PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: McEntee MHF, Foroughirad V, Krzyszczyk E, Mann J. 2023 Sex bias in mortality risk changes over the lifespan of bottlenose dolphins. *Proc. R. Soc. B* **290**: 20230675.
https://doi.org/10.1098/rspb.2023.0675

Received: 21 March 2023
Accepted: 26 June 2023

Subject Category:
Behaviour

Subject Areas:
behaviour, evolution

Keywords:
longevity, sexual selection, life course

Author for correspondence:
Molly H. F. McEntee
e-mail: mhm95@georgetown.edu

†Current institution.

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6729828.

THE ROYAL SOCIETY PUBLISHING

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

Sex bias in mortality risk changes over the lifespan of bottlenose dolphins

Molly H. F. McEntee[1], Vivienne Foroughirad[1], Ewa Krzyszczyk[1,3,†] and Janet Mann[1,2]

[1]Department of Biology, and [2]Department of Psychology, Georgetown University, Washington, DC 20057, USA
[3]School of Natural Sciences, Bangor University, Bangor, Wales LL57 2DG, UK

MHFM, 0000-0002-6616-3596

Research on sex biases in longevity in mammals often assumes that male investment in competition results in a female survival advantage that is constant throughout life. We use 35 years of longitudinal data on 1003 wild bottlenose dolphins (*Tursiops aduncus*) to examine age-specific mortality, demonstrating a time-varying effect of sex on mortality hazard over the five-decade lifespan of a social mammal. Males are at higher risk of mortality than females during the juvenile period, but the gap between male and female mortality hazard closes in the mid-teens, coincident with the onset of female reproduction. Female mortality hazard is non-significantly higher than male mortality hazard in adulthood, resulting in a moderate male bias in the oldest age class. Bottlenose dolphins have an intensely male-competitive mating system, and juvenile male mortality has been linked to social competition. Contrary to predictions from sexual selection theory, however, male–male competition does not result in sustained male-biased mortality. As female dolphins experience high costs of sexual coercion in addition to long and energetically expensive periods of gestation and lactation, this suggests that substantial female investment in reproduction can elevate female mortality risk and impact sex biases in lifespan.

1. Introduction

In mammals, female survival advantage over males has been attributed to intrasexual male competition and a male 'live fast, die young' reproductive strategy [1,2]. Recent work, however, has highlighted the diversity of sex biases in lifespan across mammals and challenged the generality of the assumption that females live longer than males [3–6]. In the most comprehensive study to date, Lemaître *et al*. [6] found female-biased longevity in 60% of the mammal populations examined, showing that female bias in longevity is common, but not ubiquitous. A growing body of research demonstrates that sex biases in longevity are context-dependent; environmental conditions [7,8], parasite [9] and pathogen loads [10], and the social environment [11–13] can all affect the direction and magnitude of sex biases in lifespan and ageing.

Traditional evolutionary theories posit that sex-specific trade-offs between reproduction and longevity result in sexual dimorphism in life-history traits and focus on the idea that males in polygynous systems invest in reproductive competition at the expense of survival [14]. In systems with intense male–male competition, males can suffer higher mortality rates and faster senescence due to costs of injury, dispersal to find mating opportunities [15], immunosuppressive effects of testosterone [16] or investment in secondary sexual traits over somatic maintenance [2]. These hypotheses predict that in systems where males compete intensively over access to females, female bias in longevity is likely to be large. In monogamous systems, where reproductive interests are relatively aligned between the sexes, sex differences in mortality and lifespan are expected to be minimal. Despite extensive theoretical treatment of these ideas, results from empirical studies are decidedly mixed. Some studies have found an association between male-biased mortality and polygynous mating

© 2023 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

systems [17,18], but more recent work using a larger mammalian dataset found no relationship between mating system and sex bias in longevity [6]. Evidence connecting sexually selected traits, such as sexual size dimorphism, relative testes size, or relative weapon size, to male-biased mortality is also mixed [1,7,19,20].

Most research on sex biases in lifespan has used summary metrics, such as median lifespan or life expectancy, to represent overall sex biases in lifespan and for comparisons across taxa. Adult and juvenile mortality are typically considered separately, or juveniles are excluded entirely. This approach assumes that the relative risk of sex-specific mortality is constant throughout life, a potentially unlikely scenario for long-lived species that experience considerable lifetime variation in social and environmental conditions. Age- and sex-specific selection pressures inevitably interact to shape overall patterns of longevity. Life course approaches that explicitly examine sex-specific mortality over the full lifespan are data-intensive, requiring detailed longitudinal data on both sexes. However, as the number and time frame of long-term longitudinal datasets continue to increase, these approaches could yield important insights into the evolutionary drivers of lifespan in the wild.

Cetaceans are a rich comparative group in which to investigate hypotheses regarding life-history evolution. The infraorder contains the largest animal to have ever evolved (the blue whale, *Balaenoptera musculus* [21]), the longest-living mammal (the bowhead whale, *Balaena mysticetus*) [22]), the only species outside of humans to evolve post-reproductive lifespans [23] and the largest brains for body size outside of humans [24]. Comprehensive life history and mortality data on cetaceans are scarce, however. Cetaceans are long-lived and often wide-ranging, making longitudinal monitoring of populations logistically difficult. The limited data that are available on sex-specific mortality in cetaceans indicate that the direction and magnitude of sex biases in mortality vary widely (see [25–29] for male-biased mortality, [30–33] for female-biased mortality). Female killer whales (*Orcinus orca*), which have the longest post-reproductive lifespan of any non-human animal, outlive males by decades [27,34]. By contrast, male bowhead whales can live to 200 years old, while it appears that few females survive past 100 [33]. This variation in sex biases in longevity, along with variation in social systems and life-history characteristics, make cetaceans a compelling system in which to investigate selection pressures that shape longevity patterns in wild populations.

We use 35 years of longitudinal demographic data on a residential population of Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia, to examine sex-specific mortality over the lifespan of a long-lived mammal. This population is stable ([35] but see [36]), and in a pristine World Heritage Site with few anthropogenic threats. Both males and females remain in their natal home ranges throughout adulthood [37]; neither sex is subject to the costs of dispersal or migration, and we can observe both sexes from birth to death. Males form stable long-term bonds with other males, and cooperate within these alliances to compete over access to mating opportunities and to mate guard and harass females [38]. While reproductive competition is costly for males [39,40], the strong male–male social bonds in the alliance structure could mitigate some of those costs. Females suffer high costs of coercive mating [39,41] and invest heavily in pregnancy, lactation and care. Gestation lasts 12 months, and lactation lasts 3–8 years [42,43]; this lengthy maternal investment in a single offspring results in an extremely male-biased operational sex ratio. Traditional theory suggests that male–male competition over mating access should result in male-biased mortality in this system.

2. Materials and methods

(a) Study site and demographic data

We used demographic data collected by the Shark Bay Dolphin Research Project on a residential population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, from 1985 to 2019. The study area covers approximately 600 km^2 of the eastern gulf of Shark Bay, within a UNESCO World Heritage Site. Dolphins are individually identified based on fin, scar and pigment matching [44,45]. This population is residential, bisexually philopatric [37] and well marked [45,46], allowing us to follow individuals of both sexes from birth to death.

Only dolphins with well-documented life histories were included in our sample. Individuals had to be sighted on a minimum of 5 separate days and have a maximum gap between sightings of 3 years or less. As survey effort increased in 1996 and was sustained thereafter, we also included individuals with larger sighting gaps pre-1996, but who were frequently sighted (less than 3-year gap) in subsequent years. To account for individuals who died early in the calf period and were seen fewer than five times before death we included all offspring of females who met our sighting requirements. Twenty-three individuals with no or poor photographic records were excluded, resulting in a total sample of 1003 individuals. Individuals in the final sample had a median number of sighting days of 23 and a median maximum lifetime sighting gap of 1.04 years.

Birth dates for individuals born after the start of the study (1985) were estimated based on consecutive observations of the mother before and after birth, calf size and the presence of fetal lines [43]. For individuals who were alive at the start of the study, or were first observed after weaning, ages were estimated based on body size and the presence and degree of ventral and dorsal speckling. Ventral speckling begins around age 10 for both sexes and increases predictably with age [47].

Death dates of dependent calves (less than 2.5 years of age, minimum weaning age) were assigned as the mid-point between consecutive observations of the mother with, and then without, the dependent calf. For juveniles and adults, death dates were calculated based on the individual's maximum sighting gap. For individuals who were rarely sighted before 1996 but regularly sighted after, their maximum sighting gap after 1996 was used. To assign a death date, a minimum of 3 years must elapse from an individual's last sighting date. The waiting period without a sighting increases proportionally to an individual's maximum sighting gap. For individuals less than 30 years old, a death date is assigned when the time since their last sighting exceeds 3 years, or three times their maximum sighting gap, whichever is longer. For individuals who are over 30 years old, a death date is assigned when the time since their last sighting exceeds 3 years or two times their maximum sighting gap. The reduced waiting time for individuals over 30 does not impact our results (electronic supplementary material). As fieldwork at the site typically runs from May to December each year, and gaps in sighting history occur from January to May, 1 May is used as the default death date. If an individual's maximum sighting gap was less than 1 year, the death date was assigned as 1 May in the year following last sighting. If the individual's maximum sighting gap exceeded 1 year, the death date was assigned as 1 May in the year of their last sighting plus their maximum sighting gap. For example, an individual under 30

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

with a maximum sighting gap of 2 years would be considered dead only after 6 years with no sightings. The death date would be assigned as 1 May, 2 years after the last sighting. These rules were suspended on the rare occasion that we recovered a body, for individuals who were seen almost daily as part of a tourist provisioning program [48], or for individuals with severe shark bite injuries that were not seen again; in such cases, death dates were assigned to the day or week in which they likely occurred.

Carcasses are only rarely recovered in this system, making the assignment of estimated death dates based on sighting history necessary. Several lines of evidence support our assignment procedure. First, we have recovered the carcasses of ten well-studied individuals, and observed four orphaned calves without their mothers, providing accurate death date information for a few individuals. In these cases, the time between an individual's last live sighting and their body being recovered, or their calf being sighted without them, ranged from zero days to 1.1 years. This suggests that setting the death date to the year following an individual's last sighting is reasonable. Second, parentage assignments via genetic sampling have never revealed that an individual who has been assigned a death date based on sighting records was still alive [49]. Third, evaluation of the rate of false adult death assignments using long-term sighting records reveals a low error rate. Applying our procedure each year from 1991 to 2014, we determined that only 4% of individuals who would have been assigned death dates by this protocol were subsequently resighted (electronic supplementary material). As false death assignments are corrected over time, we expect the error rate in the final dataset to be small. The average rate of error is 0.5 false assignments per year. Allowing for 6 years of potential uncorrected errors, we expect three individuals in the dataset to be erroneously considered dead; we do not expect that error to significantly impact our results. Further, while death dates, and therefore ages at death, are estimates, we do not expect error in these estimates to be biased with regard to sex. We did not find a difference in lifetime maximum sighting gap (Wilcoxon rank sum test, $p = 0.41$, electronic supplementary material, figure S1A), or in yearly sighting rate (GLMM, $p = 0.74$, electronic supplementary material, figure S1C and table S1) between males and females.

Individuals were sexed using observations of the genital area, observations of dependent calves and detection of sex-linked genetic markers [50,51]. Young calves are unlikely to approach the research boat to bowride, which provides a view of the genital area, and dolphins must be at least 2 years old before they are biopsied for genetic analysis. Because of this, individuals that die during the calf period are much less likely to be sexed. Our final sample included 339 unsexed individuals; 14.2% of sample individuals over the age of 3 were unsexed and 6.8% of sample individuals over the age of 10 were unsexed. We did not find a difference in the age at first documented sexing for males and females (Wilcoxon rank sum test, $p = 0.095$, electronic supplementary material, figure S1B).

(b) Analysis

We examined calf (birth–3 years old), juvenile (3–10 years old) and adult (more than 10 years old) survival and plotted Kaplan–Meier survival curves in the *survival* [52] and *survminer* [53] packages in R. Individuals who were alive when the project began were left-truncated at their age on 1 January 1985, and individuals who were still alive at the end of the data collection period were right-censored at their age on 1 January 2020. Median lifespan and 90% lifespan (the age at which 90% of individuals have died, a proxy for maximum lifespan [54]) were calculated for the overall population ($N = 1003$), and for females ($N = 308$) and males ($N = 322$) who survived to at least age three.

We modelled the effect of sex on mortality hazard, the instantaneous rate of death at time t, given that an individual has survived up to time t. We excluded unsexed individuals and individuals who died or were censored before age three and left-truncated the remaining individuals at age three (sexed sample: $N = 308$ female, $N = 322$ male). Cox regression is a commonly used semi-parametric model that can estimate the effect of a covariate on time-to-event (e.g. time-to-death) data with right-censored observations. These models are often referred to as Cox proportional hazards models; a major assumption is that the effect of the covariate on hazard is proportional, or constant, over time. Diagnostic checks of our Cox model showed that the effect of sex does not meet the proportional hazards assumption ($p = 0.003$, electronic supplementary material, figure S2). Instead, we implemented a piece-wise exponential additive model (PAM) in the *pammtools* package [55] to estimate sex-specific hazard over time. This approach applies the flexibility of generalized additive models to time-to-event data and allows for penalized estimation of baseline hazard (i.e. instantaneous rate of an event). PAMs are unconstrained by the proportional hazard assumption, and covariate effects can be nonlinear and time-varying. The baseline log-hazard is estimated semi-parametrically by piece-wise constant hazards where each unique event and censor time is a cut point. We used a stratified hazards model to separately estimate the baseline hazard for males and females and included sex as a fixed effect.

As there is some inherent uncertainty in our age-at-death estimates, we conducted sensitivity analysis by simulating age-at-death or right-censoring based on gamma error distributions and repeating the PAM analysis 100 times (electronic supplementary material). To further verify our results, we implemented a Cox regression model with an explicit linear interaction between sex and time (electronic supplementary material). We also performed Bayesian Survival Trajectory analysis (BaSTA); this approach uses capture–recapture analysis to estimate survival parameters in the absence of accurate age and death information [56]. This allowed us to construct a model completely blind to both our birth and death date estimates. Our Cox and BaSTA model results agreed with the results from the PAM model (electronic supplementary material, tables S2 and S4, and figure S4). As the PAM model allows for more flexibility in the estimation of the baseline hazard and our sensitivity analysis supported our PAM results (electronic supplementary material, figure S3), our PAM results are presented here. All analyses were conducted in R version 4.2.1 [57].

3. Results

(a) Survival summary statistics

Mortality was high throughout the calf period but was highest in the first year of life. Male, female and unsexed calves were pooled, as most individuals are not sexed until the juvenile period. Survival to age one was 80%; survival to age two and three was 72% and 67%, respectively (figure 1; electronic supplementary material, table S5). Annual mortality rate was lower in the juvenile period; 57% of all individuals survived to age 10. The median lifespan was 16.5 years, 90% lifespan was 41 years and maximum recorded lifespan was approximately 51 years.

To calculate sex-specific median and 90% lifespan, we included only individuals who survived to at least age 3. Median lifespan was slightly higher for females than males (male median lifespan = 29.5, female median lifespan =

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

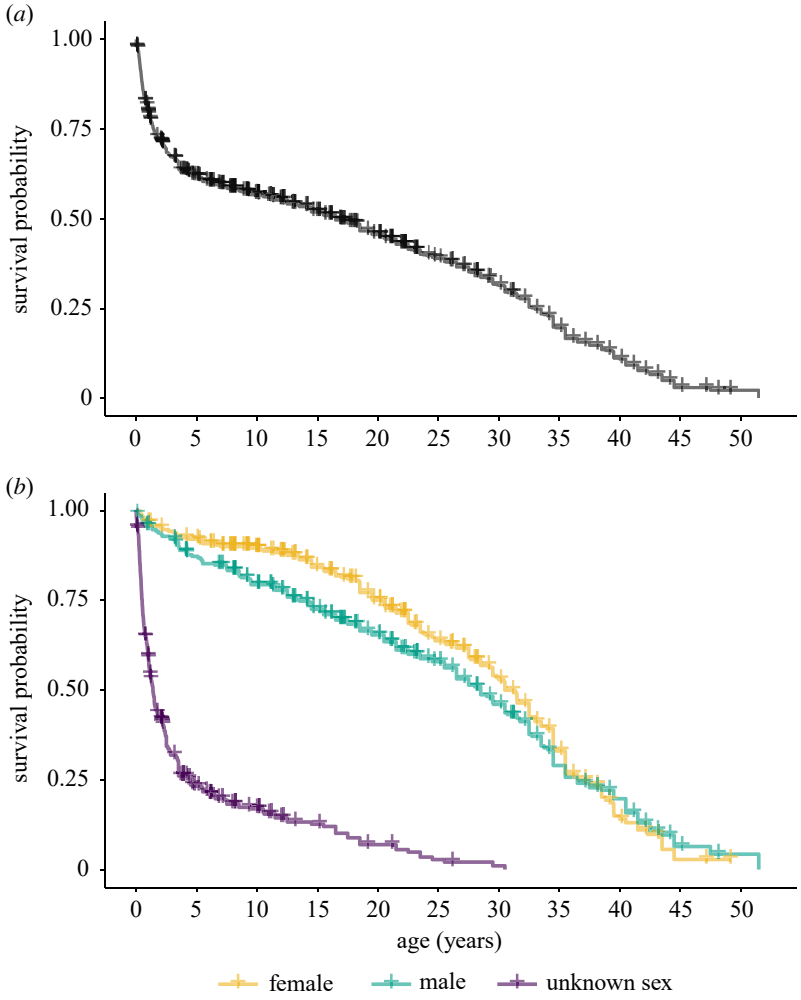

Figure 1. Kaplan–Meier survival curves for (*a*) all individuals ($N = 1003$) and (*b*) by sex ($N = 323$ female, $N = 341$ male and $N = 339$ unknown sex).

31.5). By contrast, 90% lifespan for males was slightly higher than for females (90% male lifespan = 45, 90% female lifespan = 44) (figure 1; electronic supplementary material, tables S6 and S7). Males were moderately overrepresented at the oldest age class; 61% of individuals who survived past 40 were male (25 male, 16 female). The oldest individual in our sample, a male, died at approximately 51 years old, but one female is still alive at approximately age 50 in 2023.

(b) Effect of sex on mortality hazard

Our model of mortality hazard from age 3 to maximum lifespan showed a significant main effect of sex; overall, males have higher mortality hazard than females ($p = 0.002$, table 1). The shape of the mortality hazard function differed for males and females; our PAM estimated a linear relationship between female mortality hazard and age (effective degrees of freedom = 1.00), and a nonlinear mortality hazard for males (effective degrees of freedom = 3.01, table 1). Male mortality hazard was significantly higher than female mortality hazard in the juvenile period (figure 2); at age four, male mortality rate was almost four times higher than female mortality rate (hazard ratio = 3.91, electronic supplementary material S8). The significant gap between male and female mortality hazard closed around the age of 13, coincident with the age of first reproduction in females (mean age at first birth is 12.8 years) [58]. We did not find a significant difference between male and female mortality hazard in adulthood, although estimated female mortality rate was non-significantly higher than male mortality hazard rate after age 20 (electronic supplementary material S8). Senescence, the rate of acceleration in mortality hazard with age, did not appear to differ between the sexes, but interpretation is limited by small sample sizes in the oldest age classes. These results were supported by our sensitivity analysis (electronic supplementary material, figure S3), our Cox model (electronic supplementary material, table S2) and our BaSTA model (electronic supplementary material, figure S4 and table S4).

4. Discussion

The calf period is one of high vulnerability: mortality is highest in the first year and declines continuously in the second and third years of life. Infant mortality is probably underestimated here, as some calves likely die before they are observed by researchers. Our estimate of 20% mortality should be regarded as a minimum for first-year calf mortality. One-third of calves have shark bite scars [59], and tiger shark predation is likely a major cause of calf mortality. Female reproductive success in this population is highly variable [60,61], and calf mortality is also affected by maternal condition [42,62,63]. Sex differences in calf behaviour emerge pre-weaning [64], and it is possible that sex differences in mortality occur as well. However, due to the

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

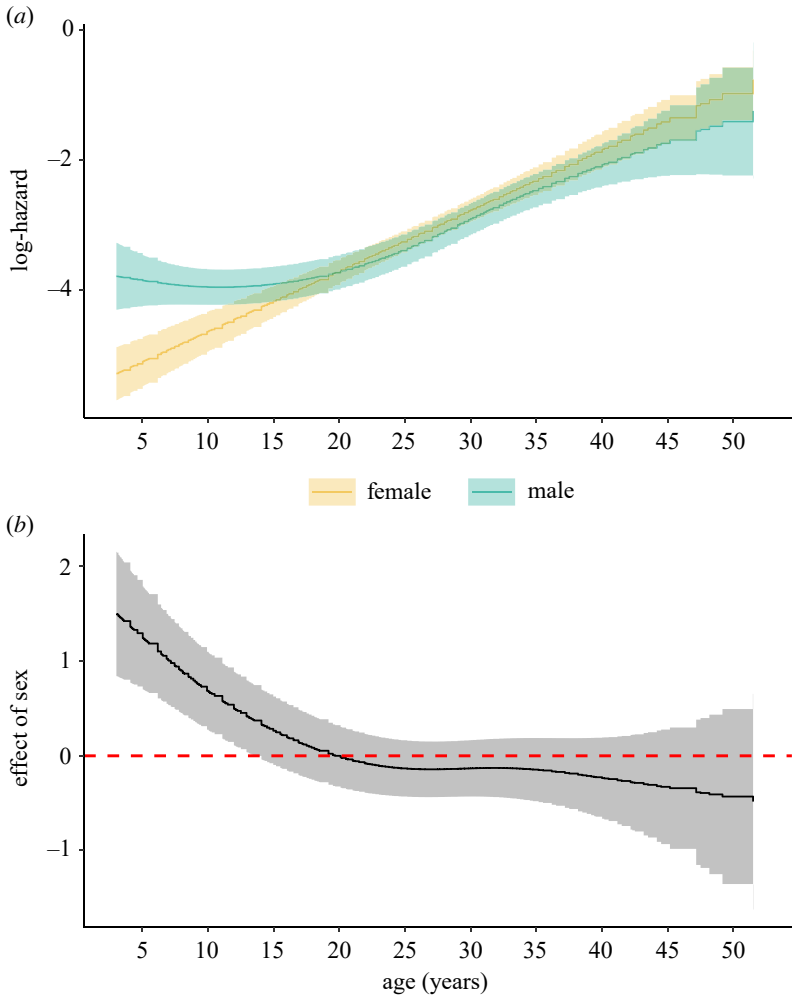

Figure 2. Estimated mortality hazard for females and males from age 3 to end of lifespan ($N = 308$ female, $N = 322$ male). (*a*) Stratified log-hazards for males and females and (*b*) effect of sex on mortality hazard over time.

Table 1. Main effects and smoothing terms from PAM-stratified hazards model. Effective degrees of freedom (EDF) for the spline representing each covariate; an EDF of 1 represents a linear relationship, while an EDF of greater than 2 represents a highly nonlinear relationship.

	estimate	s.e.	*z*-value	*p*-value
intercept	−4.19	0.12	−34.22	<0.001
sex[male]	0.49	0.16	3.15	0.002
	effective degrees of freedom	chi-square value	*p*-value	
male	3.10	89.5	<0.001	
female	1.00	133.4	<0.001	

difficulties of sexing young calves, and because the sex ratio at birth is not known, we were unable to evaluate sex differences in calf mortality.

Male mortality hazard is significantly higher than female hazard in the juvenile period. In other species, sex differences in juvenile mortality have been attributed to differential energetic requirements that put the larger sex at risk [65,66]. As Shark Bay dolphins are monomorphic [67], differential growth requirements are unlikely to play a role. Instead, the intense social competition that juvenile males experience may elevate their mortality risk relative to females. The adult alliance is a critical component of male mating strategies, and the male–male social bonds that develop into adult alliances are formed during the juvenile and early adult period [68,69]. Socially connected male calves have higher survival in the juvenile period [70], but the process of forming social bonds with age mates is risky. Juvenile males have high rates of tooth rakes from conspecific aggression [39,40], and male calves are common recipients of juvenile male socio-sexual behaviours and harassment [71]. The presence of older males appears to be stressful; male calves that associate with juvenile males are at higher mortality risk post-weaning [70], and juvenile males avoid adult males [72]. While juvenile males separate from their maternal networks to develop social bonds with peers, females maintain strong social bonds with their mothers

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

[37]. Females increase their time spent foraging during the juvenile period [72], developing the skills necessary to meet the energetic demands of gestation and lactation. These juvenile strategies reflect the sex-specific demands of adult reproduction as males invest in social bonds and females invest in foraging. The high-risk social behaviours of juvenile males, and the lower risk social and foraging behaviours of juvenile females, may ultimately contribute to high male mortality relative to females in the juvenile period.

Female mortality hazard begins to match male mortality hazard at the onset of female reproduction, in the early teens. Further work is needed to determine the role of costs of reproduction in determining female mortality hazard, but multiple stages of reproduction for females appear to carry substantial costs. First, adult females are consorted by multiple male alliances within a breeding season and can be mate guarded continuously for a month or more [38]. During consortship, females are escorted away from their preferred foraging habitats [41] and suffer increased rates of injury from male aggression [39]. Young females are particularly vulnerable to the costs of coercion, as evidenced by higher rates of inbreeding and elevated risk of received aggression [73,74]. Second, the lengthy and energetically costly periods of gestation and lactation (1 year and 3–8 years, respectively) that females face could compound the costs of consortship. While energetic requirements increase substantially during lactation [75], the demands of parental care simultaneously decrease the mother's ability to forage efficiently and may make her more vulnerable to predation. Both pregnancy and swimming close to an infant decrease the mother's swimming performance [76,77] and mothers decrease their dive durations to accommodate calves [78]. Sharks seem to target young calves, which could increase the mothers' risk as well, particularly if they intervene in attacks to defend their offspring [59]. Although grouping can mitigate predation risk, female social behaviour is constrained by foraging requirements, reflected by the fact that females spend more time alone [79] and have weaker social bonds than adult males [80].

While male and female mortality hazard in adulthood does not differ significantly, male mortality hazard starts to increase in the mid-teens, consistent with the hypothesis that male–male competition increases mortality risk. Males begin reproduction later than females and may not reach peak reproductive success until their mid-30s [49]. In early adulthood, males continue to solidify their alliance bonds [68] and may avoid conflicts over reproductive opportunities until those bonds are fortified. Scarring rates increase as males enter their prime reproductive years [40], and paternity is skewed [81], with a few males obtaining a disproportionately high number of paternities. This suggests that costs of reproductive competition are considerable; however, the strong social bonds between alliance partners may mitigate these costs and reduce mortality hazard for adult males. There is robust evidence that social bonds extend lifespan in primates [82–84], cetaceans [70,85] and other mammals [86–88]. Strong social bonds and affiliative behaviours can reduce stress responses and glucocorticoid secretion [89–91], resulting in better health and survival outcomes [88,92,93]. In Shark Bay, males have significantly stronger social bonds than females do [80]. Dyadic alliance bonds can last for decades [38], and adult male mortality risk increases significantly after the death of an alliance partner [94]. Adult males also spend less time alone and more time in large groups than females [79,95], which could lower predation risk. While strong social bonds and high social connectedness might also make males more vulnerable to pathogen transmission [96], strong male–male social bonds could extend male longevity.

Our results demonstrate that the magnitude and direction of sex bias in mortality hazard change over the lifespan of a long-lived cetacean, and highlight the potential roles of social bonds, social harassment, sexual coercion and maternal investment in mortality risk and lifespan. While strong social bonds likely reduce mortality for adult males, our results also underscore the costs of social living. Male and female dolphins are exposed to high levels of social and sexual harassment at different life stages. The process of forming male–male social bonds in the juvenile period exposes males to high levels of harassment and high mortality risk, but the bonds they develop during that time may prove protective later in life. Females, conversely, may have more social support from maternal networks and lower risk of harassment in the juvenile period, but suffer costs of sexual harassment and maternal investment during adulthood. These life stage-specific selection pressures could result in the filtering of poor-condition males out of the population in the juvenile stage, while relatively poor-condition females may survive until early adulthood, when they experience elevated energetic demands that result in increased mortality risk.

These results raise the possibility that costs of reproduction to females impact sex biases in mortality in this population. While some researchers have been careful to note that sex differences in lifespan are not reflective of reproductive costs *per se*, but rather the type and scheduling of investment [2], research on sex biases in lifespan have often defined 'reproductive investment' as male investment in competition and overlooked the costs of female investment in reproduction. In birds, parental care can incur mortality costs for both sexes [19,97] and Promislow [1] emphasized that costs of lactation and care could have a strong impact on sex-specific mortality. In feral sheep, female mortality is correlated with the number of rutting rams, resulting in a male-biased adult sex ratio [98]. Recent work even suggests that female costs of reproduction may have shaped longevity patterns in humans; the apparently robust pattern of female-biased longevity may be a recent phenomenon, mediated by a decline in birth rates in the past 200 years [99,100]. In mammals, particularly long-lived mammals with long periods of offspring dependency, female investment in reproduction could be large enough to alter expected patterns of sex-specific mortality, and explicit incorporation of selection pressures on females in studies of sex bias in longevity could help resolve inconsistencies in the literature.

Few empirical studies evaluate changes in sex-specific mortality hazard over time, and many rely on single metrics, such as median lifespan, to describe overall sex biases in lifespan. In humans, the species where we have the by far most data, women survive better than men in almost every age class and almost every context [101,102], perhaps predisposing us to assume that sex effects on mortality would be consistent with age in other species as well. Had we looked at median lifespan alone we would have concluded that females live slightly longer than males in this population and overlooked the life-history stage-specific patterns in mortality risk. Mating system categories do not capture the myriad ways that animals invest in reproduction, and each

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

life stage carries its own set of risks, challenges and trade-offs for each sex. In long-lived iteroparous mammals, variation in lifespan is a major driver of variation in reproductive success for both males and females [103,104], and the drivers of sex-specific longevity are likely under strong selection. Research that investigates the specific demographic, ecological and social conditions that produce variation in mortality hazard within populations can provide novel insights into the evolution of longevity.

Ethics. Ethical approval was obtained by the University of the Sunshine Coast (AN/S/15/35) and Georgetown University IACUC (13–069, 07–041, 10–023, 2016–1235). Research was conducted under Western Australian Department of Biodiversity, Conservation and Attractions permits (SF-009876, SF- 010347, SF-008076, SF009311, SF007457).

Data accessibility. Data and R code to reproduce models and figures are included in the electronic supplementary material [105].

Authors' contributions. M.H.F.M.: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing—original draft and writing—review and editing; V.F.: data curation, investigation, methodology, project administration and writing—review and editing; E.K.: data curation, investigation, project administration and writing—review and editing; J.M.: conceptualization, funding acquisition, investigation, project administration, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. The authors declare that they have no competing interests.

Funding. The study was funded by grants from NSF #0847922, 1755229, 0941487, 0918308, 2139712, 0316800, 2146995, 2128134, 1515197, 1559380, 0521763, 0820722, 1927619 and 9753044 (to J.M.), NSF #2106909 (to J.M. and V.F.), ONR 10230702 (to J.M.) and Georgetown University (to J.M.). M.H.F.M. received support from Williams College, NSF GRFP #1937959, NSF GROW, the American Society of Mammalogists, the Animal Behaviour Society, the Society for Integrative and Comparative Biology and the American Museum of Natural History.

Acknowledgements. We acknowledge the Malgana peoples and the traditional custodians of Gutharraguda and Irrabuga Mia where this work was conducted. We thank all members of the Shark Bay Dolphin Research Project past and present. We would also like to thank two anonymous reviewers, whose comments greatly improved this manuscript. We are grateful to the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA), the University of Western Australia, the Monkey Mia Dolphin Resort (Royal Automobile Club) and the local Shark Bay community for logistical field support.

References

1. Promislow DEL. 1992 Costs of sexual selection in natural populations of mammals. *Proc. R. Soc. Lond. B* **247**, 203–210. (doi:10.1098/rspb.1992.0030)
2. Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. 2008 Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol.* **22**, 443–453. (doi:10.1111/j.1365-2435.2008.01417.x)
3. Austad SN, Fischer KE. 2016 Sex differences in lifespan. *Cell Metab.* **23**, 1022–1033. (doi:10.1016/j.cmet.2016.05.019)
4. Tarka M, Guenther A, Niemelä PT, Nakagawa S, Noble DWA. 2018 Sex differences in life history, behavior, and physiology along a slow-fast continuum: a meta-analysis. *Behav. Ecol. Sociobiol.* **72**, 132. (doi:10.1007/s00265-018-2534-2)
5. Austad SN. 2019 Sex differences in health and aging: a dialog between the brain and gonad? *GeroScience* **41**, 267–273. (doi:10.1007/s11357-019-00081-3)
6. Lemaître JF *et al.* 2020 Sex differences in adult lifespan and aging rates of mortality across wild mammals. *Proc. Natl Acad. Sci. USA* **117**, 8546–8553. (doi:10.1073/pnas.1911999117)
7. Toïgo C, Gaillard JM. 2003 Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos* **101**, 376–384. (doi:10.1034/j.1600-0706.2003.12073.x)
8. Garratt M, Lemaître JF, Douhard M, Bonenfant C, Capron G, Warnant C, Klein F, Brooks RC, Gaillard JM. 2015 High juvenile mortality is associated with sex-specific adult survival and lifespan in wild roe deer. *Curr. Biol.* **25**, 759–763. (doi:10.1016/j.cub.2014.11.071)
9. Moore SL, Wilson K. 2002 Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* **297**, 2015–2018. (doi:10.1126/science.1074196)
10. Tidière M, Badruna A, Fouchet D, Gaillard JM, Lemaître JF, Pontier D. 2020 Pathogens shape sex differences in mammalian aging. *Trends Parasitol.* **36**, 668–676. (doi:10.1016/j.pt.2020.05.004)
11. Adler MI, Bonduriansky R. 2011 The dissimilar costs of love and war: age-specific mortality as a function of the operational sex ratio. *J. Evol. Biol.* **24**, 1169–1177. (doi:10.1111/j.1420-9101.2011.02250.x)
12. Beirne C, Delahay R, Young A. 2015 Sex differences in senescence: the role of intra-sexual competition in early adulthood. *Proc. R. Soc. B* **282**, 20151086. (doi:10.1098/rspb.2015.1086)
13. Berger V, Lemaître JF, Allainé D, Gaillard JM, Cohas A. 2018 Early and adult social environments shape sex-specific actuarial senescence patterns in a cooperative breeder. *Am. Nat.* **192**, 525–536. (doi:10.1086/699513)
14. Maklakov AA, Lummaa V. 2013 Evolution of sex differences in lifespan and aging: causes and constraints. *Bioessays* **35**, 717–724. (doi:10.1002/bies.201300021)
15. Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev.* **87**, 290–312. (doi:10.1111/j.1469-185X.2011.00201.x)
16. Foo YZ, Nakagawa S, Rhodes G, Simmons LW. 2017 The effects of sex hormones on immune function: a meta-analysis. *Biol. Rev.* **92**, 551–571. (doi:10.1111/brv.12243)
17. Clutton-Brock TH, Isvaran K. 2007 Sex differences in ageing in natural populations of vertebrates. *Proc. R. Soc. B* **274**, 3097–3104. (doi:10.1098/rspb.2007.1138)
18. Tidière M, Gaillard JM, Müller DWH, Lackey LB, Gimenez O, Clauss M, Lemaître JF. 2015 Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants. *Evolution* **69**, 3123–3140. (doi:10.1111/evo.12801)
19. Liker A, Székely T. 2005 Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* **59**, 890–897. (doi:10.1111/j.0014-3820.2005.tb01762.x)
20. Lemaître JF, Gaillard JM. 2012 Male survival patterns do not depend on male allocation to sexual competition in large herbivores. *Behav. Ecol.* **24**, 421–428. (doi:10.1093/beheco/ars179)
21. Slater GJ, Goldbogen JA, Pyenson ND. 2017 Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. *Proc. R. Soc. B* **284**, 20170546. (doi:10.1098/rspb.2017.0546)
22. Keane M *et al.* 2015 Insights into the evolution of longevity from the bowhead whale genome. *Cell Rep.* **10**, 112–122. (doi:10.1016/j.celrep.2014.12.008)
23. Ellis S, Franks DW, Nattrass S, Currie TE, Cant MA, Giles D, Balcomb KC, Croft DP. 2018 Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Sci. Rep.* **8**, 12833. (doi:10.1038/s41598-018-31047-8)
24. Marino L. 1998 A comparison of encephalization between cdontocete cetaceans and anthropoid primates. *Brain. Behav. Evol.* **51**, 230–238. (doi:10.1159/000006540)
25. Ralls K, Brownell Jr RL, Ballou J. 1980 Differential mortality by sex and age in mammals, with specific reference to the sperm whale. *Rep. Int. Whal. Comm. Spec. Issue* **2**, 233–243.
26. Kasuya T, Marsh H. 1984 Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. Int. Whal. Comm. Spec. Issue* **6**, 259–310.

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

27. Olesiuk PF, Bigg MA, Ellis GM. 1990 Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Comm. Spec. Issue* **12**, 209–243.
28. Bloch D. 1993 Age and growth parameters of the long-finned pilot whale off the Faroe Islands. *Rep. Int. Whal. Comm. Spec. Issue* **14**, 163–207.
29. Ramp C, Bérubé M, Palsbøll P, Hagen W, Sears R. 2010 Sex-specific survival in the humpback whale *Megaptera novaeangliae* in the Gulf of St. Lawrence, Canada. *Mar. Ecol. Prog. Ser.* **400**, 267–276. (doi:10.3354/meps08426)
30. Benjaminsen T, Christensen I. 1979 The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Forster). In *Behavior of marine animals: current perspectives in research* (eds HE Winn, BL Olla), pp. 143–164. Boston, MA: Springer US.
31. Heyning JE. 1989 Cuvier's beaked whale *Ziphius cavirostris* G. Cuvier, 1823. In *Handbook of Marine Mammals. Voume 4: River Dolphins and the Larger Toothed Whales* (eds SH Ridgway, R Harrison), pp. 289–308. London, UK and San Diego, California: Academic Press.
32. Kasuya T, Brownell Jr RL, Balcomb KC. 1997 Life history of Baird's beaked whales off the Pacific coast of Japan. *Rep. Int. Whal. Comm.* **47**, 969–979.
33. George JC, Bada J, Zeh J, Scott L, Brown SE, O'Hara T, Suydam R. 1999 Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* **77**, 571–580. (doi:10.1139/cjz-77-4-571)
34. Croft DP *et al.* 2017 Reproductive conflict and the evolution of menopause in killer whales. *Curr. Biol.* **27**, 298–304. (doi:10.1016/j.cub.2016.12.015)
35. Manlik O *et al.* 2016 The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecol. Evol.* **6**, 3496–3512. (doi:10.1002/ece3.2130)
36. Mann J *et al.* 2021 Elevated calf mortality and long-term responses of wild bottlenose dolphins to extreme climate events: impacts of foraging specialization and provisioning. *Front. Mar. Sci.* **8**, 219. (doi:10.3389/fmars.2021.617550)
37. Tsai YJJ, Mann J. 2013 Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Mar. Mammal Sci.* **29**, 261–279. (doi:10.1111/j.1748-7692.2011.00559.x)
38. Connor RC, Krützen M. 2015 Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Anim. Behav.* **103**, 223–235. (doi:10.1016/j.anbehav.2015.02.019)
39. Scott EM, Mann J, Watson-Capps JJ, Sargeant BL, Connor RC. 2005 Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* **142**, 21–44. (doi:10.1163/1568539053627712)
40. Lee HH, Wallen MM, Krzyszczyk E, Mann J. 2019 Every scar has a story: age and sex-specific conflict rates in wild bottlenose dolphins. *Behav. Ecol. Sociobiol.* **73**, 63. (doi:10.1007/s00265-019-2674-z)
41. Wallen MM, Patterson EM, Krzyszczyk E, Mann J. 2016 The ecological costs to females in a system with allied sexual coercion. *Anim. Behav.* **115**, 227–236. (doi:10.1016/j.anbehav.2016.02.018)
42. Karniski C, Krzyszczyk E, Mann J. 2018 Senescence impacts reproduction and maternal investment in bottlenose dolphins. *Proc. R. Soc. B* **285**, 20181123. (doi:10.1098/rspb.2018.1123)
43. Mann J, Connor RC, Barre LM, Heithaus MR. 2000 Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav. Ecol.* **11**, 210–219. (doi:10.1093/beheco/11.2.210)
44. Würsig B, Würsig M. 1977 The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* **198**, 755–756. (doi:10.1126/science.198.4318.755)
45. Bichell LMV, Krzyszczyk E, Patterson EM, Mann J. 2018 The reliability of pigment pattern-based identification of wild bottlenose dolphins. *Mar. Mammal Sci.* **34**, 113–124. (doi:10.1111/mms.12440)
46. Heithaus MR. 2001 Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. *Mar. Mammal Sci.* **17**, 526–539. (doi:10.1111/j.1748-7692.2001.tb01002.x)
47. Krzyszczyk E, Mann J. 2012 Why become speckled? Ontogeny and function of speckling in Shark Bay bottlenose dolphins (*Tursiops sp.*). *Mar. Mammal Sci.* **28**, 295–307. (doi:10.1111/j.1748-7692.2011.00483.x)
48. Foroughirad V, Mann J. 2013 Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biol. Conserv.* **160**, 242–249. (doi:10.1016/j.biocon.2013.01.001)
49. Foroughirad V, McEntee M, Kopps AM, Levengood A, Frère C, Mann J. 2022 Reproductive timing as an explanation for skewed parentage assignment ratio in a bisexually philopatric population. *Behav. Ecol. Sociobiol.* **76**, 129. (doi:10.1007/s00265-022-03233-2)
50. Krützen M, Barré LM, Möller LM, Heithaus MR, Simms C, Sherwin WB. 2002 A biopsy system for small cetaceans: darting success and wound healing in *Tursiops spp*. *Mar. Mammal. Sci.* **18**, 863–878. (doi:10.1111/j.1748-7692.2002.tb01078.x)
51. Foroughirad V, Levengood AL, Mann J, Frère CH. 2019 Quality and quantity of genetic relatedness data affect the analysis of social structure. *Mol. Ecol. Resour.* **19**, 1181–1194. (doi:10.1111/1755-0998.13028)
52. Therneau TM. 2022 A package for survival analysis in R. R package version 3.4-0, https://CRAN.R-project.org/package=survival.
53. Kassambara A, Kosinski M, Biecek P. 2021 Survminer: drawing survival curves using ggplot2. R package version 0.4.9, https://CRAN.R-project.org/package=survminer.
54. Moorad JA, Promislow DEL, Flesness N, Miller RA. 2012 A comparative assessment of univariate longevity measures using zoological animal records. *Aging Cell* **11**, 940–948. (doi:10.1111/j.1474-9726.2012.00861.x)
55. Bender A, Scheipl F. 2018 pammtools: Piece-wise exponential Additive Mixed Modeling tools. *ArXiv180601042 Stat.*
56. Colchero F, Jones OR, Rebke M. 2012 BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark–recapture/recovery data with covariates. *Methods Ecol. Evol.* **3**, 466–470. (doi:10.1111/j.2041-210X.2012.00186.x)
57. R Core Team. 2022 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
58. Mann J. 2019 Maternal care and offspring development in odontocetes. In *Ethology and behavioral ecology of odontocetes* (ed. B Würsig), pp. 95–116. Berlin, Germany: Springer.
59. Mann J, Barnett H. 1999 Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: defense and reactions by the mother. *Mar. Mammal. Sci.* **15**, 568–575. (doi:10.1111/j.1748-7692.1999.tb00823.x)
60. Strickland K, Mann J, Foroughirad V, Levengood AL, Frère CH. 2021 Maternal effects and fitness consequences of individual variation in bottlenose dolphins' ecological niche. *J. Anim. Ecol.* **90**, 1948–1960. (doi:10.1111/1365-2656.13513)
61. Mann J, Sargeant BL, Watson-Capps JJ, Gibson QA, Heithaus MR, Connor RC, Patterson E. 2008 Why do dolphins carry sponges? *PLoS ONE* **3**, e3868. (doi:10.1371/journal.pone.0003868)
62. Mann J, Watson-Capps JJ. 2005 Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Anim. Behav.* **69**, 899–909. (doi:10.1016/j.anbehav.2004.04.024)
63. Frère CH, Krützen M, Mann J, Connor RC, Bejder L, Sherwin WB. 2010 Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc. Natl Acad. Sci. USA* **107**, 19 949–19 954. (doi:10.1073/pnas.1007997107)
64. Gibson QA, Mann J. 2008 Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Anim. Behav.* **76**, 375–387. (doi:10.1016/j.anbehav.2008.01.021)
65. Clutton-Brock TH, Albon SD, Guinness FE. 1985 Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**, 131–133. (doi:10.1038/313131a0)
66. Maness TJ, Anderson DJ. 2013 Predictors of juvenile survival in birds. *Ornithol. Monogr.* **78**, 1–55. (doi:10.1525/om.2013.78.1.1)
67. van Aswegen M, Christiansen F, Symons J, Mann J, Nicholson K, Sprogis K, Bejder L. 2019 Morphological differences between coastal bottlenose dolphin (*Tursiops aduncus*) populations identified using non-invasive stereo-laser photogrammetry. *Sci. Rep.* **9**, 12235. (doi:10.1038/s41598-019-48419-3)
68. Gerber L *et al.* 2020 Affiliation history and age similarity predict alliance formation in adult male

Downloaded from https://royalsocietypublishing.org/ on 26 July 2023

bottlenose dolphins. *Behav. Ecol.* **31**, 361–370. (doi:10.1093/beheco/arz195)

69. Galezo AA, Foroughirad V, Krzyszczyk E, Frère CH, Mann J. 2020 Juvenile social dynamics reflect adult reproductive strategies in bottlenose dolphins. *Behav. Ecol.* **31**, 1159–1171. (doi:10.1093/beheco/araa068))
70. Stanton MA, Mann J. 2012 Early social networks predict survival in wild bottlenose dolphins. *PLoS ONE* **7**, e47508. (doi:10.1371/journal.pone.0047508)
71. Mann J. 2006 Establishing trust: socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. *Homosex. Behav. Anim.* **107**, 107–130.
72. Krzyszczyk E, Patterson EM, Stanton MA, Mann J. 2017 The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins. *Anim. Behav.* **129**, 43–59. (doi:10.1016/j.anbehav.2017.04.011)
73. Watson JJ. 2005 Female Mating Behavior in the Context of Sexual Coercion and Female Ranging Behavior of Bottlenose Dolphines (*Tursiops* Sp.) in Shark Bay, Western Australia. PhD Thesis, Georgetown University, Washington, DC.
74. Frère CH, Krützen M, Kopps AM, Ward P, Mann J, Sherwin WB. 2010 Inbreeding tolerance and fitness costs in wild bottlenose dolphins. *Proc. R. Soc. B* **277**, 2667–2673. (doi:10.1098/rspb.2010.0039)
75. Cheal AJ, Gales NJ. 1991 Body mass and food intake in captive, breeding bottlenose dolphins, *Tursiops truncatus*. *Zoo Biol.* **10**, 451–456. (doi:10.1002/zoo.1430100603)
76. Noren SR, Redfern JV, Edwards EF. 2011 Pregnancy is a drag: hydrodynamics, kinematics and performance in pre- and post-parturition bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.* **214**, 4151–4159. (doi:10.1242/jeb.059121)
77. Noren SR. 2008 Infant carrying behaviour in dolphins: costly parental care in an aquatic environment. *Funct. Ecol.* **22**, 284–288. (doi:10.1111/j.1365-2435.2007.01354.x)
78. Miketa ML, Patterson EM, Krzyszczyk E, Foroughirad V, Mann J. 2018 Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins. *Anim. Behav.* **137**, 107–117. (doi:10.1016/j.anbehav.2017.12.023)
79. Evans T, Krzyszczyk E, Frère CH, Mann J. 2021 Lifetime stability of social traits in bottlenose dolphins. *Commun. Biol.* **4**, 759. (doi:10.1038/s42003-021-02292-x)
80. Mann J, Stanton MA, Patterson EM, Bienenstock EJ, Singh LO. 2012 Social networks reveal cultural behaviour in tool-using dolphins. *Nat. Commun.* **3**, 1–8. (doi:10.1038/ncomms1983)
81. Krützen M, Barré LM, Connor RC, Mann J, Sherwin WB. 2004 'O father: where art thou?'—Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Mol. Ecol.* **13**, 1975–1990. (doi:10.1111/j.1365-294X.2004.02192.x)
82. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010 Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol.* **20**, 1359–1361. (doi:10.1016/j.cub.2010.05.067)
83. Archie EA, Tung J, Clark M, Altmann J, Alberts SC. 2014 Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc. B* **281**, 20141261. (doi:10.1098/rspb.2014.1261)
84. Campos FA, Villavicencio F, Archie EA, Colchero F, Alberts SC. 2020 Social bonds, social status and survival in wild baboons: a tale of two sexes. *Phil. Trans. R. Soc. B* **375**, 20190621. (doi:10.1098/rstb.2019.0621)
85. Ellis S, Franks DW, Nattrass S, Cant MA, Weiss MN, Giles D, Balcomb KC, Croft DP. 2017 Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. *Proc. R. Soc. B* **284**, 20171313. (doi:10.1098/rspb.2017.1313)
86. Barocas A, Ilany A, Koren L, Kam M, Geffen E. 2011 Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE* **6**, e22375. (doi:10.1371/journal.pone.0022375)
87. Vander Wal E, Festa-Bianchet M, Réale D, Coltman DW, Pelletier F. 2015 Sex-based differences in the adaptive value of social behaviour contrasted against morphology and environment. *Ecology* **96**, 631–641. (doi:10.1890/14-1320.1)
88. Snyder-Mackler N *et al.* 2020 Social determinants of health and survival in humans and other animals. *Science* **368**, eaax9553. (doi:10.1126/science.aax9553)
89. Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL. 2008 Focused grooming networks and stress alleviation in wild female baboons. *Horm. Behav.* **54**, 170–177. (doi:10.1016/j.yhbeh.2008.02.009)
90. Young C, Majolo B, Heistermann M, Schülke O, Ostner J. 2014 Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proc. Natl Acad. Sci. USA* **111**, 18 195–18 200. (doi:10.1073/pnas.1411450111)
91. Wittig RM, Crockford C, Weltring A, Langergraber KE, Deschner T, Zuberbühler K. 2016 Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nat. Commun.* **7**, 13361. (doi:10.1038/ncomms13361)
92. Sapolsky RM, Romero LM, Munck AU. 2000 How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* **21**, 55–89. (doi:10.1210/edrv.21.1.0389)
93. Campos FA, Archie EA, Gesquiere LR, Tung J, Altmann J, Alberts SC. 2021 Glucocorticoid exposure predicts survival in female baboons. *Sci. Adv.* **7**, eabf6759. (doi:10.1126/sciadv.abf6759)
94. Rankin RW, Foroughirad VJ, Krzyszczyk EB, Frère CH, Mann J. 2022 Changes in social position predict survival in bottlenose dolphins. *bioRxiv* 2022.08.25.505273. (doi:10.1101/2022.08.25.505273)
95. Galezo AA, Krzyszczyk E, Mann J. 2018 Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behav. Ecol.* **29**, 377–386. (doi:10.1093/beheco/arx177)
96. Leu ST, Sah P, Krzyszczyk E, Jacoby A-M, Mann J, Bansal S. 2020 Sex, synchrony, and skin contact: integrating multiple behaviors to assess pathogen transmission risk. *Behav. Ecol.* **31**, 651–660. (doi:10.1093/beheco/araa002)
97. Owens IPF, Bennett PM. 1994 Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. Lond. B* **257**, 1–8. (doi:10.1098/rspb.1994.0086)
98. Réale D, Boussès P, Chapuis JL. 1996 Female-biased mortality induced by male sexual harassment in a feral sheep population. *Can. J. Zool.* **74**, 1812–1818. (doi:10.1139/z96-202)
99. Bolund E, Lummaa V, Smith KR, Hanson HA, Maklakov AA. 2016 Reduced costs of reproduction in females mediate a shift from a male-biased to a female-biased lifespan in humans. *Sci. Rep.* **6**, 24672. (doi:10.1038/srep24672)
100. Schacht R, Macfarlan S, Meeks H, Cervantes P, Morales F. 2020 Male survival advantage on the Baja California peninsula. *Biol. Lett.* **16**, 20200600. (doi:10.1098/rsbl.2020.0600)
101. Austad SN, Bartke A. 2016 Sex differences in longevity and in responses to anti-aging interventions: a mini-review. *Gerontology* **62**, 40–46. (doi:10.1159/000381472)
102. Zarulli V, Barthold Jones JA, Oksuzyan A, Lindahl-Jacobsen R, Christensen K, Vaupel JW. 2018 Women live longer than men even during severe famines and epidemics. *Proc. Natl Acad. Sci. USA* **115**, E832–E840. (doi:10.1073/pnas.1701535115)
103. McDonald DB. 1993 Demographic consequences of sexual selection in the long-tailed manakin. *Behav. Ecol.* **4**, 297–309. (doi:10.1093/beheco/4.4.297)
104. Blomquist GE. 2009 Trade-off between age of first reproduction and survival in a female primate. *Biol. Lett.* **5**, 339–342. (doi:10.1098/rsbl.2009.0009)
105. McEntee MHF, Foroughirad V, Krzyszczyk E, Mann J. 2023 Sex bias in mortality risk changes over the lifespan of bottlenose dolphins. Figshare. (doi:10.6084/m9.figshare.c.6729828)