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Mating behaviour in a Chameleon (*Chamaeleo chamaeleon*) population in southern Spain – effects of male and female size

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Introduction

Chameleons, with their relatives in the families Iguanidae and Agamidae have a conspicuous social life. Their communication is based on postures and colour changes, with the chameleons being legendary in that respect. However, because chameleon colours may play a role both in their communication and in camouflage and thermoregulation, the meaning of their colours are not always obvious.

The social life's of several agamids and iguanids has been well studied. However, surprisingly little is known about chameleons. This is especially surprising considering the ease by which they are captured and the fact that they allow an observer at a close range without showing obvious signs of disturbance. On the other hand, they are not always easily spotted on demand!

The present report concerns an ongoing study of the social ecology of the common chameleon *Chamaeleo chamaeleon*. Data from 1993 will be presented. We will concentrate on data related to size and mating frequency. Other studied aspects that may explain mating success and mating frequency, like home range size and fighting success will not be treated in this report. Previous work on the behaviour of this species include those by BLASCO et al. (1985), FERNANDEZ (1989), and FERNANDEZ & CUADRADO (1992).

Methods

The study population: The common chameleon has a wide distribution in southern Europe and western Asia and in northern Africa. In Europe it is found in southernmost Spain (BLASCO et al. 1985, CUADRADO & RODRIGUEZ 1990), on some islands off the Turkish west coast, and on Crete.

The studied population is found in San Fernando, close to the sea in the province of Cadiz, Spain. It lives in a parklike setting totally surrounded by built up areas. Important trees and bushes are *Cupressus sempervivens*, *Eucaliptus* spp, *Morus* spp and *Retama monosperma*. The locality is the surrounding of an old astronomical observatory (Real Observatorio

de Marina) administered by the Spanish Navy. The study was concentrated to an area of 1 ha where the highest density of chameleons was found, although the total observatory park was about 3 ha.

In the study population, behaviour was observed from July 20th to October 6th 1993. Copulations were observed from August 20th to September 15th. Egg laying took place about one month later and the eggs hatched following the September, almost one year later.

Altogether 65 males and 66 females were captured in the study area. Of these, 25 males and 30 females were observed for at least 15 days (time from first to last day of observation) and at least once during the period when copulations were taking place, August 20th to September 15th. This is a minimum estimation of the breeding population.

Capture, marking and tagging: Most chameleons were captured during night when they were roosting in trees. They were easily spotted with a strong flashlight. All chameleons captured were individually marked by painting a coloured number on both sides of the body with leather paint. This seemed not to affect the helth of the animals and sloughing took place normally. 17 males and 17 females were also equipped with radio transmitters. This made it possible to quickly locate these animals and assured that they were located daily. The transmitters (Holohil BD-2G) were attached with glue and had a 10 cm wip antenna.

Some of the results presented below refer to all chameleons observed in the study area. This gives a large sample size but may introduce some bias. E.g. "copulations per day" is likely to be unrealistically high because animals are more likely to be observed during courting than at other times. However, the rate may serve as a useful index if this bias is the same for e.g. for large and small females. Other results below refer only to chameleons with radio transmitters. These give a better indication of the actual values.

Field procedure: During the period July 27th to September 30th the main study area was monitored daily by at least one person. During the main breeding period three or four persons were monitoring the animals. As many chameleons as possible, including all those with transmitters, were observed each day. At least once per hour notes were taken of the observed chameleons' position, distance to other chameleons in the vicinity and behaviour. For all those that showed sign of social interactions or for which such could be foreseen, e.g. those close to other animals, we attempted to carry out almost continuous observations. This was facilitated by the fact that the study area was restricted in area. All aggressions, active courting behaviour and matings were noted. Because mating was usually preceded by obvious courting behaviour we believe that most matings performed by the animals with transmitters were observed. However, actual physical contact only lasted for about 1 minute and at times there where conflicts as to which animal to observe when interesting interactions were taking place at different parts of the study area. Some matings might therefore have been overlooked. When chameleons moved they were controlled frequently enough to record all trees and bushes visited. This gave an accurate record of the distance moved.

Chameleon size: In this report only weight is used as size measurement. Chameleons were captured and measured at irregular intervals. Some only once but most several

times. To compare the size of different individuals a standardizing procedure had to be adopted. For all animals weighed more than once the growth rate was computed. The average of these growth rates was used to standardize all measurements to that expected at the mean date for all measurements (August 24th). This is computed as "Adjusted cell means" by SYSTAT (WILKINSON 1990). For each animal the average (if more than one) of these measurements was used as a measure of its size.

Spearman rank order correlation coefficient was computed for correlations.

Results

From the middle of July different behaviours related to courting were observed. Males and females were observed in close vicinity (< 2 m) and males started moving about more than before. Also males and females sometimes moved together (female first) over fairly long distances (several tens of meters) in a short time (a few days). This is the behaviour analyzed in figs. 5 and 11. After staying close to a female for some time, days or even weeks, males were often seen attempting to copulate with females (courting). In these cases the female either was simply not interested, actively rejected the male, even biting him, or copulation took place. Actual copulation usually lasted for less than a minute. Sometimes a male would stay close to a female for some days after copulation.

M a l e s : Males of all sizes were seen in the vicinity of females (fig. 1, $r = 0.25$, $N = 15$, $P > 0.10$). This figure and figs. 2 and 3 are based on males with transmitters only as males without transmitters are more likely to be observed near females than at other places.

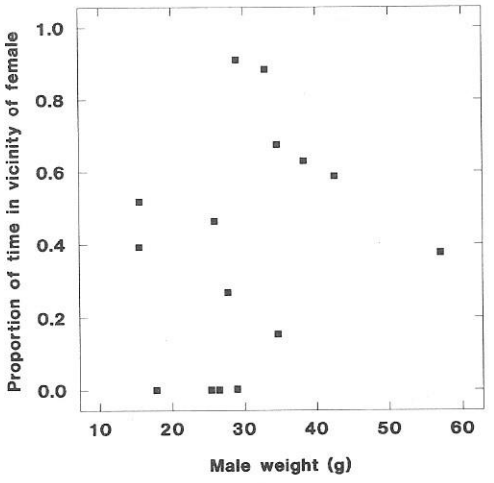

Fig. 1. Male interest in female in relation to male size. Only males with transmitters are included.

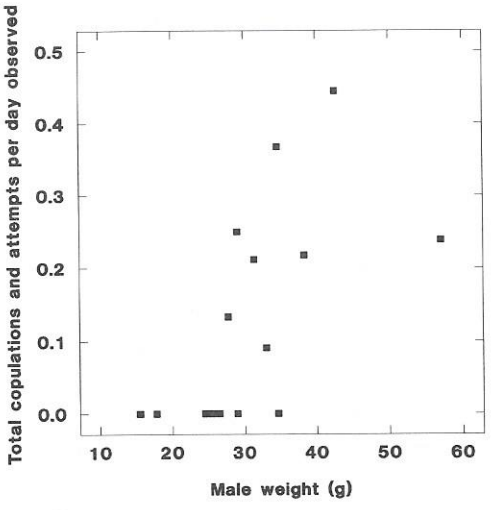

Fig. 2. Courting intensity in relation to male size. Only males with transmitters are included.

However, large males were more active than small ones with regard to active courting; attempted and successful copulations (fig. 2, r = 0.76, N = 17, P < 0.001). Also, large males actually copulated more often than small ones (fig. 3, r = 0.75, N = 17, P > 0.001).

On the other hand, per attempt, larger males were not more successful than were small ones (fig. 4, r = 0.12, N = 19, P > 0.10). This figure is based on all males observed; if a male was observed attempting copulations, there was no bias likely considering the "success" rate.

Also in another respect large males put more effort in courting; on average large males followed moving females over much longer distances (fig. 5, r = 0.62, N = 17, P < 0.01).

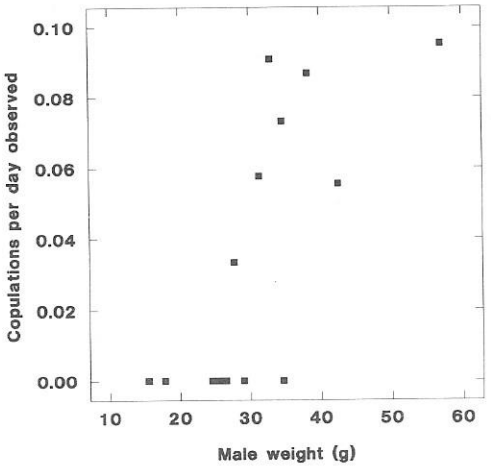

Fig.3. Rate of successful copulations in relation to male size. Only males with transmitters are included.

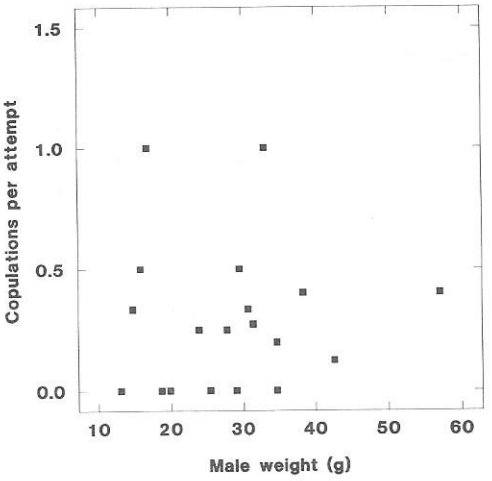

Fig. 4. Proportion of all attempted copulations that resulted in actual copulation. All observed males considered.

F e m a l e s : Only females above 20 g in weight were seen copulating. Most were only seen copulating once but some large females did so several times, up to five (fig. 6).

Analysing only females with transmitters confirmed the tendency for large females to be more sexually active than small ones (fig. 7, r = 0.53, N = 17, P = 0.05).

Males took as much interest in small as in large females to judge from the proportion of time males were seen in the vicinity of different sized females (fig. 8, r = 0.27, N = 15, P > 0.10). This was also true if one considers courtings (attempted copulations and successful copulations) per day observed for females with transmitters (fig. 9, r = 0.25, N = 16, P > 0.10). The power of these statement is however weak due to the few observations and tendencies can actually be observed. Actually, the females that were observed mating more than once were those that were above average with respect to male courting intensity (fig. 9).

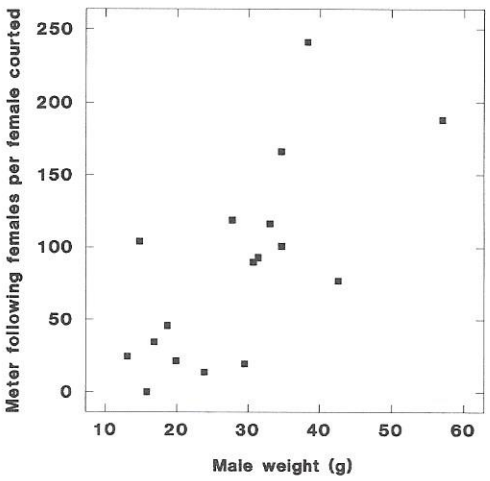

Fig. 5. Readiness to follow moving females in relation to male size. All males observed courting considered.

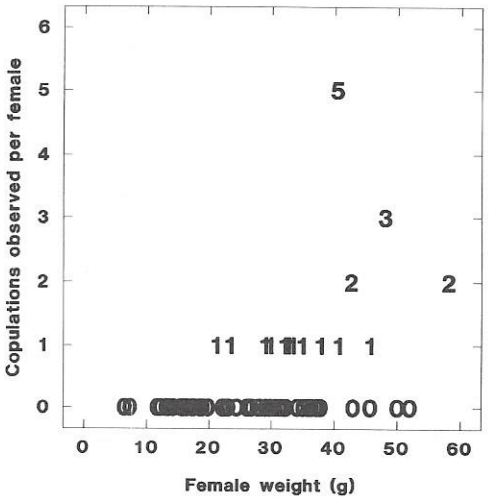

Fig. 6. Number of copulations observed per female. On this and the following figures each female's symbol is represented by the number of times she was observed copulating. All females observed in the study area considered.

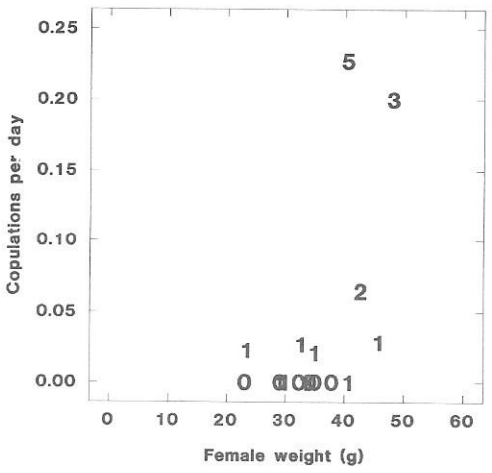

Fig. 7. Female copulation intensity. Only females with transmitters, during the period they carried these considered.

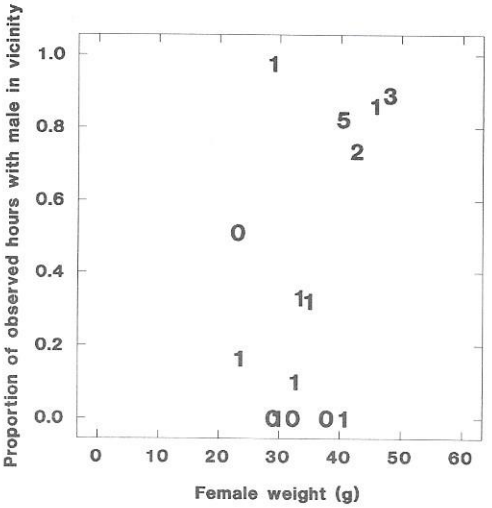

Fig. 8. Male interest in females related to female size. Only females carrying transmitters considered.

Among females over 20 g heavy, there was no obvious difference in the behaviour of large and small females. A similar proportion of all courtings resulted in copulation (fig.

10, r = 0.18, N = 18, P > 0.10) and they were almost as likely to initiate long walks between trees when courted by males (fig. 11, r = -0.62, N = 7, P > 0.10).

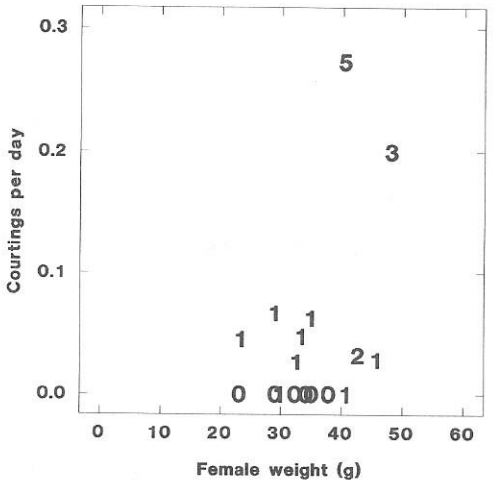

Fig. 9. Male courting intensity in relation to female size. Only females with transmitters considered.

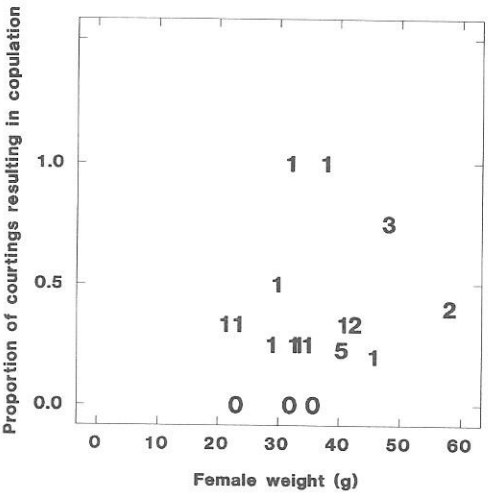

Fig. 10. Female willingness to accept courting in relation to female size. All females seen courted considered.

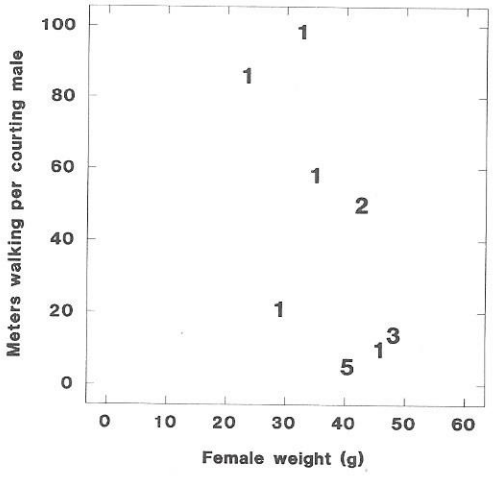

Fig. 11. Female readiness to engage in long walks when courted. Only females with transmitters considered.

Discussion

M a l e b e h a v i o u r : There was no obvious male territoriality; male home ranges overlapped widely during the breeding season. Furthermore, even small males were found near females. However, more intensive aspects of reproductive behaviour, attempted copulations and successful copulations, were mainly performed by the larger males. We interpret this as an aspect of male dominance. Indeed, FERNANDEZ & CUADRADO (1992) did find large chamaeleon males to competitively superior to smaller ones. A similar outcome of male dominance has been found for several other lizards (EDSMAN 1990). Home ranges were small and copulations usually only took place after several days of courting. This permitted larger males to monitor courting performed in their home range. A similar pattern was observed for the rainbow lizard (*Agama agama*) (MADSEN & LOMAN 1987). In that species only males displaying dull colours were permitted in the home range of large males. It was suggested that only males displaying bright colours were acceptable to the females. Dominant males could therefore accept the presence of other males, as long as they were not displaying. To what extent colour display is involved in the courting behaviour of chameleons requires further study.

F e m a l e b e h a v i o u r : Female multiple mating was here confirmed for this species. It has been shown for several other reptiles (SCHUETT & GILLINGHAM 1986, STILLE et al 1986, SCHWARTZ et al. 1989, BARRY et al. 1992, OLSSON et al. 1994). In the studied population mainly the larger females mated several times. There were indications that this was due to a more intensive male interest for these females, although a definite statement will require more data. Male preference for large females has been demonstrated in the sand lizard *Lacerta agilis* (OLSSON 1993). In many species large females produce more eggs (NUSSBAUM 1981, OLSSON 1993, BLASCO et al. 1985) which could motivate a stronger effort for the males. This assumes a similar cost for courting, regardless of female size. Such a cost could be male aggression. Although no data are presented in this report, there was frequent aggression between males, especially in near females.

There were no indications of an active female choice; courting males were as likely to be successful, regardless of size. However, the females' habit of initiating long walks when courted by males could be interpreted as a form of passive female choice. During these walks the couple was very exposed which could provoke interference from other males in the vicinity. The fact that the couple also was exposed to predators suggests that the female had reason to expect a distinct benefit from the behaviour.

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References

BARRY, F.E., WEATHERHEAD, P.J. & D.P. PHILIPP (1992): Multiple paternity in a wild population of northern water snakes *Nerodia sipedon*. – Behav. Ecol. Sociobiol., **30**: 193-199.

BLASCO, M., CANO, J., CREPILLO, E., ESCUDERO, J.C., ROMERO, J. & J.M. SANCHEZ (1985): El camaleón común (*Chamaeleo chamaeleon*) en la península Ibérica. – Monografía 43, ICONA., 1-155.

CUADRADO, M. & M. RODRÍGUEZ DE LOS SANTOS (1990) El Cameleón Común en Andalucía. – (Junta de Andalucia), 80 pp.

EDSMAN, L. (1990) Fighting for a hot spot - competitive ability and assessment in male wall lizards (*Podarcis muralis*). – In: Territoriality and competition in wall lizards. – Dissertaion (Stock hlm)

FERNANDEZ, F. (1989): Comportamiento reproductor del camaleón común (*Chamaeleo chamaeleon* L.) en el sur de Espana. – Doñana Acta Vertebrata, **16**: 5-13.

FERNANDEZ, F. & M. CUADRADO (1992): Efecto de la tala corporal, sexo y edad en el comportamiento agresivo del camaleón común (*Chamaeleo chamaeleon* L.) en cautividad. – Doñana Acta Vertebrata, **19**: 45-52.

NUSSBAUM, R.A. (1981): Seasonal shifts in clutch size and egg size in the side-blotched lizard, *Uta stansburiana* BAIRD and GIRARD. – Oecologia, **49**: 8-13.

OLSSON, M. (1993): Male preference for large females, and assortative mating for body size in the sand lizard (*Lacerta agilis*). – Behav. Ecol. Sociobiol., **32**: 337-341.

OLSSON, M., GULLBERG, A. & H. TEGELSTRÖM (1994): Sperm competition in the sand lizard, *Lacerta agilis*. – Anim. Behav., **48**: 193-200.

ROMERO, J. (1984): Contributión al conocimiento de la morfología y biología de *Chamaeleo chamaeleon* (L). – Dissertation Málaga (Univ. Málaga).

SCHUETT, G.W. & J.C. GILLINGHAM (1986): Sperm storage and multiple paternity in the copperhead *Agkistrodon contortrix*. – Copeia, **1986**: 807-811.

SCHWARTZ, J.M., MCCRACKEN, G.F. & G.M. BURGHARDT (1989): Multiple paternity in wild populations of the garter snake *Thamnophis sirtalis*. – Behav. Ecol. Sociobiol., **25**: 269-274.

STILLE, B., MADSEN, T. & M. NIKLASSON (1986): Multiple paternity in the adder *Vipera berus*. – Oikos, **47**: 173-175.

WILKINSON, L. (1990): Systat: the system for statistics. Statistics. – Evanston, Il (Systat Inc), 677 pp.

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