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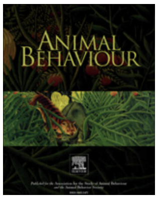

Female aggregation interacts with population structure to influence the degree of polygyny in red deer

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In polygynous systems, female aggregation may affect the degree of polygyny by increasing the variance in male mating success. However, other population features such as the sex ratio and the age structure of males may also affect the distribution of male mating success. We combined behavioural observations and genetic data to investigate the relationship between spatial distribution, population structure and degree of polygyny in 30 red deer, *Cervus elaphus*, populations in Spain. We found that although female aggregation was positively related to mean harem size, under conditions of high female aggregation males were unable to monopolize whole female groups. The relationships between female aggregation and behavioural estimates of the variance in male mating success were strongly influenced by the sex ratio and the proportion of competitive males in the population. Potential skew of male mating success and potential opportunity for sexual selection were higher in adults than in young or subadult males. Finally, the behaviourally estimated distribution of male mating success matched the genetically estimated degree of polygyny, especially under conditions of relatively high synchrony in female receptivity. Our results show how population structure can interact with female aggregation in space and time to influence the opportunity for sexual selection in red deer.

Spatial aggregation of females during the mating season favours one of the preconditions for the evolution of polygynous mating systems: the opportunity for males to monopolize multiple mates (Emlen & Oring 1977). Female aggregation may increase the mean and variance in female groups that males can monopolize and, hence, the degree of polygyny. Female aggregation is therefore a key element in the evolution of mating systems and sexually selected traits (Emlen & Oring 1977; Andersson 1994; Shuster & Wade 2003). In turn, female aggregation depends on ecological features such as habitat, food distribution or predation (Emlen & Oring 1977; Davies 1991).

In ungulate species, habitat characteristics appear to influence female aggregation patterns, which, in turn, affect mating systems and sexual dimorphism (Jarman 1974; Pérez-Barbería et al. 2002). Also, within a species, different populations might experience different conditions that modulate their mating systems (Lott 1991; Gross 1996; Carranza 2000).

Female aggregation is a key variable in polygynous systems in which males compete either directly for access to female groups or indirectly by controlling essential resources for females (Emlen & Oring 1977; Carranza et al. 1990; Carranza 2000; Shuster & Wade 2003). However, the actual degree of polygyny does not depend only on the spatial aggregation of females. The temporal distribution of female sexual receptivity, the sex ratio and the age structure of the population could also determine the distribution of males' mating success (Emlen & Oring 1977; Coltman et al. 2002; Shuster & Wade 2003; Bonenfant et al. 2004). Additionally, alternative mating tactics, such as 'sneaky' strategies, may complicate the relationship between female aggregation and the distribution of male mating success (Clutton-Brock et al. 1982; Coltman et al. 1999).

The distribution of male mating success has generally been measured by behaviourally estimated variables such as the mean or variance in harem size, proportion of successful males or variance in male mating success (see e.g. Clutton-Brock et al. 1997; Carranza & Valencia 1999). However, quantifying male mating success from behavioural observations such as harem size or harem tenure can be problematic owing to the difficulties in observing covert mating behaviour such as sneaky male strategies. In this sense, considerable progress has been made with the development of molecular techniques, which allow researchers to assess the accuracy of behavioural estimates of male mating success (Pemberton et al. 1992; Hughes 1998; Coltman et al. 1999; Say et al. 2003). The accuracy of such estimates varies between breeding systems. In some cases mating

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success can be predicted by behavioural observations (Pemberton et al. 1992; Hoelzel et al. 1999; Røed et al. 2002) but not so in others (see e.g. Amos et al. 1993; Coltman et al. 1999). In general, it is expected that the higher the importance of covert mating strategies, the lower the accuracy of behavioural estimates of male mating success.

Throughout their distribution range, red deer, *Cervus elaphus*, populations' mating systems vary in relation to local environmental conditions (see e.g. Clutton-Brock et al. 1982; Carranza et al. 1990; Bonenfant et al. 2004). In Mediterranean ecosystems, the red deer rutting season takes place after the summer (September–October), when food is scarce, patchily distributed and concentrated in certain areas (Olea et al. 2005). Under such circumstances, female distribution can be highly aggregated (Carranza et al. 1990). As a consequence of high female aggregation, male mating strategies change from harem defence polygyny, typical of northern European populations (Clutton-Brock et al. 1982), to resource defence polygyny (Carranza et al. 1990). In addition, in Spanish private hunting estates, managers normally provide supplementary food when natural food for red deer is scarce in late summer (Carranza et al. 1995). Supplementary feeding increases the aggregation of females even more and could generate a highly skewed distribution of male mating success (Sánchez-Prieto et al. 2004; Pérez-González et al. 2010a). However, if female aggregation increases too much, males may be unable to defend female groups, and sneaky strategies by subordinate males could be more successful (Shuster & Wade 1991). In this situation, despite the presence of large female groups, the actual distribution of male mating success may be much less skewed than expected under the assumption of males copulating with all (or most) females in their harems.

In this study, we investigated the relationship between female aggregation, population structure and degree of polygyny in 30 populations of Iberian red deer, *C. e. hispanicus*. First, we used spatial analyses to characterize female aggregation and population structure, as well as to quantify behavioural measures of the potential distribution of male mating success. Second, we determined how female aggregation and population structure affected the potential distribution of male mating success. Finally, we studied the relationship between the behaviourally estimated distribution of male mating success and the actual degree of polygyny estimated by genetic tools.

METHODS

Study Area

The study was conducted between 2004 and 2006 in 30 areas located in Mediterranean ecosystems in southwestern Spain (throughout Extremadura and Andalucía regions). Each area was studied in only one of the study years. Red deer stocks in these areas can be considered as isolated populations with regard to their current ranging and mating behaviour, either because of the geographical distance or because there are artificial barriers between them. Study areas averaged ca. 1000 ha in size and were located within private hunting estates. Sampled populations typically included mountain areas covered by Mediterranean shrub (*Cistus* spp., *Erica* spp., *Genista hirsuta*, *Lavandula* spp.) and forest species (*Quercus* spp., *Arbutus unedo*, *Olea europaea*, *Phyllirea* spp.), and lower, flatter land, covered by open oak woodland (*Quercus* spp.) or 'dehesa'. Within each area, deer typically use the shrub land and forest as refuge and clump in mating areas ('arenas') in open dehesas during the rut (Carranza et al. 1990; Carranza & Valencia 1999).

Measures of Population Structure and Potential Mating Success

During the rut (September–October) we made car journeys along rutting arenas to count and locate all the observed individuals (see Pérez-González et al. 2010a, b). Field data were collected in September 2004 for Extremadura region (14 populations) and September 2005 for Andalucía region (16 populations). For each population we collected census data once as close as possible to the central day of maximum activity within the rutting period (peak of rut) during the evening (daily peak in breeding activity). Environmental and population conditions may cause the rut to peak at different dates in each population (Pérez-González et al. 2010a). Our purpose was to obtain a single estimate for any population as close as possible to the several days (5 or so according to our experience) of higher activity around the peak of the rut. To do so, we were continuously informed by the managers of each estate on the progress of the rut (normally on the basis of number of stag roar counts/min, see Appendix; Fig. A1). Thus, we could schedule our field work to visit every population as close as possible to its rutting peak.

In the surveys, with the help of maps, video camera and GPS, we counted, located and georeferenced all the individuals observed, recording their sex and approximate age. Males were visually assigned to four age classes (yearlings: 1 year old; young: 2 years old; subadults: 3–4 years old; adults: older than 4 years). We categorized as yearlings those individuals with small body size and spike antlers without burr at their base. Young males were individuals with small body size but with burr and several tines in their antlers (two to five in each). Subadult males had an intermediate body size and antlers with many tines (typically more than four in each antler). Finally, we categorized as adult males larger individuals with big antlers (longer and thicker, usually with more than five tines in each). Although yearling males can be sexually mature, they were excluded from this study because many of them remain with their mothers and are not sexually motivated. As a consequence, they could bias the behavioural measures described below (see also Clutton-Brock et al. 1997 as an example of yearling exclusion in mating system studies). On the other hand, we registered all females 1 year old or older. With this census methodology (see also Pérez-González et al. 2010b) red deer densities ranged from 0.11 to 1.02 individuals/ha, averaging 0.38 individuals/ha ($N = 30$, 95% confidence interval = 0.30–0.46).

We characterized female spatial aggregation by Ripley's K approach (Ripley 1981; Pérez-González et al. 2010b). Ripley's K method describes the characteristics of the point distribution pattern over a range of distance scales, estimating the expected number of points within a distance d of an arbitrary point in the study area. Ripley's K is calculated as:

$$K(d) = \frac{A}{n^2}\sum_{i=1}^{n}\sum_{i\neq j=1}^{n} I_{ij}(d) \tag{1}$$

where $K(d)$ is an index that estimates the aggregation degree of a group of points; d is the distance assessed; A is the area of the study region; n is the number of points; $I_{ij}(d)$ is a function that takes the value of 1 when c_{ij} is lower than $d/2$ (c_{ij} is the distance between the i and j points) and 0 when c_{ij} is higher than $d/2$. The value $K(d)$ can be normalized and linearized to the $L(d)$ value with the following equation:

$$L(d) = \sqrt{\frac{K(d)}{\pi}} \tag{2}$$

The representation of $L(d) - d$ versus d shows how female spatial pattern changes at different scales. We used the first local maximum of this pattern as the spatial scale of the female distribution pattern (d^*), that is, the mean area occupied by a group of females. Once the scale was determined, we placed circles on maps of female distribution with the following preconditions (Pérez-González et al. 2010b; see section Quantification and