10.1016/S0376-6357(00)00120-0).
- Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Body condition and seabird reproductive performance: A study of three petrel species. *Ecology*, 76(7), 2240–2246. <https://doi.org/10.2307/1941698>.
- Cleasby, I. R., & Nakagawa, S. (2012). The influence of male age on within-pair and extra-pair paternity in passerines. *Ibis*, 154(2), 318–324. <https://doi.org/10.1111/j.1474-919X.2011.01209.x>.
- Cooper, W. E., & Vitt, L. J. (2002). Increased predation risk while mate guarding as a cost of reproduction for male broad-headed skinks (*Eumeces laticeps*). *Acta Ethologica*, 5(1), 19–23. <https://doi.org/10.1007/s10211-002-0058-1>.
- Cornil, C. A., & Ball, G. F. (2010). Effects of social experience on subsequent sexual performance in naïve male Japanese quail (*Coturnix japonica*). *Hormones and Behavior*, 57(4–5), 515–522. <https://doi.org/10.1016/j.yhbeh.2010.02.010>.
- Correa, S. M., Horan, C. M., Johnson, P. A., & Adkins-Regan, E. (2011). Copulatory behaviors and body condition predict post-mating female hormone concentrations, fertilization success, and primary sex ratios in Japanese quail. *Hormones and Behavior*, 59(4), 556–564. <https://doi.org/10.1016/j.yhbeh.2011.02.009>.
- Cramp, S., & Simmons, K. E. L. (1980). *Handbook of the Birds of Europe, the Middle East and North Africa* (vol. 2). Oxford, U.K.: Oxford University Press.
- Cuthill, I. (1991). Field experiments in animal behaviour: Methods and ethics. *Animal Behaviour*, 42(6), 1007–1014. [https://doi.org/10.1016/S0003-3472\(05\)80153-8](https://doi.org/10.1016/S0003-3472(05)80153-8).
- Danchin, E., Giraldeau, L. A., & Cézilly, F. (2008). *Behavioural ecology*. Oxford, U.K.: Oxford University Press.

- Dean, R., Nakagawa, S., & Pizzari, T. (2011). The risk and intensity of sperm ejection in female birds. *American Naturalist*, 178(3). <https://doi.org/10.1086/661244>.
- Delville, Y., Sulon, J., Hendrick, J. C., & Balthazard, J. (1984). Effect of the presence of females on the pituitary-testicular activity in male Japanese quail (*Coturnix coturnix japonica*). *General and Comparative Endocrinology*, 55(2), 295–305. [https://doi.org/10.1016/0016-6480\(84\)90115-1](https://doi.org/10.1016/0016-6480(84)90115-1).
- Dickinson, J. L. (1986). Prolonged mating in the milkweed leaf beetle *Labidomera divicollis clivicollis* (Coleoptera: Chrysomelidae): A test of the sperm loading hypothesis. *Behavioral Ecology and Sociobiology*, 18(5), 331–338. <https://doi.org/10.1007/BF00299664>.
- Dickinson, J. L. (1995). Trade-offs between post-copulatory riding and mate location in the blue milkweed beetle. *Behavioral Ecology*, 6(3), 280–286. <https://doi.org/10.1093/beheco/6.3.280>.
- Domjan, M., Mahometa, M. J., & Mills, A. D. (2003). Relative contributions of the male and the female to sexual behavior and reproductive success in the Japanese quail (*Coturnix japonica*). *Journal of Comparative Psychology*, 117(4), 391–399. <https://doi.org/10.1037/0735-7036.117.4.391>.
- Eberhard, W. G. (2009). Postcopulatory sexual selection: Darwin's omission and its consequences. *Proceedings of the National Academy of Sciences of the United States of America*, 106(Suppl 1), 10025–10032. <https://doi.org/10.1073/pnas.0901217106>.
- Forstmeier, W. (2002). Factors contributing to male mating success in the polygynous dusky warbler (*Phylloscopus fuscatus*). *Behaviour*, 139(10), 1361–1381. <https://doi.org/10.1163/156853902321104208>.
- Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (2nd ed.). Thousand Oaks, CA: Sage.
- Fryer, T., Cannings, C., & Vickers, G. T. (1999). Sperm competition. II-Post-copulatory guarding. *Journal of Theoretical Biology*, 197(3), 343–360. <https://doi.org/10.1006/jtbi.1998.0879>.
- Gallego, S., Puigcerver, M., Rodríguez-Teijeiro, J. D., Rodrigo-Rueda, F. J., & Roldán, G. (1993). Algunos aspectos fenológicos y de la biología de la reproducción de la codorniz (*Coturnix coturnix*) en Cataluña (España). *Historia Animalium*, 2, 125–136.
- Gallego, S., Puigcerver, M., & Rodríguez-Teijeiro, J. D. (1997). Quail *Coturnix coturnix*. In W. J. M. Hagemeijer, & M. J. Blair (Eds.), *The EBCC atlas of European breeding birds: their distribution and abundance* (pp. 214–215). London, U.K.: Poyser.
- Glütz Von Blotzheim, U. N., Bauer, K. M., & Bezzel, E. (1973). *Handbuch der Vögel Mitteleuropas*. Akademische Verlagsgesellschaft. Frankfurt am main. Germany: Aula-Verlag.
- Guyomarc'h, J. C., Combreau, O., Puigcerver, M., Fontoura, P. A., & Aebischer, N. J. (1998). *Coturnix coturnix* quail. In E. Olgiwie (Ed.), *Birds of the western Palaearctic. Update 2* (pp. 27–46). Oxford, U.K.: Oxford University Press.
- Hagelin, J. C. (2002). The kinds of traits involved in male–male competition: A comparison of plumage, behavior, and body size in quail. *Behavioral Ecology*, 13(1), 32–41. <https://doi.org/10.1093/beheco/13.1.32>.
- Harts, A. M. F., Booksmythe, I., & Jennions, M. D. (2016). Mate guarding and frequent copulation in birds: A meta-analysis of their relationship to paternity and male phenotype. *Evolution*, 70(12), 2789–2808. <https://doi.org/10.1111/evo.13081>.
- Harts, A. M. F., & Kokko, H. (2013). Understanding promiscuity: When is seeking additional mates better than guarding an already found one? *Evolution*, 67(10), 2838–2848. <https://doi.org/10.1111/evo.12163>.
- Hasselquist, D., Bensch, S., & vonSchantz, T. (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, 381(6579), 229–232. <https://doi.org/10.1038/381229a0>.
- Higaki, K., Yoshimura, Y., Tamura, T., & Okamoto, T. (1995). Localization of spermatozoa and leukocytes in vagina and uterovaginal junction after copulation in Japanese quail (*Coturnix coturnix japonica*). *Japanese poultry science*, 32(6), 387–393. <https://doi.org/10.2141/jpsa.32.387>.
- Hinde, R. A. (1964). Pair formation. In A. L. Thomson (Ed.), *A New Dictionary of Birds* (p. 928). London, U.K.: Thomas Nelson.
- Hosken, D. J., & Stockley, P. (2003). Benefits of polyandry: A life history perspective. In R. J. Macintyre, & M. T. Clegg (Eds.), *Evolutionary Biology* (vol. 33). Boston, MA: Springer. https://doi.org/10.1007/978-1-4757-5190-1_4.
- Jakob, E. M., Marshall, S. D., & Uetz, G. W. (1996). Estimating fitness: A comparison of body condition indices. *Oikos*, 77(1), 61–67. <https://doi.org/10.2307/3545585>.
- Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews*, 75(1), 21–64. <https://doi.org/10.1111/j.1469-185X.1999.tb00040.x>.
- Jones, O., & Wang, J. (2009). COLONY: A program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources*, 10(3), 551–555. <https://doi.org/10.1111/j.1755-0998.2009.02787.x>.
- Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16(5), 1099–1106. <https://doi.org/10.1111/j.1365-294X.2007.03089.x>.
- Kayang, B. B., Inoue-Murayama, M., Hoshi, T., Matsuo, K., Takahashi, H., Minezawa, M., et al. (2002). Microsatellite loci in Japanese quail and cross-species amplification in chicken and Guinea fowl. *Genetics Selection Evolution*, 34(2), 233–253. <https://doi.org/10.1186/1297-9686-34-2-233>.
- Kayang, B. B., Inoue-Murayama, M., Nomura, A., Kimura, K., Takahashi, H., Mizutani, M., et al. (2000). Fifty microsatellite markers for Japanese quail. *Journal of Heredity*, 91(6), 502–505. <https://doi.org/10.1093/jhered/91.6.502>.
- Kempnaers, B. (2007). Mate choice and genetic quality: A review of the heterozygosity theory. *Advances in the Study of Behavior*, 37, 189–278. [https://doi.org/10.1016/S0065-3454\(07\)37005-8](https://doi.org/10.1016/S0065-3454(07)37005-8).
- Kempnaers, B., Verheyen, G. R., & Dhondt, A. A. (1995). Mate guarding and copulation behaviour in monogamous and polygynous blue tits: Do males follow a best-of-a-bad-job strategy? *Behavioral Ecology and Sociobiology*, 36(1), 33–42. <https://doi.org/10.1007/BF00175726>.
- Kempnaers, B., Verheyen, G. R., & Dhondt, A. A. (1997). Extrapair paternity in the blue tit (*Parus caeruleus*): Female choice, male characteristics, and offspring quality. *Behavioral Ecology*, 8(5), 481–492. <https://doi.org/10.1093/beheco/8.5.481>.
- Kenward, R. E. (1987). *Wildlife Radio Tagging. Equipment, Field Techniques and Data Analysis*. London, U.K.: Academic Press.
- Labocha, M. K., & Hayes, J. P. (2012). Morphometric indices of body condition in birds: A review. *Journal of Ornithology*, 153(1), 1–22. <https://doi.org/10.1007/s10336-011-0706-1>.
- Lessells, C. M., & Birkhead, T. R. (1990). Mechanisms of sperm competition in birds: Mathematical models. *Behavioral Ecology and Sociobiology*, 27(5), 325–337. <https://doi.org/10.1007/BF00164003>.
- Lormée, H., Jouvantin, P., Trouve, C., & Chastel, O. (2003). Sex-specific patterns in baseline corticosterone and body condition changes in breeding Red-footed Boobies *Sula sula*. *Ibis*, 145(2), 212–219. <https://doi.org/10.1046/j.1474-919X.2003.00106.x>.
- Møller, A. P., & Birkhead, T. R. (1991). Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour*, 118(3), 170–186.
- Morales, M. B., Alonso, J. C., Martín, C., Martín, E., & Alonso, J. (2003). Male sexual display and attractiveness in the great bustard *Otis tarda*: The role of body condition. *Journal of Ethology*, 21(1), 51–56. <https://doi.org/10.1007/s10164-002-0076-5>.
- Mougeot, F., & Bretagnolle, V. (2000). Predation as a cost of sexual communication in nocturnal seabirds: An experimental approach using acoustic signals. *Animal Behaviour*, 60(5), 647–656. <https://doi.org/10.1006/anbe.2000.1491>.
- Nei, M. (1987). *Molecular Evolutionary Genetics*. New York, NY: Columbia University Press.
- Parker, G. A., & Birkhead, T. R. (2013). Polyandry: The history of a revolution. *Philosophical Transactions of the Royal Society of London – B: Biological Sciences*, 368(1613), 20120335. <https://doi.org/10.1098/rstb.2012.0335>.
- Parker, G. A., & Simmons, L. W. (1991). A model of constant random sperm displacement during mating: evidence from Scatophaga. *Proceedings of the Royal Society of London B: Biological Sciences*, 246(1316), 107–115. <https://doi.org/10.1098/rspb.1991.0131>.
- Persaud, K. N., & Galef, B. G. (2005a). Female Japanese quail (*Coturnix japonica*) mated with males that harassed them are unlikely to lay fertilized eggs. *Journal of Comparative Psychology*, 119(4), 440–446. <https://doi.org/10.1037/0735-7036.119.4.440>.
- Persaud, K. N., & Galef, B. G. (2005b). Eggs of a female Japanese quail are more likely to be fertilized by a male that she prefers. *Journal of Comparative Psychology*, 119(3), 251–256. <https://doi.org/10.1037/0735-7036.119.3.251>.
- Puigcerver, M. (1990). *Contribución al conocimiento de la biología y ecología de la codorniz (Coturnix c. coturnix) (Doctoral dissertation)*. Barcelona, Spain: Universitat de Barcelona.
- Puigcerver, M., Rodrigo-Rueda, F. J., Rodríguez-Teijeiro, J. D., & Gallego, S. (1997). On the second clutches in the common quail (*Coturnix coturnix*). *Gibier Faune Sauvage, Game Wildlife*, 14(4), 617–622.
- Puigcerver, M., Rodríguez-Teijeiro, J. D., Zijlstra, W., Bonet, V., & Gallego, S. (1999). Indicators of male quality in the call of the common quail *Coturnix coturnix*. *Hungarian Small Game Bulletin*, 5, 119–128.
- Puigcerver, M., Sanchez-Donoso, I., Vilà, C., Sardà-Palomera, F., García-Galea, E., & Rodríguez-Teijeiro, J. D. (2014). Decreased fitness of restocked hybrid quails prevents fast admixture with wild European quails. *Biological Conservation*, 171, 74–81. <https://doi.org/10.1016/j.biocon.2014.01.010>.
- R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org>.
- Reding, L. (2015). Increased hatching success as a direct benefit of polyandry in birds. *Evolution*, 69(1), 264–270. <https://doi.org/10.1111/evo.12553>.
- Reynolds, J. D. (1996). Animal breeding systems. *Trends in Ecology & Evolution*, 11(2), 68–72. [https://doi.org/10.1016/0169-5347\(96\)81045-7](https://doi.org/10.1016/0169-5347(96)81045-7).
- Richardson, D. S., & Burke, T. (2001). Extrapair paternity and variance in reproductive success related to breeding density in Bullock's orioles. *Animal Behaviour*, 62(3), 519–525. <https://doi.org/10.1006/anbe.2001.1778>.
- Rodrigo-Rueda, F. J., Rodríguez-Teijeiro, J. D., Puigcerver, M., & Gallego, S. (1997). Mate switching in a non-monogamous species? The case of the common quail (*Coturnix coturnix*). *Ethology*, 103(5), 335–364. <https://doi.org/10.1111/j.1439-0310.1997.tb00151.x>.
- Rodríguez-Teijeiro, J. D., Barroso, A., Gallego, S., Puigcerver, M., & Vinyoles, D. (2006). Orientation-cage experiments with the European Quail during the breeding season and autumn migration. *Canadian Journal of Zoology*, 84(6), 887–894. <https://doi.org/10.1139/Z06-070>.
- Rodríguez-Teijeiro, J. D., Puigcerver, M., & Gallego, S. (1992). Mating strategy in the European quail (*Coturnix c. coturnix*) revealed by male population density and sex ratio in Catalonia (Spain). *Gibier Faune Sauvage*, 9, 377–386.
- Rodríguez-Teijeiro, J. D., Puigcerver, M., Gallego, S., Cordero, P. J., & Parkin, D. T. (2003). Pair bonding and multiple paternity in the polygamous Common quail *Coturnix coturnix*. *Ethology*, 109(4), 291–302. <https://doi.org/10.1046/j.1439-0310.2003.00873.x>.
- Rodríguez-Teijeiro, J. D., Sardà-Palomera, F., Nadal, J., Ferrer, X., Ponz, C., & Puigcerver, M. (2009). The effects of mowing and agricultural landscape

- management on population movements of the common quail. *Journal of Biogeography*, 36(10), 1891–1898. <https://doi.org/10.1111/j.1365-2699.2009.02109.x>.
- Sanchez-Donoso, I., Huisman, J., Echegaray, J., Puigcerver, M., Rodríguez-Teijeiro, J. D., Hailer, F., et al. (2014). Detecting slow introgression of invasive alleles in an extensively restocked game bird. *Frontiers in Ecology and Evolution*, 2(April), 0–14. <https://doi.org/10.3389/fevo.2014.00015>.
- Sanchez-Donoso, I., Morales-Rodríguez, P. A., Puigcerver, M., Caballero de la Calle, J. R., Vilà, C., & Rodríguez-Teijeiro, J. D. (2016). Postcopulatory sexual selection favors fertilization success of restocking hybrid quails over native Common quails (*Coturnix coturnix*). *Journal of Ornithology*, 157(1), 33–42. <https://doi.org/10.1007/s10336-015-1242-1>.
- Sanchez-Donoso, I., Vilà, C., Puigcerver, M., Butkauskas, D., Caballero de la Calle, J. R., Morales-Rodríguez, P. A., et al. (2012). Are farm-reared quails for game restocking really common quails (*Coturnix coturnix*): a genetic approach. *PLoS One*, 7(6), e39031. <https://doi.org/10.1371/journal.pone.0039031>.
- Sardà-Palomera, F., Puigcerver, M., Vinyoles, D., & Rodríguez-Teijeiro, J. D. (2011). Exploring male and female preferences, male body condition, and pair bonds in the evolution of male sexual aggregation: The case of the common quail (*Coturnix coturnix*). *Canadian Journal of Zoology*, 89(4), 325–333. <https://doi.org/10.1139/Z11-005>.
- Sheldon, B. (1994). Sexually transmitted diseases in birds: Occurrence and evolutionary significance. *Philosophical Transactions of the Royal Society of London – B: Biological Sciences*, 339(1290), 491–497. <https://doi.org/10.1098/rstb.1993.0044>.
- Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies*. Princeton, NJ: Princeton University Press.
- Simmons, L. W., & Parker, G. A. (1992). Individual variation in sperm competition success of yellow dungflies, *Scatophaga stercoraria*. *Evolution*, 46(2), 366–375. <https://doi.org/10.2307/2409857>.
- Sittmann, K., & Abplanalp, H. (1965). Duration and recovery of fertility in Japanese quail (*Coturnix coturnix japonica*). *British Poultry Science*, 6, 245–250. <https://doi.org/10.1080/00071666508415580>.
- Slatyer, R. A., Mautz, B. S., Backwell, P. R. Y., & Jennions, M. D. (2012). Estimating genetic benefits of polyandry from experimental studies: A meta-analysis. *Biological Reviews*, 87(1), 1–33. <https://doi.org/10.1111/j.1469-185X.2011.00182.x>.
- Snook, R. R. (2005). Sperm in competition: Not playing by the numbers. *Trends in Ecology & Evolution*, 20(1), 46–53. <https://doi.org/10.1016/j.tree.2004.10.011>.
- Verheyen, R. (1950). *Les Colombides et les Gallinaces ainsi que les Martinets, l'engouvent, le Martin-pecheur, le Guepier, le Rollier et la Huppe de Belgique*. Bruxelles, Belgium: Institut Royal des Sciences Naturelles de Belgique.
- Webster, M. S., Pruett-Jones, S., Westneat, D. F., & Arnold, S. J. (1995). Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution*, 49(6), 1147–1157. <https://doi.org/10.2307/2410439>.
- Wedell, N., Gage, M. J. G., & Parker, G. A. (2002). Sperm competition, male prudence and sperm-limited females. *Trends in Ecology & Evolution*, 17(7), 313–320. [https://doi.org/10.1016/S0169-5347\(02\)02533-8](https://doi.org/10.1016/S0169-5347(02)02533-8).
- Zeh, J. A., & Zeh, D. W. (2001). Reproductive mode and the genetic benefits of polyandry. *Animal Behaviour*, 61(6), 1051–1063. <https://doi.org/10.1006/anbe.2000.1705>.