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

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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.

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

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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, Préault, Dubois, Faivre, & 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 km^2 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