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COPULATION DURATION DURING COURTSHIP PREDICTS FERTILITY IN THE EURASIAN KESTREL *FALCO TINNUNCULUS*

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SUMMARY.—*Copulation duration during courtship predicts fertility in the eurasian kestrel* Falco tinnunculus.

Aims: Mechanisms that reduce cuckoldry such as frequent or long copulations are adaptive for males. However, these behaviours are costly and their intensity should therefore be adjusted to the risk of extra pair copulation (EPC) as perceived by males. In addition, it has been proposed that high quality males perceive a lower risk of EPC than low quality males, and consequently show low paternity assurance responses. This hypothesis was tested in the eurasian kestrel by studying the relationship between copulation frequency and duration, and variables that are considered indexes of quality in this species (e.g. clutch size).

Location: Campo Azálvaro region (central Spain).

Methods: Nests were monitored during the pre-laying period to record copulation frequency (presence or absence) and duration.

Results: It was found that males having larger clutches showed shorter copulas. In addition, no relationships were found between copulation frequency and any of the studied indexes of male quality. As far as is known, this is the first case in which copulation behaviour co-varies negatively with an index of male quality in terms of breeding performance.

Conclusions: It is suggested that females mating with high quality males do not seek EPCs, which reduce the risk of extra-pair paternity perceived by these males.

Key words: agonistic behaviour, copulation frequency, extra-pair copulation, extra-pair paternity, mate guarding, paternity assurance.

RESUMEN.—*La duración de la copula durante el cortejo predice la fertilidad en el cernícalo vulgar* Falco tinnunculus

Objetivos: Los mecanismos que reducen la probabilidad de apareamiento fuera de la pareja como el incremento de la duración y frecuencia de las cópulas, son adaptativos para los machos. Sin embargo, estos mecanismos son costosos y su intensidad se debe ajustar por tanto al riesgo de cópula extra pareja (EPC) que perciben los machos. Por otro lado, se ha propuesto que los machos de alta calidad perciben menor riesgo de EPC que los de baja y en consecuencia mostrarán una reducción en los comportamientos dirigidos a asegurar la paternidad. En el presente estudio se explora esta hipótesis en el cernícalo vulgar analizando la relación entre la frecuencia y la duración de la cópula y variables consideradas indicadores de calidad en esta especie (p. ej. tamaño de puesta).

Localidad: Campo Azálvaro (España central).

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Métodos: Se midió la frecuencia y duración de las cópulas de las parejas en los nidos durante el periodo previo a la puesta.

Resultados: Se observó que los machos emparejados con hembras con tamaños de puesta mayores realizaron cópulas más cortas. Sin embargo, no encontramos relaciones entre la frecuencia de cópula y los indicadores de calidad del macho estudiados. Este es el primer caso en el que el comportamiento de cópula se correlaciona negativamente con un indicador de la calidad del macho en términos de éxito reproductor.

Conclusiones: Proponemos que las hembras emparejadas con machos de buena calidad no solicitan EPCs, lo que reduce el riesgo de extrapaternidad percibido por estos machos.

Palabras clave: comportamiento agonístico, frecuencia de cópula, cópula extra-pareja, paternidad extra-pareja, guarda de la pareja, protección de la paternidad.

Introduction

In those species where males provide parental care, cuckoldry decreases the fitness of the putative father and selection is strongly expected to favour male behavioural mechanisms that reduce the incidence of extra-pair copulation (EPC) and their likelihood of resulting in extra-pair paternity (EPP; Møller and Birkhead, 1991; Birkhead and Møller, 1992). In this context, behaviours such as mate guarding (Komdeur *et al*., 1999; Brylawski and Whittingham, 2004), acoustic guarding (Levin 1996), territory defense against conspecifics incorporating parts or all of the home range of a female (Davies 1991; Tobias and Seddon 2000), unpredictable male behaviour (Helfenstein *et al.,* 2004), sperm removal from the female's reproductive tract (Davies 1983) or frequent and/or long copulations (Simmons, 2001; Mougeot, 2004) may have evolved to protect paternity in animals. However, behaviours directed to prevent cuckoldry are likely to be costly (Komdeur, 2001; Low, 2006) and their intensity should therefore be adjusted to the level of sperm competition perceived by males as has been suggested for several animal taxa, such as insects (Elgar *et al*., 2003; Friberg, 2006; García-González and Gomendio, 2004; Prokop and Vaclav, 2005), fishes (Aspbury, 2007), reptiles (Moreira and Birkhead, 2004), birds (Komdeur, 2001; Mougeot *et al.,* 2006) or mammals (del Barco-Trillo and Ferkin, 2004, 2006).

In species with biparental care, it is predicted that males perceiving a reduction in their confidence of paternity should decrease the effort devoted to parental care (Whittingham *et al.,* 1992; Weatherhead *et al.,* 1994; Dixon *et al.,* 1994; Lubjuhn, 2005, but see Sheldon, 2002), with the subsequent decrease of female fitness. This reduction in female fitness (lower reproductive success) is positively associated with the male contribution to feeding offspring (Møller, 2000). Therefore, to reduce the costs of EPCs, females are expected to engage in EPCs only when they are paired with a genetically low-quality male providing low levels of parental care (Kempenears *et al.,* 1992, Lifjeld *et al.,* 1994). In this way, high quality males (at least in terms of parental care) may perceive low levels of sperm competition (e.g. low risk of EPC) and consequently should exhibit lower paternity assurance responses than low quality individuals (see Kokko and Morrel 2005). However, surprisingly, despite the large number of studies on this topic, there is little evidence supporting this idea. One of the few cases is the work recently reported by Vergara *et al.* (2007), which showed that in the eurasian kestrel *Falco tinnunculus*, high quality breeding males displayed lower paternity assurance responses (measured as aggressive behaviour against male intruders) than low quality males. This result suggests that high quality males perceive a lower risk of ECP than low quality males, and consequently, did not display costly agonistic behaviour toward in-

truders. If this is true, similar to agonistic behaviour, high quality males should spend less time on copulation (frequency and/or duration), since copulation behaviour reduces time available for other important activities, such as hunting.

The objective of the present study is to test the prediction that high quality males will display lower levels of paternity assurance than low quality ones, because the former should perceive a lower risk of EPC than the latter. Specifically, there is exploration as to whether the time spent on copulation behaviour (frequency and duration) is negatively associated with known indicators of male quality such as clutch size, laying date and age in the eurasian kestrel (Fargallo *et al.,* 2002; Korpimäki and Wiehn, 1998; Village, 1990). This species was selected because previous studies showed that copulation behaviour, both frequency and duration, are mechanisms related to paternity assurance (Korpimäki *et al.,* 1996; Ille *et al.,* 2002). By increasing copulation frequency and/or by copulating for longer periods, males may increase the sperm transferred, which has obvious benefits in terms of sperm competition and fertilization probability (Birkhead and Møller, 1992). In addition, since the risk of EPCs increases during the fertile stage (defined as the period when a copulation can lead to the fertilization of the eggs), it is predictable that copulation behaviour should also increase in frequency or duration during this period (Mougeot, 2000 ; Komdeur, 2001; Mougeot *et al.,* 2001; García and Arroyo, 2002).

Material and methods

General procedures

The eurasian kestrel (hereafter Kestrel) is a medium-sized falcon species which is typically monogamous, exhibiting courtship feeding behaviour and in which 1-year old males are sexually mature and can breed (Cramp and Simmons, 1980; Village, 1990). In the population studied, 13 % of breeding males and 30 % of breeding females were 1-year old (Vergara and Fargallo, 2007). High levels of copulation frequency began around three weeks before egg laying and reached a peak during the laying period (Village, 1990).

The study was conducted during the breeding seasons of 2006 and 2007 from March to June, in the Campo Azálvaro region (central Spain), where most kestrels breed in nest boxes (Fargallo *et al.,* 2001). The study area contains 62 nestboxes in which about 40 kestrel pairs breed each year (see Fargallo *et al.,* 2001). Nests were monitored during the pre-laying period to record copulation frequency (presence or absence) and duration in s (range 3-14). The repeatability of copulation duration (measured by two researchers simultaneously) was high ($r = 0.84$, $F_{1,4} = 20.85$, $P = 0.009$, $n = 5$; according Lessels and Boag, 1987). The mean duration of the observations was 20 min (range 15-60). Observation duration was controlled in the analyses. Observations began when at least one individual was seen in the nest or in the surrounding area. Only one case of unsuccessful copulation (without cloacal contact) was observed and that was excluded from the analyses. Observations were performed with binoculars (8 x 30) and a telescope (20 x 60-80) and were carried out between 7:00 a.m. and 5:00 p.m. by a single observer in a car situated more than 100 meters from the nest to avoid disturbance. The order in which nests were monitored each day was randomly modified to avoid daytime bias. Nests were monitored every two days to detect laying date (day of the first egg laid in the nest) and recorded clutch size (range 3 - 6). Observations ceased once females laid the first egg. Only nests with complete information regarding clutch size were included in the analyses. In total, 106 observations of 47 nests (53 observations of 21 nests in 2006 and 53 observations of 26 nests in 2007) were made. The fertile stage was con-

sidered as beginning eight days before laying and the pre-fertile stage more than eight days (range 9-46) before laying (Vergara *et al.,* 2007). Breeder's age (1-year old or + 1-year old) was later determined by capturing breeders in their nests with a trap when nestlings were 10 days old or by noting their plumage (Fargallo *et al.,* 2007; Village, 1990) during observations.

Statistical analyses

Generalised Linear Mixed Models (GLIMMIX) in SAS statistical software (SAS 1989 - 96 Institute Inc., Cary, NC, USA) with binomial error and logit link function were used to analyse copulation frequency (0 = no copulation and 1 = copulation) and General Linear Mixed Models (GLMM) to analyse copulation duration in relation to explanatory variables, such as laying date, clutch size, male's age and female's age (1 - year vs. + 1 - year old) and breeding stage (pre-fertile *vs*. fertile stage). In all models, the nest was included as a random factor to avoid pseudo-replication (Hurlbert, 1984), continuous variables as covariates and categorical variables as fixed factors. Copulation duration showed a normal distribution (Kolmogorov-Smirnov test, $P > 0.05$). Observation duration, observation day and year were not significantly correlated with copulation frequency (GLIMMIX, all $P > 0.11$) or duration (GLMM, $P > 0.21$), for which reason these variables were not included in the subsequent analyses. All tests are two-tailed. Means ± SE are given.

Results

Copulation frequency (1.1 ± 0.3 copulations per hour) was not significantly explained by any of the studied variables (GLIMMIX, all $P > 0.12$). However, copulation duration (6.4 ± 0.4 s) was significantly explained by clutch size (full model, GLMM, $F_{1,9} = 8.21$, $P = 0.01$, *estimate* = -1.82, $n = 39$), where males having larger clutches carried out shorter copulas (fig. 1). No correlation was found with any of the remaining variables (full model, GLMM, all $P > 0.27$). This correlation was also significant when excluding those non-significant variables from the model (final model, GLMM, $F_{1,12} = 18.34$, $P < 0.01$, *estimate* = -1.88, $n = 39$).

Discussion

It has been suggested that in raptor species typically breeding in open areas, such as the eurasian kestrel, males may detect extra-pair events even from long distances (Korpimäki *et al.,* 1996). If males perceive a reduction in their confidence of paternity, they should invest less in parental care (Whittingham *et al.,* 1992; Dixon *et al.,* 1994; Weatherhead *et al.,* 1994; Lubjuhn, 2005, but see Sheldon, 2002), with the subsequent decrease of female fitness (Møller, 2000). In the kestrel, females mating with high quality food providers devoted less time to hunting than females mating with low quality providers (Tolonen and Korpimäki, 1994; Wiebe *et al*., 2000). This implies that the expected decrease in male parental care in terms of food provisioning and the subsequent loss of female fitness will be more marked in females mating with high quality food provider males (Korpimäki *et al.,* 1996). Consequently, the risk of fitness reduction when trying in EPCs is higher for females mating with high quality males than those females mating with low quality males. On the other hand, high quality males should invest less in paternity assurance than low quality males. The results given support this idea, as it is shown that males of high quality in terms of food provisioning (measured as clutch size Fargallo *et al.,* 2002), performed less paternity assurance behaviour in terms of copulation duration than low quality males. Although it has been predicted (Kokko and Morrel, 2005) and observed in the

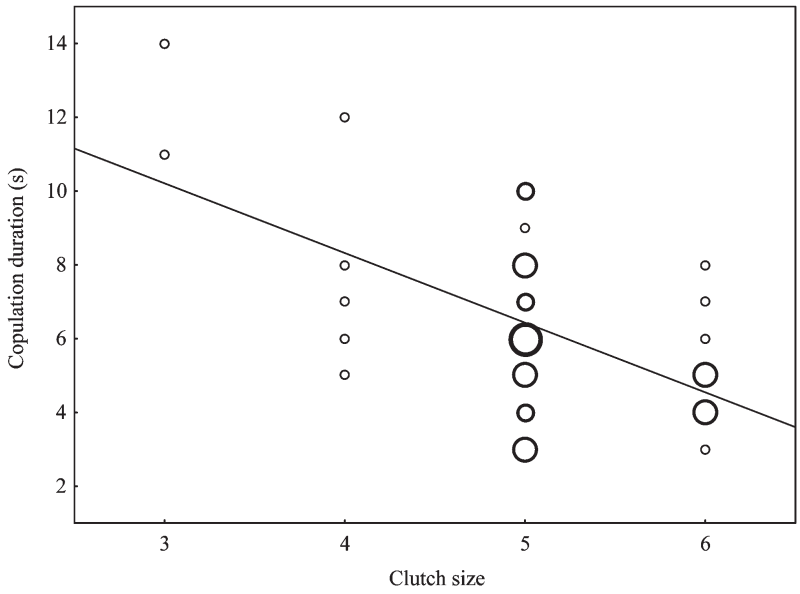

FIG. 1.—Correlation between copulation duration and clutch size. Number of cases is represented by differently sized symbols (smallest to largest, 1, 2, 3, and 6).
[Correlación entre la duración de la cópula y el tamaño de la puesta. El número de casos se representa con símbolos de distinto tamaño (del menor al mayor, 1,2, 3, y 6)]

field (Vergara *et al.,* 2007) that high quality males perform less paternity assurance responses than low quality individuals, as far as is known, the present study provides the first evidence that copulation duration is negatively correlated with male quality. Vergara *et al.,* (2007) showed that the intensity of aggressive behaviour against adult male decoys previous to laying (simulation territorial intrusions) covary negatively with clutch size in the kestrel. The present result is in agreement with that work and suggests that high quality males perceive low risk of EPC, and consequently perform low paternity assurance responses.

However, and in contrast with the predictions, none of the studied indexes of male quality were correlated with copulation frequency. There is no clear explanation for these results. One possibility is that copulation duration is a better predictor of paternity assurance than copulation frequency. Another intriguing aspect of the results is that no differences were observed in the copulation duration between adults and 1 year old kestrels, though they represent different risk levels with respect to EPCs (Mougeot *et al.,* 2006; Vergara *et al.,* 2007). It is believed that it is likely that clutch size is a better estimator of male quality than age as, obviously, clutch size is a final expression of individual quality. The fact that copulation duration was longer in 1 year old males than in adult males (7.7 ± 0.7 and 5.9 ± 0.5 respectively), although not significantly so (but univariate analyses showed that this correlation tends to be significant; GLMM, $P = 0.06$), provides support for the idea that 1-year old are individuals of lower quality and consequently perceive higher risk of EPC than adult males. Finally, the absence of differences in relationships in both copulation frequency and duration between breeding stages is an unexpected result. Future research

may help to understand this and the aforementioned unresolved questions.

Other functions than paternity assurance, such as signalling mate quality (Tortosa and Redondo 1992) have been proposed for copulation behaviour. This idea assumes that copulation behaviour can be interpreted as a signal of quality, thus being a costly activity (Zahavi 1975). Under this perspective, copulation behaviour could be an early expression of the pairs´ reproductive ability and might signal their phenotypic quality. In this sense, the expected result is a positive correlation between copulation behaviour (frequency or duration) and indexes of male quality (Tortosa and Redondo 1992; Heeb 2001). Nevertheless, copulation behaviour can have more functions in the kestrel. The early appearance of copulation behaviour in the kestrel breeding cycle and the fact that copulation attempts occur even in winter, between resident pairs, suggest that its function may be more than mere fertilisation (Village 1990). In fact, studies in other raptor species have concluded that the paternity assurance hypothesis may not fully explain the copulatory behaviour (Negro et al. 1992, 1996; Villaroel et al. 1998; Negro and Grande 2001).

In conclusion, this study provides support for the idea that high quality males perceive lower risk of EPC and consequently invest less in paternity assurance activities (copulation behaviour in our case) than low quality males.

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