Costs of mating competition limit male lifetime breeding success in polygynous mammals

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Although differences in breeding lifespan are an important source of variation in male fitness, the factors affecting the breeding tenure of males have seldom been explored. Here, we use cross-species comparisons to investigate the correlates of breeding lifespan in male mammals. Our results show that male breeding lifespan depends on the extent of polygyny, which reflects the relative intensity of competition for access to females. Males have relatively short breeding tenure in species where individuals have the potential to monopolize mating with multiple females, and longer ones where individuals defend one female at a time. Male breeding tenure is also shorter in species in which females breed frequently than in those where females breed less frequently, suggesting that the costs of guarding females may contribute to limiting tenure length. As a consequence of these relationships, estimates of skew in male breeding success within seasons overestimate skew calculated across the lifetime and, in several polygynous species, variance in lifetime breeding success is not substantially higher in males than in females.

1. Introduction

The reproductive success of male mammals varies widely [1,2], partly as a consequence of variation in mating rate and partly as a result of contrasts in longevity [1,3]. While many studies have explored the extent and causes of variation in mating rate among males within breeding seasons [4–7], relatively few have investigated the extent and causes of variation in the breeding lifespan of males [8]. Intraspecific comparisons of the breeding tenure of males show that the breeding lifespan of individual males is reduced when the intensity of competition over females is high [9,10]. Males defending large numbers of females may be faced with more frequent challenges by competitors, so that the probability that they will be displaced is relatively high [11,12]. As a result of frequent challenges, they may also experience increased risks of injury or energetic costs which reduce the chance that they will win repeated interactions [13,14]. Allocation of resources to secondary sexual characteristics or physiological traits associated with reproductive competition may also reduce the potential allocation of resources by males to somatic maintenance [15].

One consequence of the effects of male competition on the duration of male breeding tenure is that, in polygynous animals, male breeding success is often restricted to a relatively small number of years when individuals are in their prime [1,4,16–18]. As a result, estimates of standardized variance in male breeding success within years (or reproductive skew) will usually overestimate standardized variance in male success calculated over the lifetime of individuals [1,19]. As breeding in females is usually distributed across a longer period and females may show consistent individual differences in breeding success, this suggests that estimates of sex differences in reproductive skew based on data on particular seasons may often overestimate sex differences in lifetime skew by a substantial margin [20–22].

While interspecific comparisons show that the breeding tenure of male mammals is negatively associated with the degree of polygyny [8], there have been few recent attempts to examine the distribution of sex differences
in fitness variance since before 1990 [1]. A wider range of
genetic data are now available. Here, we use phylogenetic com-
parative approaches to investigate the extent and potential
causes of species differences in male breeding tenure length
among mammals and their effects on variation in male lifetime
breeding success. We focus on mammals partly because the
relative influence of competition between males varies
widely between breeding systems and partly because estimates
of male breeding tenure are available for a substantial number
of species. In addition, the median number of months that
dominant males retain their tenure has been shown to be a
good estimator of male breeding lifespan, as males sire only
few offspring outside their period of dominance [6].

We first test whether interspecific differences in median
male breeding tenure length are related to maximum longevity,
natural survival and the age of first reproduction in females in
order to determine whether male breeding tenure length is cor-
related with variation in the pace of reproduction or breeding
lifespan of females [8]. Subsequently, we investigate whether
male breeding tenure length is related to factors that are
likely to affect the intensity and frequency of competition
between males, including the number of females that males
can potentially monopolize and the rate at which females
give birth. Finally, we assess how mating rate and breeding life-
span affect variance in male lifetime fitness and compare
measures of variation in lifetime breeding success in females
and males for different mating systems.

2. Material and methods

Information on male breeding tenure length was collected by
searching ‘Web of Science ISI’, recording the median number of
months males retain the dominant position in social groups
based on records of populations in the wild (see also [23]). Breed-
ing tenure was defined to start once a male obtains a dominant
position, either by taking over a group of females or after que-
uing for dominance within a group, and ends after he is displaced
by another male and does not successfully attain dominance
again in the same or in another group. The start of males’ breed-
ing lifespan is usually several months or years after they reach
adulthood, and males might survive after their breeding lifespan
has ended. Data for the length of the inter-birth interval, maxi-
mum lifespan (separating records from the wild and captivity),
age at first reproduction and population density were drawn
from published datasets [24,25]. We extracted data on adult sur-
vival in wild populations calculated across all ages from previous
comparative studies [26,27]. We recorded the degree of sexual
dimorphism in body mass as a proxy for physical competition
[28–31] and testes mass relative to body mass as proxy for
sperm competition [32]. Data on the number of breeding adult
females and males per group were extracted from the papers
reporting male breeding tenure length or references cited there
to match them to the specific population, and we checked that
values did not represent outliers for the respective species by
comparing them to published reviews [33]. We recorded whether
a single male and a single female monopolize reproduction
(monogamous), whether a single male resides with several
breeding females (harem), or whether multiple males and
females live in social groups (multimale/polygynandrous).
Information on the reproductive share of alpha males was
obtained from [6] and used as measure of reproductive skew in
groups. In addition, for a number species which have been the
subject of long-term studies, and for which paternity has been
determined using genetic methods, we extracted information
on the lifetime breeding success of males and females by
counting the number of offspring assigned to individual males
and females. We recorded whether assigned offspring were
previously assigned or not. All studies sample offspring after the
most critical period of early offspring mortality, developmental
stage did not seem to consistently bias the measure of variance
in lifetime breeding success or affect the results, and we present
the results from the full dataset. When the information did not
specifically list the proportion of non-breeding individuals, we
estimated these given the number of surviving offspring that
were reported for the breeding individuals and calculated the
standardized variance in lifetime breeding success across both
breeders and non-breeders. The full dataset with references is
listed in the electronic supplementary material. All continuous
variables were log-transformed prior to analyses.

We performed multivariate generalized least-squares
regressions on the life-history variables while correcting for phylo-
genetic relationships. Regressions were performed in R with
functions of the packages caper [34] and geiger [35] (function
‘pgls’ and ‘gls’ with a correlation structure estimated by the func-
tion corPagel), using maximum likelihood to estimate the best
value of Pagel’s λ, and with MCMCglmm [36]. The three methods
identified the same model as best explaining the data in all cases,
and below we only report the results using the function ‘pgls’.
These methods include the phylogenetic similarity of species as a
covariance matrix, which we calculated based on the updated
mammalian supertree [37] using functions of the package APE
[38] to truncate the tree. We first compared the effect of each life-
history factor separately in explaining variation in male breeding
lifetime tenure to null models. Significance of terms was assessed
based on a comparison of Akaike (for gls) and deviance (for
MCMCglmm) information criterion values. Next, we assessed
whether any model that included interactions between the factors
provided a better explanation of the data, comparing different
combinations using the function ‘dredge’ as implemented in the
package ‘MuMIn’ [39]. Tables showing model comparisons are
provided in the electronic supplementary material.

3. Results

Across 61 species of mammals for which observational data on
variation in male breeding success were available (see the elec-
tronic supplementary material), median breeding tenure of
males varied between nine and 144 months. Closely related
taxa have similar tenure length and there is a detectable phylo-
genetic signal (maximum-likelihood estimation of λ = 0.87
(95% confidence interval: 0.71–0.97), where 1.00 indicates a per-
fact fit to the phylogenetic tree). However, the best explanatory
models described below indicate that there is no residual phylo-
genetic signal, suggesting that male breeding tenure length
adapts to changes in life history and social structure with little
evolutionary lag. Contrasts in male breeding tenure length do
not appear to reflect species’ differences in the risk of extrinsic
mortality, as variation in male breeding tenure length across
species is not associated with maximum longevity in either
sex (n = 58 species, λ = 0.84, AICc = −18.0 versus AICc of
null model = −16.7) (figure 1) or with rates of adult survival
in wild populations (n = 23 species, λ = 0.75, AICc = 13.5
versus AICc of null model = 10.4; for full model comparisons,
see the electronic supplementary material).

Across the 61 species, contrasts in male breeding tenure
length are consistently associated with: (i) the average du-
ration of inter-birth intervals among females (n = 61 species,
λ = 0.66, AICc = −46.3 versus AICc of null model = −16.6,
v = 0.47), with males remaining dominant for an average
of three breeding seasons (range 1–7) (figure 1); (ii) the
average number of females per breeding group (model including inter-birth interval and number of females per group: $n = 61$ species, $\lambda = 0.50$, $r^2 = 0.58$, AICc $= -58.4$ versus AICc of model including only inter-birth interval $= -46.3$); and (iii) whether groups contain a single or multiple males (including single- versus multimale system as a factor in the correlation: $n = 61$ species, $\lambda = 0.36$, $r^2 = 0.64$, AICc $= -61.9$ versus $-58.4$), with male breeding tenures being shorter in species with monogamous and harem systems and longer in multimale species (figure 2).

Among species in which groups contain a single breeding male, the length of the inter-birth intervals and the number of females in the group explain about 81% of the variation in male breeding tenure length. The tenure of dominants is reduced by approximately 30% of an inter-birth interval for each additional female in the group: changes from a single female (monogamy) to two females have similar effects to those of additional increases in female group size. For species living in social groups with multiple males, the best model explaining variation in tenure length included the inter-birth interval, the number of females in the group and the sex ratio in the group, explaining about 84% of the variation. Across species with multiple males per group, male breeding tenure lengths are shorter in species in which groups contain a higher number of females, each additional female leading to a decrease of approximately 10% of an inter-birth interval. The effect of the sex ratio in the group is independent of changes in female number so that, for a given sex ratio, males have longer tenures in smaller groups. This suggests that dominants may be able to defend a certain proportion of females in the group, rather than a certain number: for example, if the sex ratio is one female per male, the dominant male might defend 50% of the females and therefore have a higher mating success and shorter tenure if groups contain more females.

In groups containing multiple males, male breeding tenure is not associated with the number of males in the group, the proportion of alpha male paternity, relative testes size or the degree of sexual dimorphism in body weight, although these factors are highly correlated among themselves. As the number of male competitors in the group increases, the proportion of offspring dominant males sire in a group declines ($n = 14$ species, $\lambda = 0.0$, $r^2 = 0.67$, AICc $= 122.0$ versus null model AICc 134.8), sexual dimorphism decreases ($n = 31$ species, $\lambda = 0.93$, $r^2 = 0.32$, AICc 151.7 versus null model AICc 161.1) and relative testes sizes increase ($n = 14$ species, $\lambda = 0.0$, $r^2 = 0.75$, AICc $= 44.9$ versus 46.5). Male breeding tenure length does not differ between species in which males immigrate with relatives (as in lions) and species in which males immigrate individually and join a queue of unrelated males (as in savannah baboons).

The presence of a strong negative correlation between male breeding tenure length and the number of females per group suggests that measures of variation in reproductive skew among adult males based on data collected in single seasons will overestimate variation in lifetime breeding success. Measures of standardized variance in lifetime breeding success in both sexes are available for few species, but the data available suggest that reproductive skew among males measured

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**Figure 1.** Male breeding tenure length increases with the length of the inter-birth interval. Across mammalian species, the length of time a dominant male manages to maintain his tenure (measured in months) increases as the inter-birth interval of females increases (panel (a), measured in months). This association is not a consequence of constraints on tenure length owing to senescence as a consequence of the faster or slower life history of a species, as male breeding tenure length is not correlated with maximum longevity (panel (b), measured in months).

**Figure 2.** Male breeding tenure length decreases as the number of females per group increases. Males maintain their dominant position longer in species in which there are only few females in the group. For a given number of females in the group, tenure lengths are shorter in species in which groups contain only a single male (open squares) compared with species in which groups contain multiple females and multiple males (stars). For comparison, tenure length has been adjusted for the length of the inter-birth interval of the species.
within single breeding seasons is not a consistent predictor of standardized variance in male lifetime breeding success ($r^2 = 0.03$, $p = 0.29$, $n = 10$ species), with large values in skew consistently overestimating variance in male lifetime breeding success. Similarly, variation in breeding tenure explains only a limited portion of the species differences in standardized variance in male lifetime breeding success ($r^2 = 0.17$, $p = 0.11$, $n = 12$ species). While reproductive skew among females measured within single breeding seasons also does not predict species differences in standardized variance in female lifetime breeding success ($r^2 = 0.30$, $p = 0.12$, $n = 7$ species), differences in female breeding lifespan explain a large proportion of the species differences in standardized variance in female lifetime breeding success ($r^2 = 0.58$, $p = 0.002$, $n = 12$ species).

Across the 15 species in our sample, skew in male lifetime breeding success does not consistently exceed skew in female lifetime breeding success ($V = 28$, $p = 0.07$, $n = 15$ species) (figure 3a). This is partly owing to the high values in the standardized variance in lifetime breeding success of females observed in cooperatively breeding species, like the meerkat and red wolf (figure 3b), whereas in polygynous species skew in lifetime breeding success appears to be higher in males than in females. For both females and males, skew in lifetime breeding success is not consistently higher in species with polygynous compared with monogamous breeding systems (males: $W = 23$, $p = 0.95$; females: $W = 32$, $p = 0.21$).

4. Discussion

Our findings show that median male breeding tenure varies from less than 1 up to 12 years between species and is an important determinant of differences in male lifetime breeding success. Male breeding tenure lengths are shorter in species in which dominant males have the potential to defend a larger number of females during breeding seasons, as changes in the number of females and the sex composition of social groups are associated with interspecific contrasts in male breeding lifespan. The presence of a strong negative correlation between male breeding tenure length and the number of females per group suggests that measures of variation in reproductive skew among adult males based on data collected in single seasons will overestimate variation in lifetime breeding success. Our data on observed standardized variance in lifetime breeding success of females and males provide support to earlier studies which questioned whether variation in breeding success is consistently greater in males than females [1,12,19,22,40].

The median duration of male breeding tenure is unrelated to most life-history parameters. In most mammalian species, male breeding tenures are substantially shorter than the breeding lifespans of females [8]. This supports previous suggestions that sexual selection might act differently on males and females. Females are predicted to experience selection which either favours the rapid production of offspring which themselves reproduce quickly or which maximizes the number of breeding attempts [41]. As expected, we find that contrasts in breeding lifespan explained interspecific differences in the variance in lifetime skew in females but not in males. However, as the frequency and intensity of competition over access to females appears to limit male breeding lifespan, neither reproductive skew nor breeding tenure provides sufficient estimates of the intensity of sexual selection in males. While our results extend findings in intraspecific studies to show that contrasts between species are shaped by similar trade-offs between mating competition and male breeding tenure, more detailed long-term studies will be needed to reveal the underlying proximate cause for this relationship.

Previous studies have suggested that as male breeding tenure is relatively short in many species and is strongly affected by differences in age, estimates of standardized variation in male breeding success calculated across adults within seasons are likely to substantially overestimate variation in lifetime breeding success [1,11], and some studies have argued that the variation in male fitness may not necessarily exceed variation of female lifetime breeding success [42,43]. Our sample of data on standardized variance in lifetime breeding success in males and females support these suggestions.
that the values for males may not be substantially higher than for females in polygynous species, whereas in monogamous species maximum values for females frequently exceed values for males as a result of shorter male life spans.

These findings are relevant to our understanding of sex differences in the operation of sexual selection. The evolution of sex differences in morphology and behaviour is often explained as a consequence of increased variance in male fitness generating stronger selection pressures on traits used to compete over reproductive success in males than females. While variance in male fitness may exceed variance in female fitness in polygynous species, the available evidence of variance in lifetime breeding success in males and females suggest that the extent of sex differences in variance in fitness may not be large or consistent. These results suggest that the evolution of sex differences in morphology and behaviour may depend to a greater extent on the form of reproductive competition in males and females [44] and on the relative strength of selection operating on particular traits [12,19]. While the degree of sexual selection might be similar between the sexes and across mating systems, selection might target different traits that permit individuals to increase their breeding success. The frequently poor relationship between breeding systems and sexual dimorphism as well as the development of male weaponry or secondary sexual traits in species where variance in female breeding success exceeds variance in male breeding success [45] may be explained if in many species males still face more physical competition to increase breeding success.

References


