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Biol. Lett. 2007 **3**, 12-15

doi: 10.1098/rsbl.2006.0559

References

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The impact of climatic variation on the opportunity for sexual selection

Sean D. Twiss^{1,*}, Christopher Thomas¹,
Veronica Poland^{2,3}, Jeff A. Graves³
and Patrick Pomeroy²

¹School of Biological and Biomedical Sciences, Durham University, Durham DH1 3LE, UK

²SMRU, University of St Andrews, St Andrews, Fife KY16 8LB, UK

³School of Biology, University of St Andrews, St Andrews, Fife KY16 9TH, UK

*Author for correspondence (s.d.twiss@durham.ac.uk).

Many studies have demonstrated influences of climatic variation on a variety of ecological processes, however, its impact on the potent evolutionary force of sexual selection has largely been ignored. The intensity of sexual selection is a fundamental parameter in animal populations, which depends upon the degree of polygamy and will probably be influenced by the impact of local climatic variation upon 'environmental potential for polygamy'. Here, we provide evidence of a direct effect of local climatic variation on the intensity of sexual selection, by showing a clear correlation between local weather conditions and inter-annual changes in the degree of polygamy in a long-term study of colonially breeding grey seals (*Halichoerus grypus*). Our results show that changes in local weather conditions alter the annual proportion of males contributing to the effective population size (N_e) by up to 61%. Consequently, over the 'lifetime' of a cohort, a broader range of individuals will contribute genetically to the next generation if local weather conditions are variable. In the context of predicted future changes in climatic variation, these findings have broad implications for population genetics of socially structured animal systems through the major influence that the degree of polygamy has upon N_e .

Keywords: climate; polygyny; reproductive success; effective population size; *Halichoerus grypus*

1. INTRODUCTION

The influence of climatic variation on ecological processes is well documented (Stenseth *et al.* 2002; Walther *et al.* 2002). At the population or community level, these studies focus on phenological (Stevenson & Bryant 2000; Both *et al.* 2004) and range shifts (Warren *et al.* 2001; Crick 2004) or population dynamics and interspecific interactions (Stenseth *et al.* 2002; Walther *et al.* 2002). At the individual level, the impacts on life-history traits (Nussey *et al.* 2005) and physiological responses (Bernardo & Spotila 2006) have been demonstrated. However, the effect of climatic variation on animal mating patterns remains largely unexplored,

despite the fact that individual variation in reproductive success provides the impetus for the potent evolutionary force of sexual selection and is a primary determinant of genetically effective population size (Storz *et al.* 2001; Ardren & Kapuscinski 2003).

Changes in the degree of polygamy can have profound effects upon behavioural and demographic processes and therefore population genetics (Ardren & Kapuscinski 2003). Many factors affect variation in the degree of polygamy, in particular, the spatial and temporal distribution of resources and/or mates (Emlen & Oring 1977; Clutton-Brock 1989). Climatic variation clearly impinges upon the distribution of ephemeral resources, and consequently mates; we might therefore expect a clear link between local climate and the intensity of sexual selection in animal systems. However, this critical ecological process remains curiously absent from the literature on ecological effects of climatic variation (Stenseth *et al.* 2002; Walther *et al.* 2002).

Climate change has been linked to phenotypic changes in sexually selected traits (West & Packer 2002; Møller & Szép 2005), but the general importance of climatic variation to sexual selection is not yet known (West & Packer 2002). Here, we provide strong evidence of a direct effect of climatic variation on the intensity of sexual selection by examining individual variation in male mating success in a wild population of grey seals (*Halichoerus grypus*) in relation to changing weather conditions across nine successive breeding seasons at one colony.

Grey seals are polygynous, colonial and annual breeders with a discrete, predictable reproductive season. In the UK, adults aggregate to breed each autumn typically at remote island sites. Female dispersion patterns on the colony are determined by their pupping site preferences for fine-scale habitat features, in particular access to small pools of water necessary for behavioural thermoregulation (see electronic supplementary material). Access to preferred pupping sites confers greater success in raising their single pup (Pomeroy *et al.* 2001; Twiss *et al.* 2003). Males compete to maintain home ranges among female aggregations in order to gain copulations when females enter oestrus towards the end of lactation (Twiss *et al.* 2006). The spatio-temporal distribution of females is the ultimate determinant of environmental potential for polygamy (Emlen & Oring 1977) in grey seals as neither sex forage during the breeding season, but rely on stored energy reserves (blubber). Therefore, we predicted that inter-annual variation in rainfall, which determines pool availability, would affect the degree of polygyny in this system.

2. MATERIAL AND METHODS

(a) Quantifying the opportunity for sexual selection

Data were gathered at the North Rona colony (Scotland) from 1996 to 2004. Behavioural observations were made from hides overlooking the study area (Twiss *et al.* 2006) from the 1st to 25th of October. All males present in the study area for more than 1 h were reliably identified by pelage, scarring patterns and/or brands (Twiss *et al.* 2006). Between 101 and 153 males were individually identified in each breeding season. The majority of these males (95%) were present for three or fewer breeding seasons and only two individual males were present for all 9 years. All observed successful copulations (where intromission was clearly achieved and the copulation proceeded, uninterrupted, to completion) were recorded (Twiss *et al.* 2006). Mating success for each male was

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2006.0559> or via <http://www.journals.royalsoc.ac.uk>.

defined as the number of successful copulations with females not observed copulating previously with either the same or other males. Measures of reproductive success for a subset of genotyped males correlate well with these behavioural measures of their mating success at this colony (Twiss *et al.* 2006). Therefore, in this study, we are confident that variation in male mating success is a reliable and accurate index of variation in reproductive success and representative of the degree of polygyny. We used these measures to compute the standardized variance in male mating success ($I_{\text{males}} = \text{variance}/(\text{mean mating success}^2)$) as a measure of the opportunity for sexual selection for each breeding season (Wade & Arnold 1980).

(b) Mapping seal locations

The daily locations of all females (with identities where known), births, matings and hourly locations of all males (with identities) within the study area were recorded precisely (sub-metre accuracy) in an ARC-INFO GIS (Twiss *et al.* 2003, 2006). This spatial database permitted the computation of male home ranges (95% contours using kernel estimators) and measures of female density (median nearest neighbour distances). Examination of inter-diem locational shifts of known females provided data on the extent of female movement. Not all datasets were available for all nine seasons due to differing data collection priorities.

(c) Weather data

Total rainfall (mm) for October was obtained from the Meteorological Office. The closest consistent historic record is from the meteorological station at Stornoway Airport, 105 km Southwest of North Rona. There was no significant temporal autocorrelation in annual rainfall data. Rainfall measurements made by S.D.T on North Rona between 2001 and 2004 correlate with the Stornoway measurements, although the sample size is small ($R^2 = 0.94$, $n = 4$, $p = 0.06$).

3. RESULTS

We found a highly supported positive correlation (two-tailed Spearman's rank) between the opportunity for sexual selection (I_{males}) and rainfall (figure 1), indicating greater polygyny when pools of water were abundant on the colony. Given that a male's ability to monopolize mating opportunities is related to operational sex ratios and the spatio-temporal distribution of females (Emlen & Oring 1977), we examined if any of these factors also exhibited inter-annual relationships with either I_{males} or rainfall (see electronic supplementary material) in order to discern a potential underlying mechanism. No significant correlations were found with annual measures of (i) total number of individually identified males, (ii) total number of observed successful copulations, (iii) median duration of male stay ashore, (iv) median size of male home range, (v) mean daily female: male ratio, (vi) 'female-days' (an index of total female numbers), and (vii) median female nearest neighbour distance (index of female dispersion patterns). However, there was a negative correlation between rainfall and female movement, such that females tended to be more mobile in drier years (figure 2), although this trend was non-significant after correction for multiple tests. However, this trend supports previous observations at this colony (Redman *et al.* 2001).

4. DISCUSSION

We have shown here that the opportunity for sexual selection varies in response to climatic variation in this colony of grey seals, with a reduced degree of polygyny in drier seasons. Furthermore, our data identify a probable underlying mechanism for this relationship. The increased mobility of females in

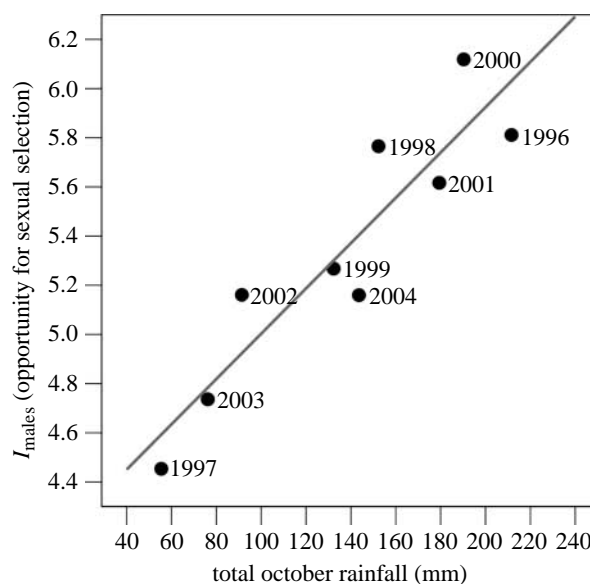


Figure 1. The standardized variation in mating success among male grey seals at North Rona was more extreme in years with heavier rainfall ($R = 0.92$, $p < 0.001$, $n = 9$).

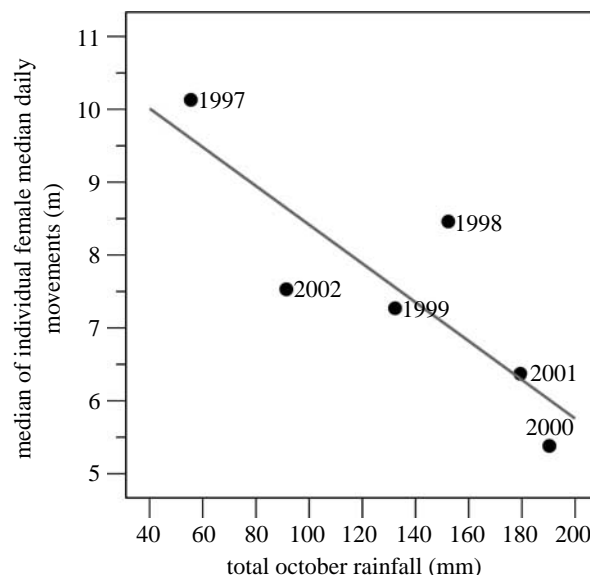


Figure 2. Female grey seals were more mobile in drier seasons ($R = -0.83$, $p = 0.042$, $n = 6$). Median of individual female median daily movements in m, which is equal to the median distance moved between successive days for each known female using their daily mapped locations, then collating these values for each year to compute an overall median for daily female movements.

drier seasons reduces the ability of dominant males to monopolize matings, allowing a greater number of less dominant males to gain matings.

Why are females more mobile in drier seasons? Female grey seals exhibit a high degree of inter-annual site fidelity on North Rona, returning to within a median distance of 39 m from their previous pupping sites (Pomeroy *et al.* 2005). Having pupped, females tend to be 'tied' to the pupping location for the remainder of their stay due to the limited mobility of pups. If the season subsequently proves to be dry with few pools, females without access to pools are forced to commute, sometimes relatively long

distances to access this important resource, and then return to nurse their pups (Redman *et al.* 2001).

Autumnal weather patterns in the UK are projected to change over this century with significant increases in inter-annual variability of precipitation and temperature (Hulme *et al.* 2002). Although many studies have examined the potential responses of a variety of ecological processes to such climate change scenarios (Stenseth *et al.* 2002; Walther *et al.* 2002), very few have explored the impact on sexual selection (Møller & Szép 2005; Spottiswoode *et al.* 2006). Our findings demonstrate changes in individual behaviour that lead to a shift in the distribution of individual reproductive success (degree of polygyny) over time within a population. Such individual level responses are potentially rapid and plastic, and have wide-ranging consequences.

The degree of polygyny is a primary determinant of genetically effective population size (N_e), and therefore changes in the variance of reproductive success can have profound consequences for the behavioural, demographic (including extinction risk) and evolutionary dynamics of populations (Storz *et al.* 2001; Laporte & Charlesworth 2002; Ardren & Kapuscinski 2003). Increases in polygyny will decrease the diversity of a population in isolation, since N_e is 'reduced by an increased male fertility variance' (Laporte & Charlesworth 2002). Temporal variation of N_e within a wild vertebrate population has only recently been shown (Ardren & Kapuscinski 2003). We have found, for the first time to our knowledge, inter-annual variation in the degree of polygyny, with its consequent impact on N_e , in relation to climatic variation. In our study, increased rainfall enhances the degree of polygyny, while dry years allow a greater number of previously unsuccessful males to sire offspring. A total of 23 males gained at least one copulation in the wettest year, compared with 37 in the driest year, representing a 61% increase in the number of males contributing to N_e . While the precise relationship in other polygamous populations or species may differ, the important conclusion is that over the 'lifetime' of a cohort, a broader range of individuals will contribute genetically to the next generation if local weather conditions are variable, than expected from the variance in mating success within a single breeding episode. This subtle effect of changing climatic variability has widespread implications, as relatively few animal populations have mating patterns in which the level and form of polygamy are not intimately linked to resource distribution (Clutton-Brock 1989).

This work was funded by a NERC grant and postdoctoral fellowships. V.P. was supported by an NSERC postgraduate scholarship. We thank R. Harcourt, S. Moss, P. Redman and S. Ruddell for their help in the field, and S. A. Richards for his helpful comments on the manuscript.

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