The red deer rut revisited: female excursions but no evidence females move to mate with preferred males

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In polygynous mammals, most variance in male reproductive success is expected to result from competition between males, and the role of female behavior remains poorly understood. Contests between red deer males during the annual rut are one of the most famous examples of male–male competition. However, anecdotal evidence suggests females in estrus make substantial movements, changing harems, and potentially disrupting the outcome of male contests. In other polygynous mammals, such movements have been interpreted as evidence of female mating preferences. Here, we use 34 years of detailed observational data on wild red deer to show that 43% of estrous females are found in different harems between successive observations and that 64% of such females make substantial movements (up to 4 km) when this occurs. Approximately 45% of these movements result in the male into whose harem a female moved fathering her offspring. We then test whether females move nonrandomly with respect to male phenotype, consistent with the hypothesis that females move to mate with preferred males. Although in general, females were more likely to be found in larger harems and the harems of younger males after harem changes, these effects were not specific to estrous females. Further, estrous females were not more likely to be found in the harems of less related males. We therefore find little support for the idea that estrous females move between harems to mate with a preferred male; as a result, the reasons females make such extraordinary movements when in estrus remain unclear. Key words: Cervus elaphus, female choice, female movements, red deer, rut excursions, sexual selection.

INTRODUCTION

In polygynous mammals that do not mate on leks, competition between males for access to receptive females was once assumed to explain a high proportion of variance in male mating success (Clutton-Brock 1989). However, discrepancies between behavioral observations and molecular analysis of paternities have revolutionized our understanding of such mating systems, suggesting dominant males may gain more or less reproductive success than indicated by behavioral observations (Pemberton et al. 1992; Hughes 1998; Colman et al. 1999; Worthington Wilmer et al. 1999; Twiss et al. 2006). This has important implications for the intensity of sexual selection (and therefore the potential for evolution) as well as the maintenance of genetic variation within a population (Hughes 1998; Colman et al. 1999; Twiss et al. 2006; Hoffman et al. 2007). Where dominant males achieve less reproductive success than expected, this can be explained by the intensity of competition between dominant males and/or the role of alternative male tactics (e.g., Hogg and Forbes 1997; Colman et al. 1999; Reichard et al. 2004); but female mating tactics may also play an important role (e.g., Travis et al. 1995; Hughes 1998).

Disentangling the roles of female behavior and male competition in polygynous species in the wild have proved challenging, because the 2 can interact either positively or negatively, either reinforcing or weakening selection on male traits (Qvarnstrom and Forsgren 1998; Wong and Candolin 2005; Hunt et al. 2009). Male competition can physically prevent females from exercising choice (Jennions and Petrie 1997; Wong and Candolin 2005) or limit choice to just a few dominant males (Hunt et al. 2009). However, females can exert choice for dominant males by inciting competition between males and mating with the winner (elephant seals, Cox and Le Boeuf 1977; bison, Wolff 1998; and elephants, Poole 1989). In several mammals, females show increased mobility during the breeding season (Byers et al. 1994; Relyea and Demarais 1994; Labisky and Fritzen 1998; San Jose and Lovari 1998; Lovari et al. 2008; Dahle and Swenson 2003; Hoffman et al. 2007; Richard et al. 2008). These include the “rut excursions” of roe deer, short term movements by females outside their home ranges, during which females visit one or more male territories to mate (San Jose and Lovari 1998; Lovari et al. 2008; Richard et al. 2008); movements of female fur and gray seals among static males (Twiss et al. 2006; Hoffman et al. 2007); and the “sampling” excursions of female pronghorn (Byers et al. 1994). Such excursion behaviors have the potential to disrupt the outcome of male competition and so influence the magnitude and direction of sexual selection, particularly if females have preferences for male traits other than those favored by male competition or if females use excursion behaviors to maximize the genetic compatibility of their mates (e.g., Hoffman et al. 2007).

Movements of breeding females during the breeding season are frequently interpreted as evidence of female choice (Byers et al. 1994; Twiss et al. 2006; Hoffman et al. 2007; Richard
et al. 2008) but may be a result of a number of nonmutually exclusive processes (Clutton-Brock and McAuliffe 2009). As well as a female mating preferences for indirect benefits in terms of offspring fitness, including both good genes (e.g., Antilocapra americana, Byers et al. 1994) and genetic compatibility or inbreeding avoidance (e.g., Arctocephalus gazelle, Hoffman et al. 2007), movements could also represent active or passive attempts to escape from harassment by males (e.g., Dama dama, Clutton-Brock et al. 1992; Equus grevyi, Sundaresan et al. 2007; and Cervus elaphus, Carranza and Valencia 1999; but see Fisher and Lara 1999, in which the moderate speed of movements in wallaby females, Onychogalea fraenata, suggests they are not trying to escape harassment). Alternatively, excursions may arise from mate-searching behaviour, if males are sparsely distributed or cannot successfully court females as they come into a brief estrus (24 h, Guinness et al. 2001; or to compare the phenotypes of the males between the breeding season, few studies of wild mammals have noted that the outcome of competition between males for females is important in explaining the distribution of reproductive success (Clutton-Brock et al. 1979, Kruuk et al. 2002). However, anecdotal evidence suggests that when females are in estrus, they sometimes leave their current harem and move substantial distances to join the harem of a different male (Clutton-Brock et al. 1982).

The present study

In this study, we use 34 years of detailed observational data on female and male location, female estrus dates, and male traits, as well as a detailed pedigree, from a wild population on the Isle of Rum, Scotland. We test whether the probability of females changing harem, and the distances they move in doing so vary with female estrus state, whether movements around estrus result in changes in the sire of a female’s offspring, and whether females move in order to mate with a preferred male. As such, in published reports, attempts to disentangle the reasons females move have frequently proved challenging or controversial (e.g., Hoffman et al. 2007; Kotiaho et al. 2008), and it has proved unclear whether movements are important relative to male competition; this is critical for our understanding of how male competition and female mating tactics interact.

In this study, we aim to test whether estrous females move to harems in order to mate with preferred males. We make the following predictions:

P1: Females will be more likely to change harem when in estrus than at other times, and will move further, to locations outside their rut home ranges, in doing so.

P2: When females change harem during estrus, the novel male will sire the females’ offspring.

P3: Females changing harem in estrus will do so nonrandomly with respect to male phenotype, moving preferentially to the harems of older males, males holding larger harems and/or the harems of less related males.

MATERIALS AND METHODS

Study population and data collection

Data were collected from a free-living red deer population living in the North Block of the Isle of Rum, off the west coast of Scotland, in which individuals of both sexes can be recognized, either from artificial marks placed at birth or individual idiosyncrasies, such as facial shape, body shape, coat coloration, or natural ear notches (Clutton-Brock et al. 1982). Individual life histories have been closely monitored in this population since...
1972 (see Clutton-Brock et al. 1982). Each year, during the rutting period (defined as 15th September–15th November), daily censuses of the study area are conducted. The identities and locations (correct to the nearest 100 m) of all females seen and all males that are with at least one female are noted during these censuses, and the identities of the females comprising the harem of each male are also recorded. It should be noted that these records provide a conservative estimate of female movement: because females are systematically recorded once per day, they may also move between harems within a day. Opportunistic sightings of behaviors indicating females are in estrus are made throughout the rutting period (see below; Clutton-Brock et al. 1997). Estrus periods in red deer usually last less than 24 h, and the majority of females mate only once (Guinness et al. 1971; Clutton-Brock et al. 1982). However, if a female fails to conceive while in estrus, she may cycle and come back into estrus after 18 days (Guinness et al. 1971). Behaviors indicative of estrus are chivvying of females (harassment) by their harem holding male, a female being in an unusual location, or a female being mounted or served (i.e., the male was seen to ejaculate) or straying, as occurs after service (Guinness F, personal communication, Clutton-Brock et al. 1982).

During the rut, female home range sizes are constricted from those occupied at other times of the year (Clutton-Brock et al. 1982). The median core home range size (see below) during the rut is 37 ha, although there is substantial variation (2–1557 ha, Stopher K, in preparation). Although this median home range size potentially encompasses multiple harems, stags invest considerable effort in herding groups of females, so that harems are typically distinct from one another (Clutton-Brock et al. 1982). However, some small movement of harems between and within days is likely to occur as grazing females move between resources; therefore, a female’s home range throughout the rut is generally larger than the area a harem occupies at any point.

During the calving season (ca. 20th May–30th June), daily observations are made to identify the calving date of each female and monitor neonatal survival (Clutton-Brock et al. 1982). Calves are caught shortly after birth, and tissue samples taken for genotyping. In addition, for possible sires not caught at birth, most have been sampled from cast antlers or by chemical immobilization or postmortem. Individuals were genotyped at up to 15 highly variable microsatellites. Paternities were assigned using the programs MasterBayes (Hadfield et al. 2006) and COLONY2 (Wang and Santure 2009) with greater than 80% individual confidence (see Walling et al. 2010, for full details).

The following variables were used as explanatory variables in our analyses:

Confidence of estrous observations
One of 3 levels of confidence was assigned to each estrous observation, based on the behavior on which the assignment was based. Confidence levels were “possible” (the female being chivvied by a male more than other females in the same harem); “likely” (the female being frequently, selectively, and intensively chivvied or being in an unusual location, see below); and “definite” (the female being mounted, served, or straining). Where more than one estrous date was recorded for a female, we used the estrus date with the highest confidence attached. Where 2 possible estrus dates were recorded with equal confidence, both observations were removed from the dataset (24 of 2236 observations).

Day relative to estrus
The number of days between the day of observation and the day on which the female was in estrus, grouped as: 1) day of estrus, 2) day before estrus, 3) day after estrus, and 4) other day in the rut.

Peak rut
This was included to account for changes in the stability of harems and change in age structure as the rut progresses (Clutton-Brock et al. 1982). It was treated as a 2 level factor denoting whether the day of observation was during the peak of the rut. Peak rut is defined as the period within a 11-day window around the average date of conception in any 1 year, where conception dates are calculated from the birth date of calves born following that rut, with gestation length taken to be 235 ± 5 days (Clutton-Brock et al. 1982).

Days between observations
The number of days between subsequent observations of a female. This was included as a covariate to correct for events in which a female was not seen on a daily census, which will increase the period and so theoretically, distance, which the female could move between observations.

Maximum temperature
This is recorded on Rum by Scottish Natural Heritage, and missing values were predicted using a regression equation from those on Tiree, a nearby island with more complete climate records, with which Rum temperatures are highly correlated (R = 0.971, for more details, see Moyes et al. 2011). For remaining gaps, temperatures were estimated from the mean temperature over the previous 3 days and subsequent 3 days (Moyes et al. 2011).

Rainfall
This was again recorded on Rum by Scottish Natural Heritage and supplemented by a regression equation used to predict the rainfall from records taken at Rhubana, Inverness-shire (Moyes et al. 2011), with which Rum rainfall is again highly correlated (R = 0.909). Data from Rhubana are less complete than Tiree; however, rainfall is much more locally variable than temperature, and therefore, it is more important to use the closest possible station proving adequate rainfall data.

Construction of rut home ranges
An average of 43.04 ± 18.94 observations were available per female per year. Females with less than 6 recorded positions were excluded, removing 4.33% of the data. This is a little less than that recommended by Borger et al. (2006), who found 10 fixes collected over a few days per month were sufficient in roe deer and kestrels for accurate home range estimation using similar methods. However, visual assessment suggested this was a sufficient number of fixes to produce sensible home range shapes. Home ranges were calculated using kernel density estimation methods (Worton 1987, 1989; Borger et al. 2006). The kernel method calculates boundaries based on the complete utilization distribution and can account for multiple centers of activity (Worton 1989; Kenward et al. 2001). The smoothing parameter, h, was selected using the reference bandwidth, h_{ref} method, as the least squares cross validation method performed poorly with home ranges with small numbers of fixes (as predicted by other studies, Seaman and Powell 1996). The h_{ref} method tends to oversmooth home ranges(Huck et al. 2008), which also makes it a more conservative smoothing algorithm in this analysis (see below) than the least squares cross validation method. Home ranges were calculated in “R” version 2.8.1 (R Development Core Team 2008) using the “adehabitat” 1.6 package (Calenge 2006) and then imported to ArcMap. In this study, we used 65%, 85%, and 90% isopleths. Borger et al. (2006) recommend using...
isopleths between 50% and 90%, as larger and smaller isopleths are subject to greater bias. Determination of whether female locations fell within calculated home ranges was done using the “intersect point tool” in Hawth’s Analysis Tools for ArcGIS (Beyer 2004), so that each position a female was recorded in was assigned a 0 if it fell outside the female’s rut home range and a 1 if it fell inside.

Statistical analysis

For this study, we use data from the ruts in years 1974–2007, excluding 2000 in which there is no estrus data available. All statistical analyses were conducted using the statistical package R version 2.8.1 (R Development Core Team 2008) or Genstat version 11.1 (Payne et al. 2009). Model selection was based on sequential removal of variables with nonsignificant Wald statistics (Crawley 2007).

Female movements and their reproductive consequences

We used (generalized) linear mixed-effects models, (G)LMMs, to test how day relative to estrus influenced a female’s probability of changing harem between observations, and how far she moved in doing so. Harem change was modeled as a binary variable denoting whether a female was in the harem of the same male (1) or a novel male (0) compared with the last observation of that female. Observations where the identity of the previous or current male was unknown were not assigned values. The distance moved by a female between successive observations was measured as the distance in meters between the female’s previous position (position to the nearest 100 m) and the female’s current position. Occasionally, the fact a female has traveled a long distance from her normal location is taken as an indication that she is in estrus; this presents obvious circularities in our analyses, and such observations were therefore excluded from all analyses. Secondly, individual males do not rut for the entire season, but at some point terminate their rutting activities, typically as a result of defeat in a fight and/or exhaustion (Clutton-Brock et al. 1982). When this occurs, they are often observed to leave the rutting areas for a sustained period of time, or even for the remainder of that season. Such male turnover events will result in females being found in a different harem because of exclusively male, not female, behavior. We therefore excluded from analyses all observations in which the harem holder a female had been seen with initially was not holding a harem at the subsequent female observation.

To test whether females were more frequently observed to change harems on the day of estrus than at other times during the rut, as was suggested by earlier studies conducted on this population (Clutton-Brock et al. 1982), we fitted a GLMM of harem change with a binomial error structure. Day since 1st September and female identity were included as random effects. Fixed effects were day relative to estrus, year of observation, confidence level of estrous observation, peak rut, daily rainfall, and minimum temperature.

To test whether females in estrus made movements of unusual distance, which resulted in them being associated with a different male, we fitted an LMM of the distance between the female’s current and previous location (to the nearest 100 m). Distance moved was log transformed, and residual errors checked for normality. Again, day since 1st September and female identity were included as random effects. Fixed effects included were day relative to estrus, change in male, year, confidence level, daily rainfall, minimum temperature, days between observations, and peak rut. An interaction was fitted between day relative to estrus and change in male to examine how the distances moved by females changing harem and not changing harem varied with estrous state.

We also investigated how often the movements of females between harems in different estrous states resulted in females moving away from their rut home ranges. This analysis was conducted using data from 2003 to 2007 only. The aim of this analysis was to determine whether the probability of a female being outside her “rut home range” increased when the female was in estrus. We first calculated the rut home range for each female, using each position in which a female was recorded during the daily rut censuses. Each home range was calculated at 3 isopleths: 65%, 85%, and 90%. A 65% isopleth home range represents a core home range for each female (Moyes 2007), whereas 85% and 90% represent progressively more inclusive ranges, so that in a 90% home range, only 10% of a female’s locations will fall outside of its boundary. We then determined whether female locations fell within calculated home ranges using the “intersect point tool” in Hawth’s Analysis Tools for ArcGIS (Beyer 2004). These data were collated for all females as proportion data grouped according to whether a female changed harem because her previous observation, and her day relative to estrus, or for which the male they moved to was not known, were excluded. We then calculated the proportion of offspring born to females which 1) changed harem in estrus and 2) changed harem and were defined as “movers,” that were sired by the novel male.

Analysis of male phenotypic traits and relatedness to focal female

To determine whether the likelihood of females changing harem was correlated with male phenotypic traits, we compared the trait values of males holding harems, which females were scored as ‘‘0’’ and males that changed males when in estrus. For which we did not have an observation on both the day before and the day of estrus, or for which the male they moved to was not known, were excluded. We then calculated the proportion of offspring born to females which 1) changed harem in estrus and 2) changed harem and were defined as “movers,” that were sired by the novel male.

To determine the reproductive outcome of movements by estrous females, we tested whether paternities were gained by males as a result of such movements. To test this, we defined a subset of females as “movers” if they changed male and moved further than the median distance moved by females that changed males when in estrus. Females for which we did not have an observation on both the day before and the day of estrus, or for which the male they moved to was not known, were excluded. We then calculated the proportion of offspring born to females which 1) changed harem in estrus and 2) changed harem and were defined as “movers,” that were sired by the novel male.

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well as year of observation and confidence of observation. We fitted an interaction between day relative to estrus and the difference between male phenotypes to test whether female preference varied with estrus state. The random selection of a focal male/nonfocal males and GLMM analyses were repeated 1000 times to ensure the random selection of focal/nonfocal male was not driving any significant results. Due to the computational time required to do this, it was not possible to simplify these models using stepwise deletion of non-significant terms. Because harem size is known to be closely correlated with age (Nussey et al. 2009), we also ran similar models in which the difference in each male trait was tested separately, without the other traits. These models included the same other fixed effects as before and again were tested with and without an interaction term fitted between difference in male trait and female estrus state. Again, the random selection of a focal male/nonfocal males and GLMM analyses were repeated 1000 times.

In a second analysis of male phenotype, we asked whether females changing harem moved further depending on the difference between male phenotypes and whether this changed when females were in estrus. This analysis was an extension of the previous analysis of distance moved by females, with explanatory variables as above, and also, fitted as a fixed effects, the difference between male trait values for age, harem size, and relatedness to the focal female, as the trait value of male joined by the female minus the trait value of male left by the female, and the interaction between the difference in male trait and female estrous state. Female identity and the identity of the pair of males which females moved between were fitted as random effects.

RESULTS

Harem changes, female movements, and reproductive consequences

Females were more likely to change harem when in estrus than either the day before estrus, the day after estrus or other days in the rut (Figure 1, in a GLMM of harem change, with a binomial error structure, with days since 1st September and female identity as random effects, $F_{3,15707.0} = 5.00, P = 0.002$). Combining “day after,” “day before,” and “other days,” we found that females were more likely to change harem when in estrus than on other days in the rut (42.7% of females changed harem on the day of estrus compared with 34.3% on other days in the rut; $F_{1,15745.1} = 13.36, P < 0.001$). However, harem change on the day after estrus and the day before were both not different than other non-estrus days in the rut (day after vs. “other,” 39.3% vs. 34.3%, $F_{1,15194.9} = 1.54, P = 0.215$; day before vs. other, 33.4% vs. 34.2%, $F_{1,19185.8} = 0.06, P = 0.801$).

The likelihood of females changing harem also varied with year ($F_{5,6011.7} = 4.59, P < 0.001$) and decreased as rainfall increased ($F_{1,15788.5} = 35.46$). There was no effect of confidence of estrous observation, timing in relation to the peak of the rut, or temperature (in the full GLMM of harem change—containing fixed effects of day relative to estrus, year of observation, confidence level of estrous observation, peak rut, daily rainfall, and minimum temperature, as well as random effects of days since September 1st and female identity—confidence $F_{3,5588.5} = 1.85, P = 0.139$, peak rut $F_{1,14795.2} = 1.01, P = 0.316$, minimum temperature $F_{1,19032.4} = 2.23, P = 0.136$).

Females that changed harems tended to move further between observations when they were in estrus than at other times in the rut (Figure 2). In an LMM of distance moved by females between successive observations, the interaction between day relative to estrus and whether a female changed male on the distance moved by a female was highly significant (day relative to estrus by change in male interaction; $F_{3,4993} = 6.55, P < 0.001$, Table 1). As Figure 2 shows, females that changed harem moved further when in estrus than at other times in the rut, but females remaining within the same harem moved similar distances whether in estrus or not.

The distances females moved also varied between years and were positively correlated with the number of days between observations of that female (see Table 1). Females moved shorter distances between observations during the peak of the rut than moved further when rainfall was higher and when the minimum daily temperature was warmer (see Table 1).

Females were also more likely to be outside their rut home range when in estrus than at other times in the rut (Figure 2). In a GLMM of distance moved by females between successive observations, the interaction between day relative to estrus and whether a female changed harem tends to move further when in estrus than at other times in the rut; there was a interaction between day relative to estrus and whether a female changed harem on the likelihood of being outside her rut home range ($F_{3,4993} = 6.4183, P = 0.005$, see Figure 3 and Table 2). However, this was only true for rut home ranges

![Figure 1](https://example.com/figure1.png)

**Figure 1** Percentage of females changing harem by day of observation relative to estrus.

![Figure 2](https://example.com/figure2.png)

**Figure 2** Plot showing the effects of day relative to estrus and whether the female had changed harem on the distance a female moved between successive observations. Day relative to estrus is grouped into day of estrus, day before estrus, day after estrus, and other days in the rut.
**Table 1**

Results from the minimum adequate behavioral estrus dataset movement model in which the response variable is distance moved: an LMM, based on 14,748 observations

<table>
<thead>
<tr>
<th>Term</th>
<th>Estimate</th>
<th>SE</th>
<th>F value</th>
<th>df</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>5.504</td>
<td>0.102</td>
<td>2804.91</td>
<td>1, 9323</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Day relative to estrus</td>
<td></td>
<td></td>
<td>7.16</td>
<td>3, 4993</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Day relative to estrus (before)</td>
<td>0.143</td>
<td>0.164</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Day relative to estrus (exact)</td>
<td>0.543</td>
<td>0.129</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day relative to estrus (after)</td>
<td>0.283</td>
<td>0.141</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td>1290.51</td>
<td>1, 4993</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Male (same)</td>
<td>−1.206</td>
<td>0.034</td>
<td>4.99</td>
<td>1, 4993</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Year</td>
<td>0.097</td>
<td>0.020</td>
<td>24.66</td>
<td>1, 4993</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Days between observations</td>
<td></td>
<td></td>
<td>13.09</td>
<td>1, 4993</td>
<td>0.02</td>
</tr>
<tr>
<td>Peak rut</td>
<td>−0.124</td>
<td>0.034</td>
<td>17.28</td>
<td>1, 4993</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Peak rut (TRUE)</td>
<td>0.006</td>
<td>0.001</td>
<td>6.55</td>
<td>3, 4993</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Minimum temperature</td>
<td>0.011</td>
<td>0.005</td>
<td>4.26</td>
<td>1, 4993</td>
<td>0.04</td>
</tr>
<tr>
<td>Day relative to estrus × Male</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day relative to estrus (before) × Male (same)</td>
<td>−0.347</td>
<td>0.203</td>
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<tr>
<td>Day relative to estrus (exact) × Male (same)</td>
<td>−0.391</td>
<td>0.171</td>
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<tr>
<td>Day relative to estrus (after) × Male (same)</td>
<td>−0.435</td>
<td>0.178</td>
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</tbody>
</table>

The estimated effect size and standard error (SE) from the LMM are given, with F values and P values tested based on type II sums of squares. Effect sizes for each year are not shown.

calculated at a 65% isopleth. Again, grouping day relative to estrus into 2 factor levels showed that females that changed male were more likely to be outside their home range when in estrus than at other times in the rut (t = 4.899, degrees of freedom [df] = 54, P < 0.0001) but were not more likely to be outside their home range on the day after estrus than at other times (t = −1.488, df = 54, P = 0.142, see Figure 3a). This indicates that females return to their rut home range after estrus. Although not significant, the patterns were broadly similar for home ranges calculated at 85% and 90% isopleths (see Table 2, Figure 3b,c).

In analyzing the reproductive consequences of female movements, we identified 40.5% (202 of 499) of estrous females considered in this analysis which were positively identified as being with a different male when in estrus compared with the previous observation, 68.3% of which (106 of 202) moved further than the median distance moved by females when changing harem. Of all females, which changed harem when in estrus, 95 produced a calf that could be assigned a sire from the pedigree, and of females, which both changed harem and moved further than the median distance, when in estrus, 53 produced a calf that could be assigned a sire from the pedigree. For individuals that changed male when in estrus, the assigned sire matched the male the female moved to when in estrus in 43.2% (41 of 95) cases. For individuals which changed male and moved further than the median distance, the assigned sire matched the male the mother moved to when in estrus in 45.0% (24 of 53) cases.

Male phenotypic traits and relatedness analysis

Throughout the rut, females changing harem tended to do so from older to younger males (independent of harem size, average estimated effect of age difference = −0.325, average standard error = 0.034, average Wald value = 94.054, average P value < 0.001, see Figure 4a, Table 3) and smaller to larger harem sizes (independent of male age, average estimate = 0.104, average standard error = 0.009, average Wald value = 122.103, P < 0.001, see Figure 5, Table 3), but there was no association with relatedness of the male to the focal female. In the full model, testing for interactions between male phenotypic traits and female estrus, there was no significant interaction between day relative to estrus and female preferences: the effects of male phenotype on female harem changing were the same for estrous and non-estrous females (see Table 4). However, when male age was considered without the other traits in the model, there was a weak trend toward an interaction between female estrous state and difference in male age (average Wald value = 3.110, average P value = 0.102); this indicates that females in estrus were less likely to move to younger males (see Figure 4b). This discrepancy between models including all male phenotype differences and the model including only male age difference is likely to be due to correlations between harem size and male age, and so the result should be treated with caution—this finding does not provide evidence of mating preference. Considering harem size or relatedness to the female without other male traits in the model had no difference on our findings (in such models, main effect of harem size, average Wald value = 112.794, average P < 0.001, main effect of relatedness, average Wald value = 0.162, average P = 0.749).

Neither differences between males in their age or harem size nor differences in their relatedness to the focal female, had an effect on the distance which females moved when changing harem: After simplification, this model retained no main effects of these terms nor any interactions between these terms and a female’s estrous state (interactions with day relative to estrus in full model: difference in male age: $F_{1,3929.4} = 1.05$, $P = 0.31$, difference in harem size: $F_{1,4606.8} = 0.02$, $P = 0.90$, and difference in relatedness: $F_{1,4391.6} = 0.01$, $P = 0.90$, see Table 5). This indicates that male phenotype and relatedness to the female had no effect on the distance moved by either estrous or non-estrus females.

**DISCUSSION**

In this study, we have shown that the red deer rut, a famous and well-studied example of male competition, is a more complex and dynamic process than previously appreciated. Changes in harem membership are common, with at least a third of females being found in different harem groups on consecutive observations. Moreover, changes in harem membership increase when females come into estrus, a finding in agreement with previous studies of this population, conducted early...
in the study period (Clutton-Brock et al. 1982). In this study, we have also demonstrated that when changing harem, estrous females move substantial distances, up to 4 km, to locations outside of their normal rut home ranges. These distances are further than females changing harem at other times in the rut. That females leave their home ranges during these estrus movements indicate that these behaviors are deviations from normal spatial behavior. Moreover, such excursions are clearly tightly linked to timing of mating, given that on the day after estrus, females were not more likely to be outside their home range than at other times in the rut. Further, around 45% of estrous excursions result in the male into whose harem a female moved gaining paternity of the female’s offspring. This indicates that female excursions have the potential to affect individual male reproductive success and so, potentially, sexual selection on male traits.

Excursions by breeding females, such as those described here, have been noted in other polygynous mammals, but the causes and significance of the behavior are often poorly understood or controversial (Hoffman et al. 2007; Kotiaho et al. 2008; Richard et al. 2008). We predicted that females in estrus move between harems in order to mate with males, which can provide them with direct or indirect fitness benefits, and as such, that female excursions would be nonrandom with respect to male phenotype. Further, given such movements are likely to be costly (Byers et al. 2005), we expected females to accept greater costs, that is to move further, when the fitness benefits were higher: when the magnitude of the difference between the male left and the male joined was larger, suggesting females do not move further when the potential benefits are greater. However, it should be noted that the interpretation of this latter result is dependent on the spatial distribution of males with respect to trait values: if for example, males rutting in similar locations had similar trait values, then females moving further would inevitably move to more dissimilar males.

Our results do show that, throughout the rut, when females changed harem, they were more likely to enter the harems of younger males (see Figure 4a). That said, when male age was considered without correcting for female tendency to join larger harems, we found females in estrus did not show

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**Table 2**

Results from an LM in which the response variable was the proportion of females outside their home range

<table>
<thead>
<tr>
<th>Isopleth %</th>
<th>Term</th>
<th>df</th>
<th>F value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>65</td>
<td>Day relative to estrus</td>
<td>3, 109</td>
<td>6.9301</td>
<td>0.0003</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>1, 108</td>
<td>23.4540</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>85</td>
<td>Day relative to estrus</td>
<td>3, 110</td>
<td>1.4927</td>
<td>0.2210</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>1, 109</td>
<td>6.4409</td>
<td>0.0126</td>
</tr>
<tr>
<td>90</td>
<td>Day relative to estrus</td>
<td>1, 110</td>
<td>1.6356</td>
<td>0.1855</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>1, 109</td>
<td>1.7325</td>
<td>0.1910</td>
</tr>
</tbody>
</table>

Results reported here are F values and P values tested based on type II sums of squares for an LM, testing the effects of day relative to estrus and whether females changed harem on the proportion of females outside their rut home range. Results are given for home ranges calculated at 3 isopleths: 65%, 85%, and 90%.
a tendency to preferentially join older or younger males (Figure 4b). In general, our results provide little evidence that females have preferences for mating with younger males. Female choice for mating with younger males is not generally predicted by theory (although females may prefer young males if, for example, viability/fertility in old age is negatively genetically correlated with early adult viability/fertility, Trivers 1972; Hansen and Price 1995; Brooks and Kemp 2001), and there is no reason to expect older males to be better able to protect females from harassment. The effect of male age on female harem changing therefore seems less likely to be the result of female mate preference than an artifact of attempts by young males to segregate small groups of females from harems during fights between more dominant males, or of females having to cross the peripheral harems of young males to move between feeding sites (Clutton-Brock et al. 1982). Clutton-Brock et al. (1982) found females were less likely to mate with younger males and that the potential costs of mating with inexperienced males were high in terms of injuries gained when mating. Our results hint that females may avoid young males when in estrus, given the presence of a weak trend for an estrous female to be less likely to be found with young males after changing harem than females not in estrus (Figure 4).

Secondly, throughout the rut, when females changed harem, they were also more likely to be found in larger harems independent of the effect of male age; however, again this was not specific to nor changed when females were in estrus. Females may have preferences for larger harems because harem size is an indicator of male quality (mediated through male–male competition, Clutton-Brock et al. 1979) or because of a tendency to join other females, as has been described in lekking ungulates (Clutton-Brock and McComb 1993). Females may benefit from reduced per capita rates of harassment in larger harems (Clutton-Brock et al. 1992; Carranza and Valencia 1999). Alternatively, given male harem size is linked to fighting ability, males with large harems may be more likely to obtain females through male–male competition (Clutton-Brock et al. 1982). However, given the tendency of females to be found in larger harems after changing harem was not specific to estrous females, our findings do not indicate positive evidence that movements of females when in estrus are a result of female preferences for mating with males holding larger harems.

Overall therefore, although we show movements of females in this population are clearly associated with the timing of mating and frequently result in mating with the novel male, our results do not support the prediction that females in estrus systematically move between harems in order to mate with preferred males. Of course, it is important to note that females may show preferences for traits other than those considered here: for example, various studies have suggested female preferences for properties of the male roar (McComb 1991; Reby et al. 2001, 2010; Reby and McComb 2003; Charlton et al. 2007a, 2007b, but see Charlton et al. 2008). It is also worth considering that the optimal mate may not be the same male for all females: for example, females may trade off mating with a male which can provide additive genetic benefits with mating with males which are more genetically compatible (Mays and Hill 2004; Neff and Pitcher 2005); particularly if the optimal balance varies depending on the likely sex of their offspring (Carranza et al. 2009). Alternatively, females may vary in their ability to exert mate preferences with condition or experience (Jennions and Petrie 1997).

![Figure 4](https://academic.oup.com/beheco/article-abstract/22/4/808/299167)

**Table 3**

Results of GLMM, testing the main effects of differences in male phenotype on the probability of a female moving between pairs of males

<table>
<thead>
<tr>
<th>Term</th>
<th>Estimate</th>
<th>SE</th>
<th>Wald value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Av.</td>
<td>0.05</td>
<td>0.95</td>
<td>Av.</td>
</tr>
<tr>
<td>Difference in age</td>
<td>-0.325</td>
<td>-0.351</td>
<td>-0.302</td>
<td>0.034</td>
</tr>
<tr>
<td>Difference in harem size</td>
<td>0.104</td>
<td>0.098</td>
<td>0.110</td>
<td>0.009</td>
</tr>
<tr>
<td>Difference in relatedness</td>
<td>2.550</td>
<td>-1.277</td>
<td>3.892</td>
<td>2.611</td>
</tr>
</tbody>
</table>

Results reported here are average and 5th and 95th percentiles, for estimates, standard errors (SE), Wald and P values from Wald tests for differences in male traits and relatedness to the focal female, for 1000 runs of the GLMM.
Such variation may mask female preferences for male phenotypes in our study. Further, given females are highly philopatric, and unpublished data suggest males show some consistency in rutting location between years (Stopher K, in preparation), it is possible females do not move to a preferred male but to a “different” male; one with whom they had not mated in previous years. Such behavior could be favored either to maximize diversity of paternal genetic combinations (Worthington-Wilmer 2000), or because of knowledge of reproductive failure in previous breeding attempts with that male, analogous to “divorce” observed in monogamous birds (reviewed in Choudhury 1995). However, in general, it appears most likely that much of the harem change we observe amongst females results from passive responses to male disturbance (fights, harassment, and so on) rather than preferences for male phenotypic traits, and the reasons for the sometimes extraordinary distances moved by females when in estrus remain unclear. In contrast to other polygynous mammals (e.g., roe deer, Lovari et al. 2008), in the harem-defense system of red deer, where males defend groups of females at close proximity rather than territories, females are unlikely to have to search for a mate. Further, although we have found effects of rain and temperature on the distances females move each day, after accounting for these effects females in estrus still moved significantly further than females not in estrus. Therefore, these excursions are unlikely to be a result of environmental effects (cf. Twiss et al. 2007). Further work is therefore needed to unravel why females in estrus make such long distance movements, and particularly to explore the link between rates of male disturbance within the harems of different males and both the propensity of females to change harems and the distances traveled by females when disturbed.

Understanding the ultimate causes and consequences of excursions of breeding females in polygynous mammals requires data to link excursions with reproductive state of females, to compare male phenotypes and to assess whether excursions affect which males gain paternity of a female’s offspring. Using a uniquely detailed long-term behavioral data, we have identified unusual movements of red deer females at close proximity rather than territories, females are unlikely to have to search for a mate. Further, although we have found effects of rain and temperature on the distances females move each day, after accounting for these effects females in estrus still moved significantly further than females not in estrus. Therefore, these excursions are unlikely to be a result of environmental effects (cf. Twiss et al. 2007). Further work is therefore needed to unravel why females in estrus make such long distance movements, and particularly to explore the link between rates of male disturbance within the harems of different males and both the propensity of females to change harems and the distances traveled by females when disturbed.

### Table 4

Results of a GLMM, testing interactions between day relative to estrus and effect of differences in male phenotype on the probability of a female moving between pairs of males

<table>
<thead>
<tr>
<th>Interaction term</th>
<th>Wald value</th>
<th>0.05</th>
<th>0.95</th>
<th>0.05</th>
<th>0.95</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day relative to estrus × difference in age</td>
<td>2.394</td>
<td>0.907</td>
<td>4.277</td>
<td>0.155</td>
<td>0.039</td>
</tr>
<tr>
<td>Day relative to estrus × difference in harem size</td>
<td>0.143</td>
<td>0.001</td>
<td>0.512</td>
<td>0.768</td>
<td>0.474</td>
</tr>
<tr>
<td>Day relative to estrus × difference in relatedness</td>
<td>0.181</td>
<td>0.006</td>
<td>0.587</td>
<td>0.718</td>
<td>0.444</td>
</tr>
</tbody>
</table>

Results reported here are average and 5th and 95th percentiles, for estimates, standard errors, Wald and P values from Wald tests for the interaction between differences in male traits and relatedness to the focal female and day relative to female estrus, for 1000 runs of the GLMM.
females linked specifically to estrus and have shown that these movements have consequences for the reproductive success of individual males. However, the harem changing and movements we observe in estrous females appear to be random with respect to male phenotype, suggesting these are passive responses to male–male competition and turnover; yet if this is true, it remains unclear why females move such long distances in their response. It is therefore clear that excursions of females should not be assumed to be expression of female mate choice. However, there remains potential for such movements to affect male mating success, as demonstrated by the number of paternities resulting from female movements in this study. If the causes of movement can be understood, the excursions of female polygynous mammals are therefore likely to be a fertile area for future research in understanding conflict between female and male mating behavior in such systems.

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Natural Environmental Research Council (NERC) PhD studentship to K.Y.S. (NE/F008945/1) and additional funding from the Macaulay Institute, Aberdeen. The Rum Red deer project has been funded by a succession of NERC grants (the final of which relevant to this study was NERC grant NE/B504314/1).

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