A R T I C L E

Marine Mammal Science 🌊

Offspring sex ratio increases with paternal reproductive success in a colony of southern elephant seals

Hassen Allegue[1] 🆔 | **Christophe Guinet**[2] 🆔 | **Samantha C. Patrick**[3] 🆔 |
Cécile Ribout[2] | **Coraline Bichet**[2] 🆔 | **Olivier Lepais**[4] 🆔 |
Denis Réale[1] 🆔

[1]Département des Sciences Biologiques, Université du Québec à Montréal, Québec, Canada

[2]Centre d'Etudes Biologiques de Chizé, CNRS-La Rochelle Université, Villiers en Bois, France

[3]School of Environmental Sciences, University of Liverpool, Liverpool, UK

[4]Université de Bordeaux, INRAE, BIOGECO, Cestas, France

Correspondence
Hassen Allegue, Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC, Canada.
Email: h.all@disroot.org

Funding information
Fond de Recherche du Québec - Nature et Technologies, Grant/Award Number: 283511; Institut polaire français Paul-Émile Victor; French National Centre for Scientific Research; Natural Sciences and Engineering Research Council of Canada, Grant/Award Numbers: 2020-04745, CGSD3-504399-2017

Abstract

In polygynous species, male reproductive success is often determined by their ability to dominate female harems. Harem-holders sire a disproportionate number of offspring. Male dominance tends to correlate with age, but intense competition and early male mortality limit most males from achieving high social status. To maximize reproductive success despite low rank, offspring sex ratio adjustment may have evolved, favoring the sex with higher fitness. If traits influencing dominance are heritable and confer reproductive advantages, we expect fathers with higher reproductive success to produce more sons, as they are more likely to become dominant. In contrast, subordinate males with lower success may benefit from siring more daughters. We tested this hypothesis on a colony of southern elephant seals breeding on the Kerguelen Archipelago. We used genetic markers to link the paternity of 540 pups to 58 breeding males. We found that the probability of siring a son increases from 43% to 54% with paternal relative reproductive success, supporting the offspring sex ratio adjustment hypothesis. Given that various factors influence sex ratio in a population, future studies should tease apart these ecological processes (e.g., paternal dominance,

maternal condition, local density, or adult sex ratio) and investigate how they interact with each other.

1 | INTRODUCTION

In polygynous mating systems, commonly found in mammalian species (Clutton-Brock, 1989), sexual selection favors male phenotypes that promote the monopolization of receptive females (Andersson, 1994). The strength of selection depends on the ability of males to defend female groups, which could vary with females' distribution in space and time, predation pressures, costs of social living, and activity of competitors (Clutton-Brock, 1989; Emlen & Oring, 1977). When females are highly aggregated and predictable in space and time, most dominant males defend and control aggregations of females (also called harems), resulting in strong reproductive skew favoring harem-holders (Clutton-Brock, 1985; Hoelzel et al., 1999; Hoffman et al., 2003; Lukas & Clutton-Brock, 2014). Male dominance rank is typically assumed to increase with age as males acquire key physical attributes (e.g., body size and secondary sexual characteristics) and experience to compete successfully against other males (Festa-Bianchet, 2012; Heckel & Helversen, 2002). However, when intermale competition is extremely strong combined with high mortality rates over successive life stages, most males in the population fail in holding a harem. This results in a strongly skewed distribution in reproductive success among males and null or very low lifetime reproductive success for most of them (Clinton & Le Boeuf, 1993; Clutton-Brock, 2007; Loison et al., 1999).

In this context, the adaptive adjustment of offspring sex ratio (defined as the proportion of offspring that are males) weakens the strength of sexual selection, which stabilizes the variance of the fitness among males (Booksmythe et al., 2013; Fawcett et al., 2011). Parents should bias the sex ratio of their offspring towards the sex that will have the greatest improvement on their fitness (Charnov, 1982; Trivers & Willard, 1973). The reproductive benefit of producing a male or a female offspring for parents should depend on the relative fitness of sons and daughters, the costs of producing and rearing each sex, and the sex differences in any future competition or cooperation with parents or other kin (Clutton-Brock & Iason, 1986; Emlen et al., 1986; Frank, 1986).

The most influential hypothesis on offspring sex ratio adjustment—the Trivers and Willard hypothesis—predicts that, when variation in reproductive success is higher in males than in females and maternal condition has a stronger effect on the fitness of sons than daughters, females in good condition should produce more sons, whereas females in poor condition should produce more daughters (Trivers & Willard, 1973). The Trivers and Willard hypothesis can be generalized and applied to any factor that has a differential effect on the fitness of sons and daughters (West, 2009), such as local density (local resource competition; Silk, 1983), the need for helpers (local resource enhancement; Komdeur et al., 1997), or parents' phenotype (male attractiveness and female mating preference; Burley, 1981; Kirkpatrick, 1982).

The mate attractiveness hypothesis posits that females can manipulate the sex ratio of their progeny according to their mate's attributes (Burley, 1981; Pen & Weissing, 2001). Females breeding with attractive males (e.g., larger body size, weapons, or ornaments), should capitalize on this advantage by biasing their offspring production in favor of sons, because sons of attractive males are more likely to have higher fitness than daughters (Cox & Calsbeek, 2010; Fawcett et al., 2007). In contrast, females breeding with nonattractive males make the best of a bad job by biasing their progeny in favor of daughters, because sons of nonattractive males may have a lower fitness than daughters (Burley, 1981; Cox & Calsbeek, 2010; Fawcett et al., 2007). Various cryptic choice mechanisms may allow females to bias sex determination in response to male attractiveness. This can be done from differential mortality or

fertilization of X- and Y-chromosome bearing spermatozoa (CBS) in the female reproductive tract (Grant & Chamley, 2010; Krackow, 1995; Navara, 2013) which could be driven by levels of testosterone, glucose, estrogen, and stress (Geiringer, 1961; Helle et al., 2008; Lane & Hyde, 1973; Perret, 2005).

Trivers and Willard (1973) originally assumed that only mothers influence offspring sex determination. Recent evidence, however, shows that fathers may also drive offspring sex ratio—especially in mammalian males as they are the heterogametic sex (Douhard & Geffroy, 2021; Edwards & Cameron, 2014). For example, red deer (*Cervus elaphus*) hinds, artificially inseminated with no knowledge of male phenotypes, produced twice as many sons than daughters when the sire's fertility was higher (Gomendio et al., 2006). Fathers may influence offspring sex ratio by varying the proportion of the X- and Y-CBS as a higher proportion of Y-CBS results in a higher probability of producing a son (Chandler et al., 2007; Douhard & Geffroy, 2021; Edwards et al., 2016; Saragusty et al., 2012). Variation in X- and Y-CBS proportions could be driven by mating frequency (James, 1996), hormonal variation (James, 2008), competitiveness between X- and Y-CBS (Malo et al., 2005), and seminal fluid composition (Edwards & Cameron, 2017).

The objective of this study was to test for the relationship between father's phenotypes and offspring sex ratio in a highly polygynous species, the southern elephant seal (*Mirounga leonina*). Elephant seals gather on land once a year for the breeding season (Figure 1). Males arrive before females, and immediately begin interacting with each other to establish dominance hierarchy (Le Boeuf, 1974; McCann, 1981). Pregnant females arrive a few weeks later and gather in harems of high density. Females give birth ca. 5 days after hauling out and nurse their pup for ca. 24 days. Females come into estrus the last ca. 4 days before returning to sea to forage (Laws, 1956; Le Boeuf, 1972). Dominant males adopt a central position in harems and actively prevent other males from accessing females, while subordinate males stay at the periphery and opportunistically look for copulation attempts. Reproductive success in males is highly skewed, with harem holders generally siring more than 75% of the pups (Fabiani et al., 2004; Modig, 1996). Variance in lifetime reproductive success is approximately four times greater in males than in females (Le Boeuf & Reiter, 1988). For example, in northern elephant seals (*Mirounga angustirostris*), successful males inseminate up to 121 females (Le Boeuf & Reiter, 1988), whereas most successful females give birth to 20 pups (Le Boeuf et al., 2019) during their lifetime. Holding a harem is a highly successful mating tactic. However, intermale competition is intense and mortality rate is high, and most of the males die
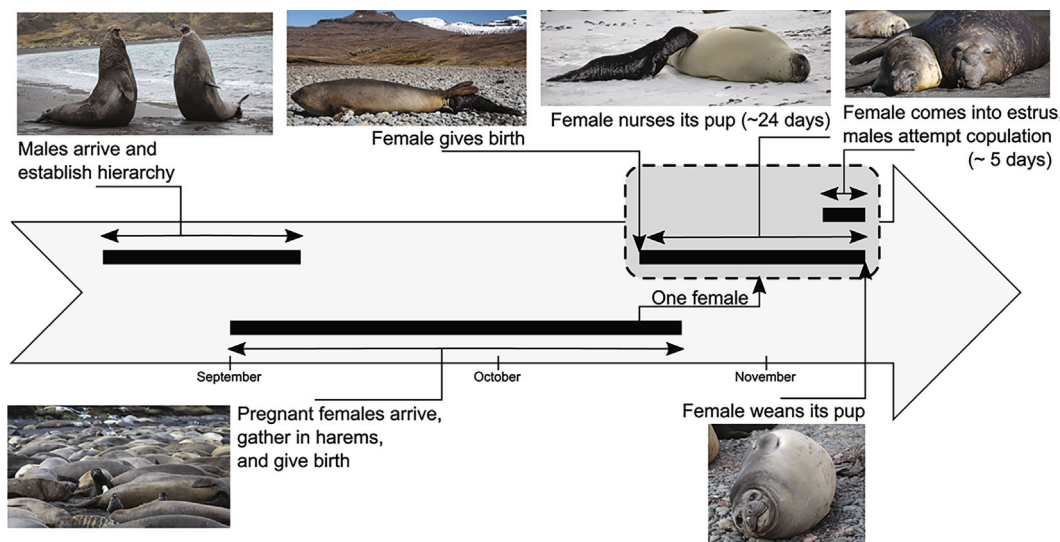

FIGURE 1 Diagram summarizing approximately the progression of the breeding season in southern elephant seals.

before reaching the physical condition and the experience required to hold a harem (Clinton & Le Boeuf, 1993; Le Boeuf, 1974; Lloyd et al., 2020).

We hypothesize that, in southern elephant seals, a polygynous species where the probability of a male holding a harem (i.e., high reproductive success) is extremely low, natural selection will favor offspring sex ratio adjustment as one of the mechanisms stabilizing fitness variance among males. We expect offspring sex ratio to vary with the siring probability of males. Assuming that breeding males with high reproductive success sire sons with higher average fitness than daughters, and that breeding males with low reproductive success sire sons with lower average fitness than daughters, we should find a positive relationship between the probability that a breeding male sires a son and its relative reproductive success.

2 | METHODS

2.1 | Study site, observations, and sample collection

We tested our hypothesis on a colony of southern elephant seals breeding at the *Rivière du Nord* (RdN) site between September 2 and November 10, 2017. The RdN breeding site is located north of the Kerguelen Archipelago (49.176°S, 70.138°E) and is characterized by 500 m long sandy beaches mixed with pebbles. We walked around the colony, almost daily, to record the presence of each male. Individuals were photographed at the first encounter, then identified according to their body scars. We used a 3-m-long aluminum pole equipped with a stainless-steel biopsy tip with barb (7 mm diameter and 40 mm length) to sample tissue biopsies from the lateral back area of the seals. We sampled 74 breeding males among all males ($n = 113$) accessible at RdN. We could not sample the remaining males because they were never accessible, i.e., stayed at RdN for short time or were most of the time inside a harem. In 2018, we returned to RdN and sexed all accessible weaned pups ($n = 951$, approximately 80% to 95% of all pups) in addition to sampling tissue biopsies from the trailing edge of one of their hind flippers using dissecting scissors. We conducted these manipulations while two people were restraining the pup. All tissue samples were preserved in 70% ethanol until laboratory genetic analysis for paternity assignment. Pre-weaning mortality in elephant seals generally ranges between 2% and 8% (Campagna et al., 1993; Hindell & Burton, 1987; McMahon & Hindell, 2003; Pistorius et al., 2001), and there is no evidence for differential mortality between the sexes (Le Bœuf et al., 1989).

2.2 | Relative body length

We estimated the relative body length of the breeding male seals from photos taken when they were laying straight and flat on the ground (Bell et al., 1997). We used a Canon camera (EOS 5D 12.8 MP DSLR) with a 100–400 mm zoom lens to take the photographs. We photographed the seal at a distance of about 10 m, perpendicularly to the longitudinal axis of its body, and approximately at the height of the center of its body. We placed a calibrated rope (marked every 50 cm) along the seal's body and used it as a reference for the scale. We disregarded the caudal flippers and the head of the seal as their position varied between the photographs. We considered the length of the seal from the eye to the base of the hind flippers. This measure correlates with the total length, i.e., from the tip of the nose to the end of hind flippers $r = 0.99$, Carlini et al., 2006). We measured the body length of 80 seals from the photos using the software ImageJ version 1.53f51. As we took multiple photographs per seal ($M = 2.3$ photographs, range $= 1$–8; Supplementary Material 1), we estimated a unique value of the relative body length for each seal by extracting the best linear unbiased predictors from an univariate linear mixed-effect model fitted in a Bayesian framework using the brms R package (Bürkner, 2017). The model included the body length as response variable and the seal identifier as random intercept (Supplementary Material 1). We calculated the repeatability of body

length according to Nakagawa and Schielzeth (2010). The repeatability is used as an indicator of the error in measuring body length of the same individual between photographs.

2.3 | Genetic analysis

2.3.1 | DNA extraction

The samples of skin biopsies were digested with proteinase K. We then extracted DNA using the Nucleospin 96 Tissue Kit (Macherey-Nagel), following the manufacturer's instructions, and randomly distributed samples into the plates. We replicated 50 individuals twice at the extraction stage to check the repeatability of the results. We assessed DNA concentration and purity with Qubit DSDNA Assay kit (ThermoFisher) on a Berthold Tristar2 microplate reader.

2.3.2 | Microsatellite development and sequence-based microsatellite genotyping

We identified microsatellite markers from a random shotgun sequencing of a DNA pool extracted from ten individuals purified using 1.8X Agencourt AMPure XP beads (Beckman Coulter, High Wycombe, UK) and quantified with a Qubit 2.0 fluorometer (ThermoFisher). We prepared the DNA library using QIASeq FX DNA library kit (Qiagen) and sequenced it on an Illumina MiSeq sequencer using a v2 nano sequencing kit (2×250 bp). Raw sequences are publicly available in the European Nucleotide Archive accession number ERR10752787. We used the software BBmerge v38.87 (Bushnell et al., 2017) to merge paired reads and the software QDD v3.1.2 (Meglécz et al., 2014) to discover microsatellites. We fixed the QDD primer design parameters to target amplicon lengths between 100 and 180 bp and optimized them for multiplex PCR (Lepais et al., 2020). We selected 60 primer pairs based on different criteria to increase polymorphism content and amplification success (Meglécz et al., 2014). We tagged the locus-specific primers at 5 -end with universal Illumina adapter overhang sequences: TCGTCGGCAGCGTCAGATGTGTATA AGAGACAG for forward primers and GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG for reverse primers (Supplementary Material 2). We tested the amplification of each of the 60 primer pairs in a simplex PCR performed on the DNA pool of the elephant seals. We prepared the PCR in a volume of 10 l containing 2 L of 5X Hot Firepol Blend master mix (Solis Biodyne), 1 L of 2 M primer pairs, 1 l of DNA pool (10 ng/L), and 6 L of PCR-grade water. We performed the PCR on a Veriti 96-Well Fast thermal cycler (ThermoFisher) which consisted in an initial denaturation at 95°C for 15 min, followed by 35 cycles of denaturation at 95°C for 20 s, annealing at 59°C for 60 s, extension at 72°C for 30 s, and a final extension step at 72°C for 10 min. We checked the amplification on a 3% agarose gel.

We validated the developed markers by repeated genotyping of a set of 95 samples. We performed a multiplexed PCR amplification of the 60 markers in a volume of 10 L using 2 L of 5X Hot Firepol Multiplex master mix (Solis Biodyne), 1 L of multiplex primer mix (0.5 M of each primer), 2 L of DNA (10 ng/L), and 5 L of PCR-grade water. We performed the PCR on a Veriti 96-Well Fast thermal cycler (ThermoFisher), which consisted of an initial denaturation at 95°C for 12 min followed by 30 cycles of denaturation at 95°C for 30 s, annealing at 59°C for 180 s, extension at 72°C for 30 s, and a final extension step at 72°C for 10 min. We performed a second PCR to attach the adapters and sample-specific pairs of indexes (8 bp unique sequences) to each side of the amplicons by targeting the universal sequence attached to the locus-specific primers. We carried out this indexing PCR in a volume of 20 L using 5X Hot Firepol Multiplex master mix (Solis Biodyne), 5 L of amplicon, and 0.5 M of each of the forward and reverse adapters. The PCR conditions consisted in an initial denaturation at 95°C for 12 min followed by 15 cycles of denaturation at 95°C for 30 s, annealing at 59°C for 90 s, extension at 72°C for 30 s, and a final extension step at 72°C for 10 min. We then pooled the libraries and purified them with 1.8X Agencourt AMPure XP beads (Beckman

Coulter). We checked quality on a Tapestation 4200 (Agilent) and conducted the quantification using QIAseq Library Quant Assay kit (Qiagen, Hilden, Germany) in a Roche LightCycler 480 quantitative PCR. We sequenced the pool on an iSeq 100 sequencer (Illumina, San Diego, CA) with a 2 × 150 bp kit.

We used the bioinformatics pipeline (Lepais et al., 2020) integrating the FDSTools software (Hoogenboom et al., 2017) to call genotypes from raw sequences. We performed a first analysis on the 95 repeated samples for which we used a negative control to optimize the bioinformatic pipeline to each locus, to estimate the locus-level allelic error rate, and to select the loci that produced repeatable genotypes for the final genotypic data set.

For the final genotyping, we performed a multiplex PCR on the validated markers in 384 format plates in a volume of 5 L using 1 L of 5X Hot Firepol Multiplex master mix (Solis Biodyne), 0.5 L of multiplex primer mix (0.5 M), 1 L of DNA (10 ng/L), and 2.5 L of PCR-grade water. We realized the second PCR in a volume of 5 L using 1 L of 5X Hot Firepol Multiplex master mix (Solis Biodyne), 1.25 L of amplicon, and 0.5 L of each of the forward and reverse adapters (5 M). The PCR conditions for these two PCR are the same as for genotyping validation except the reactions were performed on a Veriti 384-Well thermal cycler (ThermoFisher). We then pooled the libraries from 384 samples, purified them with 1.8X Ampure beads, and quantified them with QIAseq Library Quant Assay kit. We sequenced each pool on an iSeq 100 sequencer (Illumina) with a 2 × 150 bp kit. We performed genotyping analysis with the same bioinformatics pipeline (see above) using optimized parameters determined during the validation phase (Supplementary Material 2).

All the 60 developed primer pairs from the whole genome shotgun sequencing produced specific amplification and were kept in the multiplexed PCR (Supplementary Material 2). Among the 60 loci, 37 produced repeatable genotypes with low missing data (<30%) and were polymorphic, representing a total of 363 alleles that showed differences in their sequences ($M = 9.8$ alleles per loci) and only 253 alleles that showed differences in their sizes ($M = 6.8$ alleles per loci) with an average of 0.7% of allelic error among the 95 repeatedly genotyped samples (Supplementary Material 2).

The 37 loci were tested from Hardy–Weinberg equilibrium and their frequency of null alleles were determined using the software CERVUS 3.0.7 (Kalinowski et al., 2007). Only one locus (SSRseqMir_002) exhibited significant deviation from Hardy–Weinberg equilibrium and a high frequency of null alleles (0.10; Supplementary Material 2) and was, therefore, eliminated for further analyses. According to Waits et al. (2001), we calculated the probability of observing identical genotypes (P_{ID}) between two different individuals using the function *pid* implemented in the R package "PopGenUtils" (Tourvas, 2023). This probability was very low (7.94×10^{-12}). Although fathers can sire multiple offspring within the same breeding season, mothers produce one pup per year and twinning is extremely rare (McMahon & Hindell, 2003).

2.4 | Paternity analyses

Genotypes were excluded from the paternity analyses when less than 15 loci were typed ($n = 5$ for the pups and $n = 0$ for the candidate fathers). The average inbreeding coefficient within the candidate fathers was estimated at -0.004 ± 0.009 *SE*. The mean relatedness between the candidate fathers was estimated at -0.014 ± 0.001. Both estimators were obtained using the R package "related" (Pew et al., 2014) using the methods described by Lynch and Ritland (1999).

The paternity assignment analyses were conducted using CERVUS 3.0.7 (Kalinowski et al., 2007) for a set of 36 polymorphic microsatellite loci (Supplementary Material 3) typed on 74 males (candidate fathers), and 946 pups. The proportion of loci typed was 0.94 and the nonexclusion probability was 2.5×10^{-9}.

A male was considered as a likely father when no mismatches were detected between the pup genotype and the candidate male genotype (81% of the pup-father pairs). When a candidate male exhibited one single mismatch with the pup genotype, we considered this male as the father only if the pair confidence was 95% (or more, i.e., strict confidence, 19% of the pup-father pairs). When the confidence of the pair was too low and/or the number of mismatches higher than 1, we considered that we did not sample the father of this pup.

2.5 | Statistical analysis

We ran all our analysis on R (R Core Team, 2021). We used a test to compare the number of male and female weaned pups in RdN in 2018. To test for our hypothesis that offspring sex ratio in southern elephant seals varies with paternal relative reproductive success, we used a generalized linear model with a binomial distribution to model the probability of siring a son as a function of the relative reproductive success of the male. The response variable was the number of sons relative to the number of pups each male sired. We calculated each male relative reproductive success as the number of pups sired by a male divided by the mean number of pups sired by all breeding males. Note that the sex ratio of pups is taken at weaning, which we refer to as offspring sex ratio in our analysis. Reproductive success strongly increases with age in southern elephant seals (Clinton & Le Boeuf, 1993; Lloyd et al., 2020), and paternal age was shown to affect offspring sex ratio in other mammalian species (Edwards & Cameron, 2014; Santos et al., 2015; Tanaka et al., 2019). We, thus, added the relative body length to our model as a proxy for age (McLaren, 1993). The model included all seals that sired at least one pup and for which we measured body size (n = 57). We found that some males that sired few pups were sighted for a brief period or only at the beginning of the breeding season before females arrived. We concluded that these fertilizations must have occurred in a neighboring breeding site and that females moved to RdN the following year (2018) when we sampled skin biopsies on the pups. This means that the number of pups sired and the offspring sex ratio for these males may not be representative of their actual reproductive status. To minimize the effect of these off-site copulations, we weighted our model by the tenure of each male, i.e., the number of days they spent at RdN (Supplementary Material 4). We also weighed all computed statistics related to male reproductive success by the tenure such as the mean and the standard deviation of the number of sired pups.

We used a Bayesian framework to fit our model using the brms R package (Bürkner, 2017; Supplementary Material 4). We normalized all predictors, i.e., mean centered and unit variance. To investigate for potential collinearity issues in our model, we computed the correlation between the relative reproductive success and the relative body length by extracting the regression coefficient from a linear regression between both normalized variables (Supplementary Material 5). This approach allowed us to weight the correlation value between the relative reproductive success and the relative body length by the number of days individuals spent at RdN.

3 | RESULTS

3.1 | Paternity assignments

We found that 58 out of 74 candidate fathers sired 540 (437 with zero mismatch and 103 with one mismatch but with at least 95% pair confidence) out of 946 pups. The number of pups sired was highly skewed with a weighted mean of 12.7 pups and a weighted sd of 17.5 (Figure 2). Approximately 20% of the sampled males were responsible for siring 80% of the pups with the known sire. The maximum number of pups sired by the same male was 66 pups (7%).

3.2 | Weanling sex ratio model

The proportion of sons among all the weaned pups observed at RdN in 2018 did not differ from 0.5 (474 sons and 472 daughters; proportion test: $\chi^2 = 0.00$, $p = .97$). We found a positive effect between a male relative reproductive success and its probability of producing a son, and the 95% credible intervals did not overlap with zero (Figures 3 and 4, Table 1). According to our model, the male with the lowest relative reproductive success has a probability of 43% to produce a son and the one with the highest relative reproductive success has a probability of 54%. We did
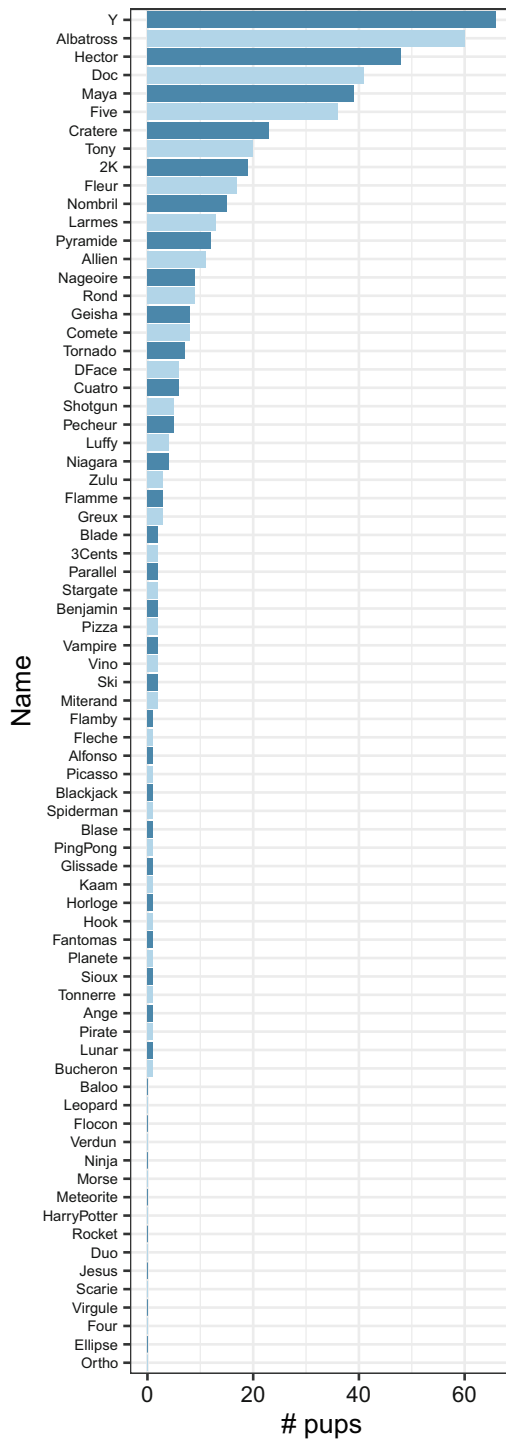
FIGURE 2   The number of pups sired by each male southern elephant seal in our sample of pups.

not find any evidence that the effect of the relative body length (used as a proxy for age) on the probability of producing a son was different from zero as the posterior distribution of the effect estimate had a great dispersion and overlapped with zero (Figure 3, Table 1). The mean (± SE [95%CI]) repeatability of body length was 0.94 ± 0.01 [0.91,
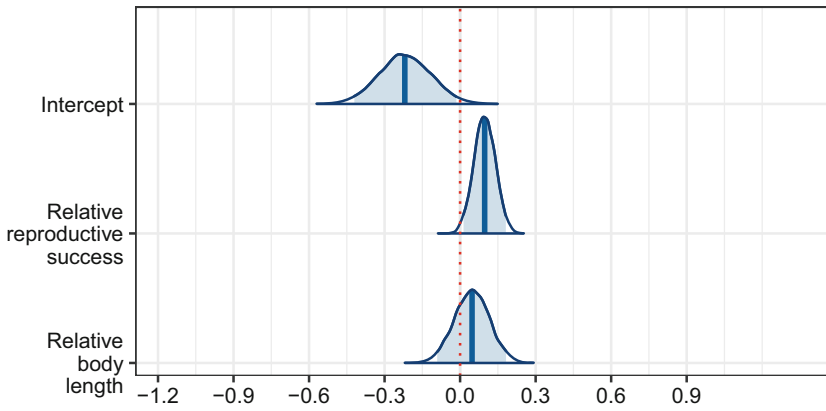
FIGURE 3 Parameter posterior distributions of the generalized linear model predicting the probability that a male southern elephant seal sires a son as a function of its relative reproductive success and relative body length (a proxy for age). The relative reproductive success is calculated as the number of offspring sired by a male divided by the mean number of offspring sired by all sampled males. The mean of the parameter posterior distribution is marked by a vertical dark blue line and the area representing the 95% credible intervals is colored in light blue.
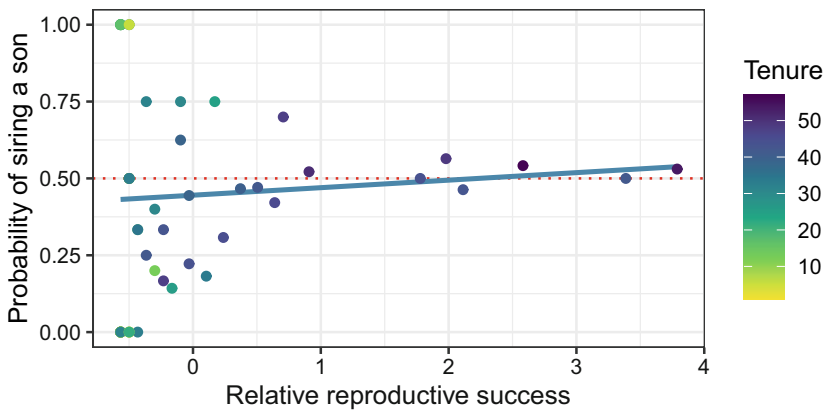

FIGURE 4 The predictive probability that a male southern elephant seal sires a son as a function of its relative reproductive success. The relative reproductive success is calculated as the number of offspring sired by a male divided by the mean number of offspring sired by all sampled males. 95% credible intervals (gray area) were added around the mean effect (blue line). Points represent the proportion of sons each male sired and are colored by the seal tenure at the RdN site.

TABLE 1 Parameter mean estimates of the generalized linear model predicting the probability that a male southern elephant seal sires a son as a function of its relative reproductive success and relative body length (a proxy for age). The relative reproductive success is calculated as the number of offspring sired by a male divided by the mean number of offspring sired by all sampled males. Parameter mean estimates are presented with standard errors (*SE*) and 95% credible intervals (CI).

Parameter	Estimate	*SE*	CI
Intercept	−0.22	0.10	[−0.42, −0.01]
Relative reproductive success	0.10	0.04	[0.01, 0.18]
Relative body length	0.05	0.07	[−0.09, 0.18]

0.96] and the weighted correlation between male relative reproductive success and relative body length was 0.40 ± 0.09 [0.23, 0.57], which we do not consider large enough to lead to concerning collinearity issues.

4 | DISCUSSION

We found that sex ratio of weaned pups increased with paternal relative reproductive success in a colony of southern elephant seals breeding on the Kerguelen Archipelago. This is consistent with previous studies on polygynous species showing a general positive trend between male attributes and offspring sex ratio (e.g., Douhard et al., 2016; Gomendio et al., 2006; Malo et al., 2017; Perret, 2018; Røed et al., 2007). We found that the probability of producing a son increases by 11% with parental relative reproductive success, which is slightly lower compared to other similar studies (e.g., 29%, Douhard et al., 2016; 35%, Gomendio et al., 2006; 20%, Røed et al., 2007). Nonetheless, few studies explicitly showed that the relationship between paternal reproductive success and offspring sex ratio can be adaptive (Cox & Calsbeek, 2010; Douhard et al., 2016). The effect size estimated by our model was weak (Table 1) as predicted by theoretical models (Booksmythe et al., 2013; Fawcett et al., 2007) and supported by a meta-analysis on empirical studies, albeit mostly on bird species (Booksmythe et al., 2017).

4.1 | Adaptive offspring sex ratio adjustment

The capacity of offspring sex ratio adjustment to evolve with paternal reproductive success in polygynous species may depend on the heritability of the competitive ability of males and the resulting differential fitness outcome of sons and daughters (Clutton-Brock & Iason, 1986; Trivers & Willard, 1973). In elephant seals, reproductive success increases with the competitive capacity of males to hold a harem (Hoelzel et al., 1999). We expect the traits that influence this ability, such as large body size, physical stamina, aggressiveness, and boldness, to be heritable (e.g., Kruuk et al., 2000). A harem holder would benefit from producing sons that inherit its competitive ability which will also increase their likelihood to hold a harem. In contrast, peripheral (subordinate) males should benefit more from producing daughters if the average fitness of daughters exceeds the fitness of sons that never hold a harem. Sexually antagonistic genetic variance for fitness could be a genetic mechanism favoring the evolution of offspring sex ratio adjustment (Blackburn et al., 2010). Variation of some specific alleles may be beneficial to one sex but deleterious to the other, leading to a trade-off between optimal genotypes for males and females (Connallon & Jakubowski, 2009; Fedorka & Mousseau, 2004; Foerster et al., 2007). Given the very small proportion of males that reach dominant status, and a high reproductive success, biasing offspring sex ratio in favor of sons corresponds to a high-risk high-reward strategy, whereas biasing it in favor of females corresponds to a bet-hedging strategy (Gillespie, 1974; Slatkin, 1974). Bet hedging can help explain the maintenance of these two alternative strategies, even if at first sight lifetime reproductive success in polygynous species can be much higher for males than females (Simons, 2011). Offspring sex ratio adjustment is thus expected to erode the strength of sexual selection by stabilizing the fitness variance among males and consequently preventing an evolutionary collapse due to traits that are "too exaggerated" (Iwasa & Pomiankowski, 1995).

In our study, we did not measure the differential relative fitness between producing sons and daughters in relation to paternal reproductive success and, to our knowledge, this has not been measured in any other colony of elephant seals studied so far. However, this has been investigated in others polygynous species. For example, the fitness outcome of producing daughters in bighorn rams (*Ovis canadensis*; Douhard et al., 2016) with lower reproductive success and in brown anole lizard males (*Anolis sagrei*; Cox & Calsbeek, 2010) with smaller sizes is greater than of producing sons, supporting the adaptive relationship between male attractiveness and offspring sex ratio.

Although we based our hypothesis on how offspring sex ratio affects the variance of male fitness, it also affects the variance of female fitness (Booksmythe et al., 2013). Both effects can be in agreement or in conflict depending on the differential costs females pay to raise a son or a daughter (Clutton-Brock & Iason, 1986). In elephant seals, several studies found that weaning sons is more costly than daughters as sons weigh more than daughters at weaning and have longer lactation periods (Carrick et al., 1962; Reiter et al., 1978). The underlying reason for this is not clear. For example, it could be because sons are heavier than daughters at birth (Arnbom et al., 1994; Le Boeuf et al., 1989) or sons need to be heavier than daughters to reach equivalent postweaning survival rates (McMahon et al., 2000). Therefore, mothers may favor the production of sons over daughters only if they can afford the extra energetic costs as suggested by the Trivers and Willard hypothesis (Trivers & Willard, 1973).

In accordance with the Trivers and Willard hypothesis, young and small female elephant seals produce more daughters than sons, conversely to larger and older females that favor the production of sons (Arnbom et al., 1994; Le Boeuf et al., 1989, 2019; Wilkinson & Aarde, 2001). Additionally, in southern elephant seals breeding on Macquarie Island, larger females devote more energy to their sons than to their daughters whereas smaller females devote more energy to their daughters than to their sons (McMahon et al., 2017). Le Boeuf et al. (1989) also found that young mother northern elephant seals were less successful at raising sons than daughters compared to older mothers. Therefore, it seems that both effects of offspring sex ratio adjustment by males and females are in accordance when harem-holders breed more often with older and larger females. Otherwise, both effects of offspring sex ratio adjustment are in conflict resulting in a canceled overall effect.

We did not design our study to identify the mechanisms causing offspring sex ratio adjustment, similarly to most previous studies on this topic (Cameron, 2004; Helle et al., 2008). Although initial hypotheses assumed that mothers exclusively control offspring sex ratio (Burley, 1981; Trivers & Willard, 1973), recent evidence shows that offspring sex ratio can be driven by fathers, mothers, or both simultaneously (Douhard & Geffroy, 2021; Edwards & Cameron, 2014). In the following sections, we discuss some possible causal mechanisms of these different pathways that could explain the result we found in this study on southern elephant seals.

4.2 | Offspring sex ratio adjustment by females

Accordingly with the differential allocation and the mate attractiveness hypotheses (Burley, 1981; Sheldon, 2000), mothers may adjust the sex of their offspring in response to fathers' phenotypes in a way to maximize their long-term fitness output (Booksmythe et al., 2017). Mating with an attractive male increases the probability of producing sons, as they inherit the phenotypes of their fathers (e.g., ornaments, armaments, or dominance rank, Burley, 1981; Cox & Calsbeek, 2010; Ellegren et al., 1996).

Elephant seal females may perceive the quality of males through their physical attributes, such as body size or their dominance status (i.e., harem-holder vs. peripheral) (Carlini et al., 2006; Hoelzel et al., 1999; Modig, 1996). For example, elephant seal females resist and protest more against copulation attempts of low rank males than higher rank males (Galimberti et al., 2000a). Dependent on the male attractiveness, various mechanisms of cryptic choice can allow females to skew their offspring sex ratio. This can be done through differential mortality or fertilization success of the X- and Y-CBS in the reproductive tract (Grant & Chamley, 2010; Krackow, 1995; Navara, 2013). For example, female field voles (*Microtus agrestis*) with higher levels of testosterone and glucose (Helle et al., 2008) and female gray mouse lemurs (*Microcebus murinus*) with lower levels of estrogen (Perret, 2005) produced male-biased litters. In highly dense harems, such as in elephant seals, more centrally located females are more protected from harassment by peripheral males and are more likely to mate with harem-holders (Le Boeuf, 1972, 1974). Females reproductive experience and dominance capacity seem to drive their spatial structure (McMahon & Bradshaw, 2004; Reiter et al., 1981). Testosterone levels may play an important role here as it is associated with social dominance (Rada et al., 1976; Williamson et al., 2017) and offspring sex ratio adjustment (Navara, 2013). Females with higher levels of testosterone may monopolize more central locations in harems and thus more likely to mate with harem-

holders. At the same time, higher testosterone levels promote the production of sons, for example, via a higher fertilization probability of Y-CBS (Grant et al., 2008), which benefits centrally located females because their sons may inherit the capacity of their fathers to obtain a high lifetime reproductive success.

Stress may also be an important factor influencing offspring sex ratio adjustment by mothers (Navara, 2018). Females experiencing higher levels of stress tend to produce more daughters than sons (Geiringer, 1961; Lane & Hyde, 1973). For example, female house mice (*Mus musculus domesticus*) exposed to higher density of males were more stressed (higher blood corticosterone levels) and produced female-biased offspring sex ratios (Firman, 2020). Stress alters the mother's physiology and thus, similarly, may induce a sex chromosome-specific mortality or fertilization (Ideta et al., 2009; Navara, 2018). According to harem characteristics, elephant seal females experience different levels of male harassment (Galimberti et al., 2000a,b) resulting in varying stress levels among females. Females that are more subject to male harassment (higher stress levels) are less likely to be fertilized by harem-holders and thus benefit to produce more daughters than sons.

4.3 | Offspring sex ratio adjustment by males

In mammals, males are the heterogametic sex producing X- and Y-CBS which determine the sex of the offspring. Hence, paternal offspring sex ratio adjustment represents a parsimonious explanation compared to maternal offspring sex ratio adjustment in response to male attributes (Douhard & Geffroy, 2021; Edwards & Cameron, 2014). Fathers may adjust offspring sex ratio by varying the proportion of the X- and Y-CBS, where a higher proportion of Y-CBS results in a higher probability of producing a son (Chandler et al., 2007; Edwards et al., 2016; Saragusty et al., 2012).

Variation in the proportion of X- and Y-CBS may be driven by mating frequency variation between harem-holders and peripheral males. Harem holders that have a higher mating frequency compared to peripheral males may produce more Y-CBS because they are smaller—i.e., less costly to produce—than X-CBS which contains 4% more DNA (Douhard & Geffroy, 2021; Seidel, 1999). For example, the proportion of X-CBS in humans (*Homo sapiens*) increased with sexual abstinence (Hilsenrath et al., 1997) and mating frequency influences offspring sex ratio in horses, rabbits, rats, and mice (James, 1996). As the breeding season progresses, harem-holders become exhausted resulting in increasing the production of Y-CBS and thus the likelihood of siring sons. Older females arrive at breeding sites later than younger females (McMahon & Bradshaw, 2004), which may lead to positive assortative mating as older females are more likely to bear the additional energetic costs of rearing a son (Arnbom et al., 1994; Le Boeuf et al., 1989). Furthermore, the date at which females arrive to breed is heritable ($h^2 = 0.4$; Oosthuizen et al., 2023), which reinforces the evolutionary potential of the positive assortative mating between males and females.

Variation in the proportion of X- and Y-CBS may also be driven by hormonal variation among males correlated to their breeding status and performance (James, 2008). Social dominance increases with testosterone through more aggressive behaviors (Rada et al., 1976; Williamson et al., 2017). For example, castrated rats showed a decrease in aggressiveness with a loss of social dominance (Albert et al., 1986). Testosterone level is also higher in harem-holders in various species of deer (Chunwang et al., 2004) and horse (McDonnell & Murray, 1995). Testosterone levels in blood and semen are correlated to Y-CBS in bulls (Kholghi et al., 2020). Therefore, testosterone levels may link social dominance (reproductive success) with offspring sex ratio adjustment. For example, in spotless starling females (*Sturnus unicolor*), ibex females (*Capra nubiana*), and grey mouse lemur males, high levels of testosterone were associated with higher social ranks and son-biased offspring sex ratio (Perret, 2018; Shargal et al., 2008; Veiga et al., 2004).

4.4 | Conclusion

Our study shows that offspring sex ratio increased with paternal relative reproductive success in a colony of southern elephant seals breeding on the Kerguelen Archipelago. This finding brings additional support to the potential

adaptive adjustment of offspring sex ratio by parents. However, we could not identify the underlying mechanisms driving the relationship between offspring sex ratio adjustment and paternal relative reproductive success.

Studies on offspring sex ratio adjustment have produced inconsistent and contradictory results in many vertebrate species (Clutton-Brock & Iason, 1986; Cockburn et al., 2002; Douhard, 2017; Silk et al., 2005). This can be explained by the complexity of the factors influencing offspring sex ratio (Brown, 2001; Komdeur & Pen, 2002; Packer et al., 2000). For example, three interacting processes such as maternal condition (the Trivers-Willard hypothesis; Trivers & Willard, 1973), local density (the local resource competition hypothesis; Schaik & Hrdy, 1991), and adult sex ratio (the homeostatic hypothesis; Hamel et al., 2016) may result in an unbiased or biased sex ratio towards either males or females (Wild & West, 2007). This was empirically demonstrated in red deer, where the offspring son-biased production by dominant females declined with population density and winter rainfall, both environmental factors associated with preparturition nutritional stress (Kruuk et al., 1999). In elephant seals, offspring sex ratio was shown to vary with maternal age (Le Boeuf et al., 2019), maternal body condition in relation to preparturition environmental conditions (Lee & Sydeman, 2009; Vergani et al., 2004), and paternal reproductive success (this study). We, therefore, advocate that future studies should be specifically designed to tease apart the different ecological and evolutionary processes responsible for the offspring sex ratio adjustment as understanding these mechanisms may have important wildlife management and conservation implications (Clout et al., 2002; Vetter & Arnold, 2018).

AUTHOR CONTRIBUTIONS

Hassen Allegue: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing. **Christophe Guinet:** Conceptualization; funding acquisition; methodology; project administration; supervision; validation; writing – review and editing. **Samantha C. Patrick:** Supervision; validation; writing – review and editing. **Cécile Ribout:** Data curation; formal analysis; methodology; writing – review and editing. **Coraline Bichet:** Data curation; formal analysis; methodology; validation; writing – review and editing. **Olivier Lepais:** Data curation; formal analysis; methodology; validation; writing – review and editing. **Denis Reale:** Conceptualization; funding acquisition; investigation; methodology; supervision; validation; writing – review and editing.

AVAILABILITY OF DATA AND MATERIALS

Data are available on Zenodo: https://doi.org/10.5281/zenodo.7418941

The random shotgun sequencing reads from a pool of 10 individuals for microsatellite discovery are available at NCBI SRA under the accession number ERR10752787.

CONFLICT OF INTEREST DISCLOSURE

The authors declare that they have no competing of interest concerning the content of the manuscript.

ORCID

Hassen Allegue https://orcid.org/0000-0001-9357-9151

Christophe Guinet https://orcid.org/0000-0003-2481-6947

Samantha C. Patrick https://orcid.org/0000-0003-4498-944X

Coraline Bichet https://orcid.org/0000-0003-0255-4966

Olivier Lepais https://orcid.org/0000-0002-6102-9478

Denis Réale https://orcid.org/0000-0002-0419-7125

REFERENCES

Albert, D. J., Walsh, M. L., Gorzalka, B. B., Siemens, Y., & Louie, H. (1986). Testosterone removal in rats results in a decrease in social aggression and a loss of social dominance. *Physiology & Behavior*, *36*(3), 401–407. https://doi.org/10.1016/0031-9384(86)90305-7

Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.

Arnbom, T., Fedak, M. A., & Rothery, P. (1994). Offspring sex ratio in relation to female size in southern elephant seals, Mirounga leonina. *Behavioral Ecology and Sociobiology*, *35*(6), 373–378. https://doi.org/10.1007/BF00165838

Bell, C. M., Hindell, M. A., & Burton, H. R. (1997). Estimation of body mass in the southern elephant seal, *Mirounga leonina*, by photogrammetry and morphometrics. *Marine Mammal Science*, *13*(4), 669–682. https://doi.org/10.1111/j.1748-7692.1997.tb00090.x

Blackburn, G. S., Albert, A. Y. K., & Otto, S. P. (2010). The evolution of sex ratio adjustment in the presence of sexually antagonistic selection. *American Naturalist*, *176*(3), 264–275. https://doi.org/10.1086/655220

Booksmythe, I., Mautz, B., Davis, J., Nakagawa, S., & Jennions, M. D. (2017). Facultative adjustment of the offspring sex ratio and male attractiveness: a systematic review and meta-analysis. *Biological Reviews*, *92*(1), 108–134. https://doi.org/10.1111/brv.12220

Booksmythe, I., Schwanz, L. E., & Kokko, H. (2013). The complex interplay of sex allocation and sexual selection. *Evolution*, *67*(3), 673–678. https://doi.org/10.1111/evo.12003

Brown, G. R. (2001). Sex-biased investment in nonhuman primates: can Trivers & Willard's theory be tested? *Animal Behaviour*, *61*(4), 683–694. https://doi.org/10.1006/anbe.2000.1659

Bürkner, P.-C. (2017). brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Burley, N. (1981). Sex ratio manipulation and selection for attractiveness. *Science*, *211*(4483), 721–722. https://doi.org/10.1126/science.211.4483.721

Bushnell, B., Rood, J., & Singer, E. (2017). BBMerge – Accurate paired shotgun read merging via overlap. *PLoS ONE*, *12*(10), Article e0185056. https://doi.org/10.1371/journal.pone.0185056

Cameron, E. Z. (2004). Facultative adjustment of mammalian sex ratios in support of the Trivers–Willard hypothesis: evidence for a mechanism. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1549), 1723–1728. https://doi.org/10.1098/rspb.2004.2773, Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism

Campagna, C., Lewis, M., & Baldi, R. (1993). Breeding biology of southern elephant seals in Patagonia. *Marine Mammal Science*, *9*(1), 34–47. https://doi.org/https://doi.org/10.1111/j.1748-7692.1993.tb00424.x

Carlini, A. R., Poljak, S., Daneri, G. A., Márquez, M. E. I., & Negrete, J. (2006). The dynamics of male harem dominance in southern elephant seals (*Mirounga leonina*) at the South Shetland Islands. *Polar Biology*, *29*(9), 796–805. https://doi.org/10.1007/s00300-006-0117-6

Carrick, R., Csordas, S. E., & Ingham, S. E. (1962). Studies on the southern elephant seal, *Mirounga leonina* (L.). IV. Breeding and development. *CSIRO Wildlife Research*, *7*(2), 161–197. https://doi.org/10.1071/CWR9620161

Chandler, J. E., Taylor, T. M., Canal, A. L., Cooper, R. K., Moser, E. B., McCormick, M. E., Willard, S. T., Rycroft, H. E., & Gilbert, G. R. (2007). Calving sex ratio as related to the predicted Y-chromosome-bearing spermatozoa ratio in bull ejaculates. *Theriogenology*, *67*(3), 563–571. https://doi.org/10.1016/j.theriogenology.2006.09.006

Charnov, E. L. (1982). *The theory of sex allocation*. Princeton University Press.

Chunwang, L., Zhigang, J., Yan, Z., & Caie, Y. (2004). Relationship between serum testosterone, dominance and mating success in Père David's deer stags. *Ethology*, *110*(9), 681–691. https://doi.org/10.1111/j.1439-0310.2004.01003.x

Clinton, W. L., & Le Boeuf, B. J. (1993). Sexual selection's effects on male life history and the pattern of male mortality. *Ecology*, *74*(6), 1884–1892. https://doi.org/10.2307/1939945

Clout, M. N., Elliott, G. P., & Robertson, B. C. (2002). Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biological Conservation*, *107*(1), 13–18. https://doi.org/10.1016/S0006-3207(01)00267-1

Clutton-Brock, T. H. (1985). Reproductive success in red deer. *Scientific American*, *252*(2), 86–93.

Clutton-Brock, T. H. (1989). Review lecture: mammalian mating systems. *Proceedings of the Royal Society B: Biological Sciences*, *236*(1285), 339–372. https://doi.org/10.1098/rspb.1989.0027

Clutton-Brock, T. H. (2007). Sexual selection in males and females. *Science*, *318*(5858), 1882–1885. https://doi.org/10.1126/science.1133311

Clutton-Brock, T. H., & Iason, G. R. (1986). Sex ratio variation in mammals. *Quarterly Review of Biology*, *61*(3), 339–374. https://doi.org/10.1086/415033

Cockburn, A., Legge, S., & Double, M. C. (2002). Sex ratios in birds and mammals: can the hypotheses be disentangled? In I. C. W. Hardy (Ed.), *Sex ratios: Concepts and research methods* (pp. 266–286). Cambridge University Press.

Connallon, T., & Jakubowski, E. (2009). Association between sex ratio distortion and sexually antagonistic fitness consequences of female choice. *Evolution*, *63*(8), 2179–2183. https://doi.org/10.1111/j.1558-5646.2009.00692.x

Cox, R. M., & Calsbeek, R. (2010). Cryptic sex-ratio bias provides indirect genetic benefits despite sexual conflict. *Science*, *328*(5974), 92–94. https://doi.org/10.1126/science.1185550

Douhard, M. (2017). Offspring sex ratio in mammals and the Trivers-Willard hypothesis: In pursuit of unambiguous evidence. *BioEssays*, *39*(9), 1700043. https://doi.org/10.1002/bies.201700043

Douhard, M., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Paternal reproductive success drives sex allocation in a wild mammal. *Evolution*, *70*(2), 358–368. https://doi.org/10.1111/evo.12860

Douhard, M., & Geffroy, B. (2021). Males can adjust offspring sex ratio in an adaptive fashion through different mechanisms. *BioEssays*, *43*(5), Article 2000264. https://doi.org/10.1002/bies.202000264

Edwards, A. M., & Cameron, E. Z. (2014). Forgotten fathers: paternal influences on mammalian sex allocation. *Trends in Ecology & Evolution*, *29*(3), 158–164. https://doi.org/10.1016/j.tree.2013.12.003

Edwards, A. M., & Cameron, E. Z. (2017). Cryptic male choice: experimental evidence of sperm sex ratio and seminal fluid adjustment in relation to coital rate. *Reproduction, Fertility and Development*, *29*(7), 1401–1404. https://doi.org/10.1071/RD16123

Edwards, A. M., Cameron, E. Z., Pereira, J. C., & Ferguson-Smith, M. A. (2016). Paternal sex allocation: how variable is the sperm sex ratio? *Journal of Zoology*, *299*(1), 37–41. https://doi.org/10.1111/jzo.12317

Ellegren, H., Gustafsson, L., & Sheldon, B. C. (1996). Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(21), 11723–11728. https://doi.org/10.1073/pnas.93.21.11723

Emlen, S. T., Emlen, J. M., & Levin, S. A. (1986). Sex-ratio selection in species with helpers-at-the-nest. *American Naturalist*, *127*(1), 1–8. https://doi.org/10.1086/284463

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223. https://doi.org/10.2307/1744497

Fabiani, A., Galimberti, F., Sanvito, S., & Hoelzel, A. R. (2004). Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behavioral Ecology*, *15*(6), 961–969. https://doi.org/10.1093/beheco/arh112

Fawcett, T. W., Kuijper, B., Pen, I., & Weissing, F. J. (2007). Should attractive males have more sons? *Behavioral Ecology*, *18*(1), 71–80. https://doi.org/10.1093/beheco/arl052

Fawcett, T. W., Kuijper, B., Weissing, F. J., & Pen, I. (2011). Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(38), 15925–15930. https://doi.org/10.1073/pnas.1105721108

Fedorka, K. M., & Mousseau, T. A. (2004). Female mating bias results in conflicting sex-specific offspring fitness. *Nature*, *429*(6987), 65–67. https://doi.org/10.1038/nature02492

Festa-Bianchet, M. (2012). The cost of trying: weak interspecific correlations among life-history components in male ungulates. *Canadian Journal of Zoology*, *90*(9), 1072–1085. https://doi.org/10.1139/z2012-080

Firman, R. C. (2020). Exposure to high male density causes maternal stress and female-biased sex ratios in a mammal. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1926), Article 20192909. https://doi.org/10.1098/rspb.2019.2909

Foerster, K., Coulson, T., Sheldon, B. C., Pemberton, J. M., Clutton-Brock, T. H., & Kruuk, L. E. B. (2007). Sexually antagonistic genetic variation for fitness in red deer. *Nature*, *447*(7148), 1107–1110. https://doi.org/10.1038/nature05912

Frank, S. A. (1986). Hierarchical selection theory and sex ratios I. General solutions for structured populations. *Theoretical Population Biology*, *29*(3), 312–342. https://doi.org/10.1016/0040-5809(86)90013-4

Galimberti, F., Boitani, L., & Marzetti, I. (2000a). Female strategies of harassment reduction in southern elephant seals. *Ethology Ecology & Evolution*, 12(4), 367–388. https://doi.org/10.1080/08927014.2000.9522793

Galimberti, F., Boitani, L., & Marzetti, I. (2000b). The frequency and costs of harassment in southern elephant seals. *Ethology Ecology & Evolution*, 12(4), 345–365. https://doi.org/10.1080/08927014.2000.9522792

Geiringer, E. (1961). Effect of ACTH on sex ratio of the albino rat. *Proceedings of the Society for Experimental Biology and Medicine*, 106(4), 752–754. https://doi.org/10.3181/00379727-106-26464

Gillespie, J. H. (1974). Natural selection for within-generation variance in offspring number. *Genetics*, 76(3), 601–606. https://doi.org/10.1093/genetics/76.3.601

Gomendio, M., Malo, A. F., Soler, A. J., Fernández-Santos, M. R., Esteso, M. C., García, A. J., Roldan, E. R. S., & Garde, J. (2006). Male fertility and sex ratio at birth in red deer. *Science*, 314(5804), 1445–1447. https://doi.org/10.1126/science.1133064

Grant, V. J., & Chamley, L. W. (2010). Can mammalian mothers influence the sex of their offspring peri-conceptually? *Reproduction*, 140(3), 425–433. https://doi.org/10.1530/REP-10-0137

Grant, V. J., Irwin, R. J., Standley, N. T., Shelling, A. N., & Chamley, L. W. (2008). Sex of bovine embryos may be related to mothers' preovulatory follicular testosterone. *Biology of Reproduction*, 78(5), 812–815. https://doi.org/10.1095/biolreprod.107.066050

Hamel, S., Festa-Bianchet, M., & Côté, S. D. (2016). Offspring sex in mountain goat varies with adult sex ratio but only for mothers in good condition. *Behavioral Ecology and Sociobiology*, 70(1), 123–132. https://doi.org/10.1007/s00265-015-2031-9

Heckel, G., & Helversen, O. von. (2002). Male tactics and reproductive success in the harem polygynous bat *Saccopteryx bilineata*. *Behavioral Ecology*, 13(6), 750–756. https://doi.org/10.1093/beheco/13.6.750

Helle, S., Laaksonen, T., Adamsson, A., Paranko, J., & Huitu, O. (2008). Female field voles with high testosterone and glucose levels produce male-biased litters. *Animal Behaviour*, 75(3), 1031–1039. https://doi.org/10.1016/j.anbehav.2007.08.015

Hilsenrath, R. E., Swarup, M., Bischoff, F. Z., Buster, J. E., & Carson, S. A. (1997). Effect of sexual abstinence on the proportion of X-bearing sperm as assessed by multicolor fluorescent in situ hybridization. *Fertility and Sterility*, 68(3), 510–513. https://doi.org/10.1016/S0015-0282(97)00247-1

Hindell, M. A., & Burton, H. R. (1987). Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Zoology*, 213(2), 365–380. https://doi.org/10.1111/j.1469-7998.1987.tb03712.x

Hoelzel, A. R., Le Boeuf, B. J., Reiter, J., & Campagna, C. (1999). Alpha-male paternity in elephant seals. *Behavioral Ecology and Sociobiology*, 46(5), 298–306. https://doi.org/10.1007/s002650050623

Hoffman, J. I., Boyd, I. L., & Amos, W. (2003). Male reproductive strategy and the importance of maternal status in the antarctic fur seal *Arctocephalus gazella*. *Evolution*, 57(8), 1917–1930. https://doi.org/10.1111/j.0014-3820.2003.tb00598.x

Hoogenboom, J., Gaag, K. J. van der, Leeuw, R. H. de, Sijen, T., Knijff, P. de, & Laros, J. F. J. (2017). FDSTools: A software package for analysis of massively parallel sequencing data with the ability to recognise and correct STR stutter and other PCR or sequencing noise. *Forensic Science International: Genetics*, 27, 27–40. https://doi.org/10.1016/j.fsigen.2016.11.007

Ideta, A., Hayama, K., Kawashima, C., Urakawa, M., Miyamoto, A., & Aoyagi, Y. (2009). Subjecting holstein heifers to stress during the follicular phase following superovulatory treatment may increase the female sex ratio of embryos. *Journal of Reproduction and Development*, 55(5), 529–533. https://doi.org/10.1262/jrd.20209

Iwasa, Y., & Pomiankowski, A. (1995). Continual change in mate preferences. *Nature*, 377(6548), 420–422. https://doi.org/10.1038/377420a0

James, W. H. (1996). Evidence that mammalian sex ratios at birth are partially controlled by parental hormone levels at the time of conception. *Journal of Theoretical Biology*, 180(4), 271–286. https://doi.org/10.1006/jtbi.1996.0102

James, W. H. (2008). Evidence that mammalian sex ratios at birth are partially controlled by parental hormone levels around the time of conception. *Journal of Endocrinology*, 198(1), 3–15. https://doi.org/10.1677/JOE-07-0446

Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16(5), 1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x

Kholghi, M., Rostamzadeh, J., Razmkabir, M., & Heidari, F. (2020). Blood testosterone level affects sex ratio of bull semen. *Concepts of Dairy & Veterinary Sciences*, 4(1), 363–369. https://doi.org/10.32474/CDVS.2020.04.000177 Research

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution*, 36(1), 1–12. https://doi.org/10.2307/2407961

Komdeur, J., Daan, S., Tinbergen, J., & Mateman, C. (1997). Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature*, 385(6616), 522–525. https://doi.org/10.1038/385522a0

Komdeur, J., & Pen, I. (2002). Adaptive sex allocation in birds: the complexities of linking theory and practice. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 357(1419), 373–380. https://doi.org/10.1098/rstb.2001.0927

Krackow, S. (1995). Potential mechanisms for sex ratio adjustment in mammals and birds. *Biological Reviews*, 70(2), 225–241. https://doi.org/10.1111/j.1469-185X.1995.tb01066.x

Kruuk, L. E. B., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M., & Guinness, F. E. (1999). Population density affects sex ratio variation in red deer. *Nature*, 399(6735), 459–461. https://doi.org/10.1038/20917

Kruuk, L. E. B., Clutton-Brock, T. H., Slate, J., Pemberton, J. M., Brotherstone, S., & Guinness, F. E. (2000). Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Sciences of the United States of America*, 97(2), 698–703. https://doi.org/10.1073/pnas.97.2.698

Lane, E. A., & Hyde, T. S. (1973). Effect of maternal stress on fertility and sex ratio: a pilot study with rats. *Journal of Abnormal Psychology*, 82(1), 78–80. https://doi.org/10.1037/h0034851

Laws, R. M. (1956). The elephant seal (*Mirounga leonina* Linn.): II. General, social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports*, 13, 1–88.

Le Boeuf, B. J. (1972). Sexual behavior in the northern elephant seal Mirounga angustirostris. *Behaviour*, 41, 1–26. https://doi.org/10.2307/4533425

Le Boeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14, 163–176. https://doi.org/10.2307/3881981

Le Boeuf, B. J., Condit, R., & Reiter, J. (2019). Lifetime reproductive success of northern elephant seals (Mirounga angustirostris). *Canadian Journal of Zoology*, 97(12), 1203–1217. https://doi.org/10.1139/cjz-2019-0104

Le Boeuf, B. J., Condit, R., & Reiter, J. (1989). Parental investment and the secondary sex ratio in northern elephant seals. *Behavioral Ecology and Sociobiology*, 25(2), 109–117. https://doi.org/10.1007/BF00302927

Le Boeuf, B. J., & Reiter, J. (1988). Lifetime reproductive success in northern elephant seals. In T. Clutton-Brock (Ed.), *Reproductive success* (pp. 344–362). University of Chicago Press.

Lee, D. E., & Sydeman, W. J. (2009). North Pacific climate mediates offspring sex ratio in northern elephant seals. *Journal of Mammalogy*, 90(1), 1–8. https://doi.org/10.1644/08-MAMM-A-130.1

Lepais, O., Chancerel, E., Boury, C., Salin, F., Manicki, A., Taillebois, L., Dutech, C., Aissi, A., Bacles, C. F. E., Daverat, F., Launey, S., & Guichoux, E. (2020). Fast sequence-based microsatellite genotyping development workflow. *PeerJ*, 8, Article e9085. https://doi.org/10.7717/peerj.9085

Lloyd, K. J., Oosthuizen, W. C., Bester, M. N., & Bruyn, P. J. N. de. (2020). Trade-offs between age-related breeding improvement and survival senescence in highly polygynous elephant seals: dominant males always do better. *Journal of Animal Ecology*, 89(3), 897–909. https://doi.org/https://doi.org/10.1111/1365-2656.13145

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. T., & Jullien, J.-M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, 80(8), 2539–2554. https://doi.org/10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2

Lukas, D., & Clutton-Brock, T. (2014). Costs of mating competition limit male lifetime breeding success in polygynous mammals. *Proceedings of the Royal Society B: Biological Sciences*, 281(1786), Article 20140418. https://doi.org/10.1098/rspb.2014.0418

Lynch, M., & Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics*, 152(4), 1753–1766. https://doi.org/10.1093/genetics/152.4.1753

Malo, A. F., Garde, J. J., Soler, A. J., García, A. J., Gomendio, M., & Roldan, E. R. S. (2005). Male fertility in natural populations of red deer is determined by sperm velocity and the proportion of normal spermatozoa. *Biology of Reproduction*, 72(4), 822–829. https://doi.org/10.1095/biolreprod.104.036368

Malo, A. F., Martinez-Pastor, F., Garcia-Gonzalez, F., Garde, J., Ballou, J. D., & Lacy, R. C. (2017). A father effect explains sex-ratio bias. *Proceedings of the Royal Society B: Biological Sciences*, 284(1861), 20171159. https://doi.org/10.1098/rspb.2017.1159

McCann, T. S. (1981). Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *Journal of Zoology*, 195, 295–310. https://doi.org/10.1111/j.1469-7998.1981.tb03467.x

McDonnell, S. M., & Murray, S. C. (1995). Bachelor and harem stallion behavior and endocrinology. *Biology of Reproduction*, 52(monograph_series1), 577–590. https://doi.org/10.1093/biolreprod/52.monograph_series1.577

McLaren, I. A. (1993). Growth in pinnipeds. *Biological Reviews of the Cambridge Philosophical Society*, 68(1), 1–79. https://doi.org/10.1111/j.1469-185x.1993.tb00731.x

McMahon, C. R., & Bradshaw, C. J. A. (2004). Harem choice and breeding experience of female southern elephant seals influence offspring survival. *Behavioral Ecology and Sociobiology*, 55(4), 349–362. https://doi.org/10.1007/s00265-003-0721-1

McMahon, C. R., Burton, H., McLean, S., Slip, D., & Bester, M. (2000). Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Veterinary Record*, 146(9), 251–254. https://doi.org/10.1136/vr.146.9.251

McMahon, C. R., Harcourt, R. G., Burton, H. R., Daniel, O., & Hindell, M. A. (2017). Seal mothers expend more on offspring under favourable conditions and less when resources are limited. *Journal of Animal Ecology*, 86(2), 359–370. https://doi.org/10.1111/1365-2656.12611

McMahon, C. R., & Hindell, M. A. (2003). Twinning in southern elephant seals: the implications of resource allocation by mothers. *Wildlife Research*, 30(1), 35–39. https://doi.org/10.1071/WR01069

Meglécz, E., Pech, N., Gilles, A., Dubut, V., Hingamp, P., Trilles, A., Grenier, R., Martin, J.-F. (2014). QDD version 3.1: a user-friendly computer program for microsatellite selection and primer design revisited: experimental validation of variables determining genotyping success rate. *Molecular Ecology Resources*, 14(6), 1302–1313. https://doi.org/10.1111/1755-0998.12271

Modig, A. O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Animal Behaviour*, 51(6), 1295–1306. https://doi.org/10.1006/ANBE.1996.0134

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85(4), 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Navara, K. J. (2013). Hormone-mediated adjustment of sex ratio in vertebrates. *Integrative and Comparative Biology*, 53(6), 877–887. https://doi.org/10.1093/icb/ict081

Navara, K. J. (2018). *Choosing sexes: Mechanisms and adaptive patterns of sex allocation in vertebrates*. Springer. https://doi.org/10.1007/978-3-319-71271-0

Oosthuizen, W. C., Pistorius, P. A., Bester, M. N., Altwegg, R., & Bruyn, P. J. N. de. (2023). Reproductive phenology is a repeatable, heritable trait linked to the timing of other life-history events in a migratory marine predator. *Proceedings of the Royal Society B: Biological Sciences*, 290(2003), Article 20231170. https://doi.org/10.1098/rspb.2023.1170

Packer, C., Collins, D. A., & Eberly, L. E. (2000). Problems with primate sex ratios. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355(1403), 1627–1635. https://doi.org/10.1098/rstb.2000.0725

Pen, I., & Weissing, F. J. (2001). Sexual selection and the sex ratio: an ESS analysis. *Selection*, 1(1–3), 111–122. https://doi.org/10.1556/select.1.2000.1-3.11

Perret, M. (2005). Relationship between urinary estrogen levels before conception and sex ratio at birth in a primate, the gray mouse lemur. *Human Reproduction*, 20(6), 1504–1510. https://doi.org/10.1093/humrep/deh802

Perret, M. (2018). Revisiting the Trivers-Willard theory on birth sex ratio bias: role of paternal condition in a malagasy primate. *PLoS ONE*, 13(12), Article e0209640. https://doi.org/10.1371/journal.pone.0209640

Pew, J., Wang, J., Muir, P., & Frasier, T. (2014). *Related: An r package for analyzing pairwise relatedness data based on codominant molecular markers*. https://r-forge.r-project.org/projects/related/

Pistorius, P. A., Bester, M. N., Kirkman, S. P., & Taylor, F. E. (2001). Pup mortality in southern elephant seals at Marion Island. *Polar Biology*, 24(11), 828–831. https://doi.org/10.1007/s003000100285

R Core Team. (2021). R: a language and environment for statistical computing (Version 4.2.3) [Computer software]. R Foundation for Statistical Computing.

Rada, R. T., Kellner, R., & Winslow, W. W. (1976). Plasma testosterone and aggressive behavior. *Psychosomatics*, 17(3), 138–142. https://doi.org/10.1016/S0033-3182(76)71132-0

Reiter, J., Panken, K. J., & Le Boeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Animal Behaviour*, 29(3), 670–687. https://doi.org/https://doi.org/10.1016/S0003-3472(81)80002-4

Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: The transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, 3(4), 337–367. https://doi.org/10.1007/BF00303199

Røed, K. H., Holand, Ø., Mysterud, A., Tverdal, A., Kumpula, J., & Nieminen, M. (2007). Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. *Proceedings of the Royal Society B: Biological Sciences*, 274(1610), 727–733. https://doi.org/10.1098/rspb.2006.0214

Santos, M. M., Maia, L. L., Nobre, D. M., Oliveira Neto, J. F., Garcia, T. R., Lage, M. C. G. R., Vaz de Melo, M. I., Viana, W. S., Palhares, M. S., Monteiro da Silva Filho, J., J. M., Santos, R. L., & Valle, G. R. (2015). Sex ratio of equine offspring is affected by the ages of the mare and stallion. *Theriogenology*, 84(7), 1238–1245. https://doi.org/10.1016/j.theriogenology.2015.07.001

Saragusty, J., Hermes, R., Hofer, H., Bouts, T., Göritz, F., & Hildebrandt, T. B. (2012). Male pygmy hippopotamus influence offspring sex ratio. *Nature Communications*, 3(1), 697. https://doi.org/10.1038/ncomms1700

Schaik, C. P. van, & Hrdy, S. B. (1991). Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. *American Naturalist*, 138(6), 1555–1562. https://doi.org/10.1086/285300

Seidel, G. E. J. (1999). Sexing mammalian spermatozoa and embryos–state of the art. *Journal of Reproduction and Fertility Supplement*, 54, 477–487.

Shargal, D., Shore, L., Roteri, N., Terkel, A., Zorovsky, Y., Shemesh, M., & Steinberger, Y. (2008). Fecal testosterone is elevated in high-ranking female ibexes (*Capra nubiana*) and associated with increased aggression and a preponderance of male offspring. *Theriogenology*, 69(6), 673–680. https://doi.org/10.1016/j.theriogenology.2007.11.017

Sheldon, B. C. (2000). Differential allocation: tests, mechanisms and implications. *Trends in Ecology & Evolution*, 15(10), 397–402. https://doi.org/10.1016/S0169-5347(00)01953-4

Silk, J. B. (1983). Local Resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *American Naturalist*, 121(1), 56–66. https://doi.org/10.1086/284039

Silk, J. B., Willoughby, E., & Brown, G. R. (2005). Maternal rank and local resource competition do not predict birth sex ratios in wild baboons. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1565), 859–864. https://doi.org/10.1098/rspb.2004.2994

Simons, A. M. (2011). Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1601–1609. https://doi.org/10.1098/rspb.2011.0176

Slatkin, M. (1974). Hedging one's evolutionary bets. *Nature*, *250*(5469), 704–705. https://doi.org/10.1038/250704b0

Tanaka, Y., Fukano, Y., & Nakamura, M. (2019). Effect of paternal age on the birth sex ratio in captive populations of aye-aye (*Daubentonia madagascariensis* (Gmelin)). *Zoo Biology*, *38*(4), 389–392. https://doi.org/10.1002/zoo.21487

Tourvas, N. (2023). *PopGenUtils: A collection of useful functions to deal with genetic data in R* [Computer software]. https://github.com/nikostourvas/PopGenUtils/

Trivers, R. L., & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, *179*(4068), 90–92.

Veiga, J. P., Viñuela, J., Cordero, P. J., Aparicio, J. M., & Polo, V. (2004). Experimentally increased testosterone affects social rank and primary sex ratio in the spotless starling. *Hormones and Behavior*, *46*(1), 47–53. https://doi.org/10.1016/j.yhbeh.2004.01.007

Vergani, D. F., Stanganelli, Z. B., & Bilenca, D. (2004). Effects of El Niño and La Niña events on the sex ratio of southern elephant seals at King George Island. *Marine Ecology Progress Series*, *268*, 293–300. https://doi.org/10.3354/meps268293

Vetter, S. G., & Arnold, W. (2018). Effects of population structure and density on calf sex ratio in red deer (*Cervus elaphus*)—implications for management. *European Journal of Wildlife Research*, *64*(3), 30. https://doi.org/10.1007/s10344-018-1190-1

Waits, L. P., Luikart, G., & Taberlet, P. (2001). Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Molecular Ecology*, *10*(1), 249–256. https://doi.org/10.1046/j.1365-294X.2001.01185.x

West, S. A. (2009). Sex allocation. *Monographs in Population Biology*, *44*. https://doi.org/10.1515/9781400832019

Wild, G., & West, S. A. (2007). A sex allocation theory for vertebrates: combining local resource competition and condition dependent allocation. *American Naturalist*, *170*(5), E112–E128. https://doi.org/10.1086/522057

Wilkinson, I. S., & Aarde, R. J. van. (2001). Investment in sons and daughters by southern elephant seals, *Mirounga leonina*, at Marion Island. *Marine Mammal Science*, *17*(4), 873–887. https://doi.org/10.1111/j.1748-7692.2001.tb01303.x

Williamson, C. M., Lee, W., Romeo, R. D., & Curley, J. P. (2017). Social context-dependent relationships between mouse dominance rank and plasma hormone levels. *Physiology & Behavior*, *171*, 110–119. https://doi.org/10.1016/j.physbeh.2016.12.038

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.