LETTER

https://doi.org/10.1038/s41586-018-0020-7

High male sexual investment as a driver of extinction in fossil ostracods

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Sexual selection favours traits that confer advantages in the competition for mates. In many cases, such traits are costly to produce and maintain, because the costs help to enforce the honesty of these signals and cues[1]. Some evolutionary models predict that sexual selection also produces costs at the population level, which could limit the ability of populations to adapt to changing conditions and thus increase the risk of extinction[2–4]. Other models, however, suggest that sexual selection should increase rates of adaptation and enhance the removal of deleterious mutations, thus protecting populations against extinction[3,5,6]. Resolving the conflict between these models is not only important for explaining the history of biodiversity, but also relevant to understanding the mechanisms of the current biodiversity crisis. Previous attempts to test the conflicting predictions produced by these models have been limited to extant species and have thus relied on indirect proxies for species extinction. Here we use the informative fossil record of cytheroid ostracods—small, bivalved crustaceans with sexually dimorphic carapaces—to test how sexual selection relates to actual species extinction. We show that species with more pronounced sexual dimorphism, indicating the highest levels of male investment in reproduction, had estimated extinction rates that were ten times higher than those of the species with the lowest investment. These results indicate that sexual selection can be a substantial risk factor for extinction.

Sexual selection favours traits that confer advantages to competition for access to mates, often leading to the evolution of costly, exaggerated characteristics[7,8]. The evolutionary costs of such traits help to enforce the honesty of the associated displays[1], but can also reduce fitness of populations in general and thereby increase the risk of population extinction in response to environmental change[2–4]. Alternatively, sexual selection could instead reinforce natural selection, more effectively remove deleterious mutations, and thereby speed up adaptation, which could decrease the risk of extinction[3,5,6,9]. The conflicting predictions generated by these two types of evolutionary models have prompted empirical tests of the relationship between sexual selection and extinction risk. Experiments on laboratory populations have found adaptation to be more effective in the presence of sexual selection in some cases[5,10], but not others[11]. Studies of wild populations have not found evidence that sexual selection protects against extinction, but have instead suggested that it either increases extinction risk[12–15] or that it has no effect[16–18]. Notably, all of these studies have examined extant species and have therefore been limited to studying indirect proxies of extinction rather than true lineage terminations. Such proxies have included population decline[17,18], local extirpation[12,14,19] and conservation status[13,16]. Because the models predict evolutionary outcomes, it is important that we investigate patterns of actual species extinction in association with changes in the strength of sexual selection.

The fossil record has documented the origin, persistence and extinction of a large number of species. Palaeontologists routinely compare the longevities of fossil taxa to test factors that have been hypothesized to increase or decrease extinction risk[20,21]. These approaches have not yet been applied to sexual selection, because males and females can seldom be distinguished in fossil remains and, therefore, we usually know very little about sexual dimorphism and sexual selection in extinct species[22]. Cytheroid ostracods, however, are a notable exception to this rule. Males in extant members of this superfamily can be distinguished from females by their relatively elongated carapaces[23] (Fig. 1). This shape difference arises from an expansion of the posterior region that accommodates the large sperm pumping and copulatory apparatus of males[23]. Because this difference is expressed in the mineralized and readily preserved carapace, sexes can be discerned even in extinct populations. Reports from living cytheroids have suggested that sexual differences in carapace size and shape can reflect differences in male investment in reproduction: males with larger carapaces bear

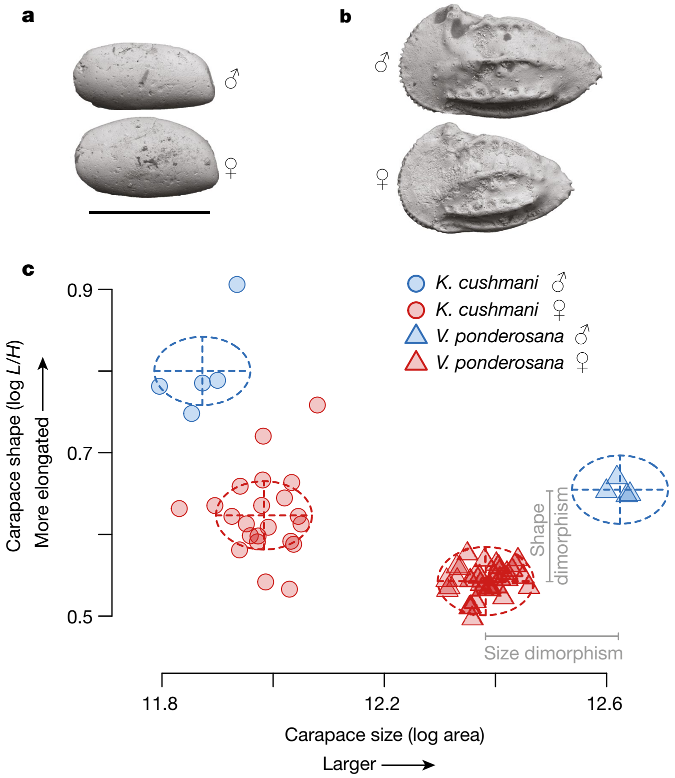

Fig. 1 | Sexual dimorphism in two species of cytheroid ostracods. **a**, **b**, Example males (top) and females (bottom) of *Krithe cushmani* (**a**) and *Veenia ponderosana* (**b**). **c**, Carapace size versus shape (circles, *K. cushmani*, $n = 27$; triangles, *V. ponderosana*, $n = 39$) with separate sex clusters for each species (blue, males, red, females). Magnitudes of sexual dimorphism were computed as male minus female means. Scale bar, 200 μm (applies to all specimens). These fossils were sampled from the Marlbrook Marl (*K. cushmani*) and Annona Chalk (*V. ponderosana*) in Arkansas, USA.

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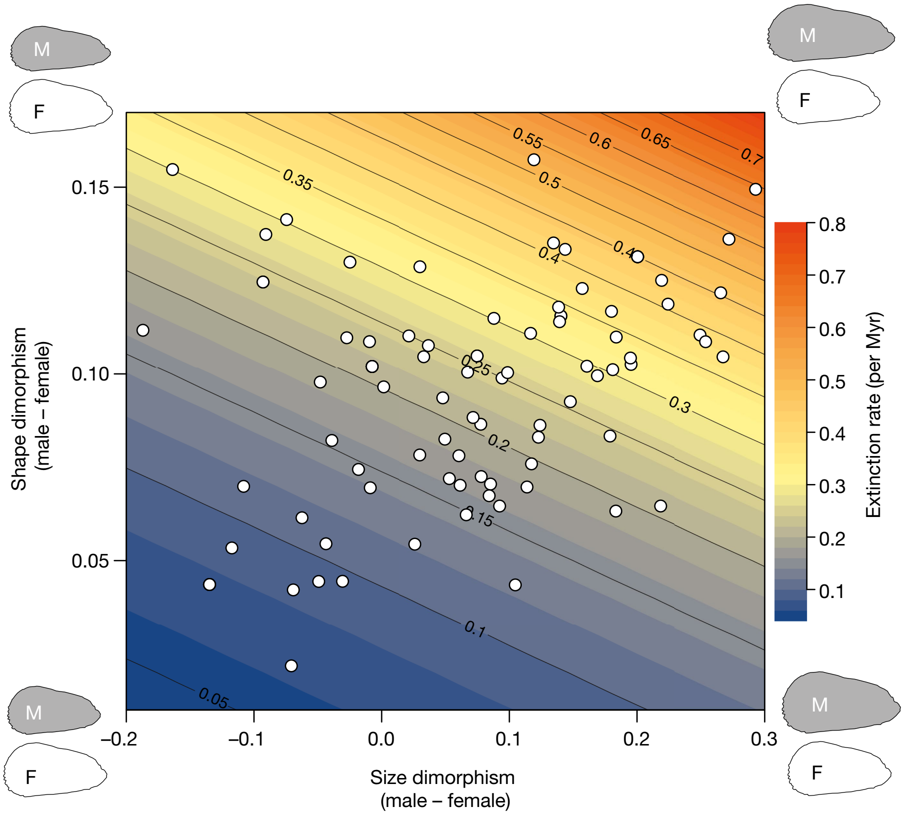

Fig. 2 | Model-predicted extinction rate according to sexual size and shape dimorphism. Magnitudes of sexual size and shape dimorphism were computed as male minus female means. Each dot represents the size and shape dimorphism of a species ($n = 93$), with colour contours corresponding to per-Myr extinction rates predicted by capture–mark–recapture modelling. Silhouettes illustrate sexual dimorphism patterns at each corner of the plot (male, grey; female, white).

disproportionately larger sex organs[24] and the relative elongation of males can be related to the relative size of their copulatory organs[25].

Recent work has comprehensively documented magnitudes of sexual size and shape dimorphism in cytheroid ostracod fauna from the Late Cretaceous epoch (approximately 84–66 million years ago) of the US coastal plain[26]. Species of this fauna vary greatly in their sexual dimorphism: males range from 30% larger to 20% smaller than females, with abundant variation in shape dimorphism as well (Fig. 2). To test whether this large variation in male investment among species has consequences for extinction risk, we combined these data with a high-resolution study of the stratigraphic occurrences of 93 species in Late Cretaceous strata in eastern Mississippi[27] (Extended Data Fig. 1). Using capture–mark–recapture methods[28], we fitted a series of 576 models in which probabilities of extinction, speciation and preservation are constant over time, variable over time or dependent on covariates, such as the magnitude of sexual dimorphism or on other traits that may be related to evolutionary outcomes. The key assessment of the influence of sexual selection on extinction hinges on comparisons between models in which extinction depends on sexual dimorphism versus those in which it does not.

The fits of these models strongly indicate that extinction probabilities increase with male reproductive investment as reflected by sexual dimorphism. Only twenty models receive non-trivial support[29] (difference in corrected Akaike information criterion (ΔAICc) < 10; higher values indicate lower support), and all of these models except for one have extinction probabilities that depend on sexual dimorphism in size, shape or both (Table 1; full model results are in Supplementary Table 1). Support for the best model in which extinction is independent of sexual dimorphism is almost negligible compared to that of the best-supported model (model 18, ΔAICc $= 9.25$). Overall, models in which extinction depends on sexual dimorphism collectively account for 99.3% of the available model support (that is, Akaike weight).

Estimated coefficients averaged across models indicate that extinction risk increases markedly with size and shape dimorphism (Fig. 2): predicted extinction rates are approximately tenfold higher for the most dimorphic species (0.64 per million years (Myr^{-1})) compared to the species with dimorphism that are indicative of the lowest levels of male investment in reproduction (0.06 Myr^{-1}). These differences in extinction rate correspond to expected species durations of 1.6 and 15.5 Myr, respectively. The similarity of estimated coefficients across models (Extended Data Fig. 2) emphasizes the consistent signal of increased extinction risk in taxa with males that are larger and more elongated than females (see also Extended Data Fig. 3).

Extinction in the best-supported model increases with shape dimorphism (Table 1), and the model-averaged 95% confidence interval for this coefficient excludes zero (Extended Data Fig. 2). Size dimorphism does affect extinction in some well-supported models (Table 1), but the effect is less consistent (Extended Data Fig. 2) and these data cannot decisively determine whether extinction risk increases only with size dimorphism, only with shape dimorphism or with both. Previous work[30] has suggested that speciation might also be facilitated by sexual selection, but we find little evidence for this relationship: speciation probabilities increase with magnitudes of sexual dimorphism in some models, but not in any of the ones with the highest support (Table 1).

Behavioural observations from living cytheroids show no indication that the sexual dimorphism of the carapace is related to pre-copulatory signalling to females or to direct contests among males[31]. Rather, it is more likely that this dimorphism reflects investment in sexual reproduction itself. In extant species of the cytheroid genus *Cyprideis*, sexual size dimorphism is correlated with the size of the male genitalia. The strongest correlations with size involve the large, muscular sperm pump[24], suggesting that size dimorphism might relate to the quantity, size or transfer efficiency of sperm. Resources devoted to sperm competition are unavailable for other functions needed for survival

Table 1 | Best-supported models for speciation and extinction

Rank	Extinction	Speciation	ΔAICc
1	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Occupancy + family	0.00
2	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Occupancy + family	1.00
3	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Occupancy	2.63
4	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy	Occupancy + family	3.32
5	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Occupancy	3.38
6	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Constant	4.82
7	$\mathrm{DM}_{\mathrm{size}}$ + occupancy + family	Occupancy + family	4.85
8	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Constant	6.06
9	$\mathrm{DM}_{\mathrm{size}}$ + occupancy + family	Occupancy	6.56
10	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	$\mathrm{DM}_{\mathrm{size}}$	6.66
11	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	$\mathrm{DM}_{\mathrm{shape}}$	6.86
12	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Family	7.09
13	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	$\mathrm{DM}_{\mathrm{size}}$	7.47
14	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy	Occupancy	7.80
15	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	$\mathrm{DM}_{\mathrm{shape}}$	8.11
16	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	Family	8.46
17	$\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$	8.73
18	Occupancy + family	Occupancy + family	9.25
19	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + occupancy + family	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$	9.53
20	$\mathrm{DM}_{\mathrm{size}}$ + occupancy + family	Constant	9.80

Models are listed in order of decreasing model support as measured by ΔAICc. Under extinction and speciation the covariates are listed that modify speciation and extinction probabilities for those models. The top twenty models include all of those with non-negligible[29] model support (ΔAICc < 10); in all of these models except for one (model 18), extinction risk depends on sexual dimorphism. $\mathrm{DM}_{\mathrm{size}}$, sexual size dimorphism; $\mathrm{DM}_{\mathrm{shape}}$, sexual shape dimorphism. Occupancy measures how widely a species is found and family indicates the taxonomic family. Constant indicates that speciation or extinction probabilities are the same in each time interval and do not depend on sexual dimorphism or any other covariate. Results for the full set of models are given in Supplementary Table 1.

and ejaculates themselves may be costly to produce[32]. Increased sperm competition may also be harmful to females who, in turn, may evolve increasingly costly counter-adaptations[33]. Therefore, the dimorphism that we have documented here is likely costly at the population level and could contribute to the increased extinction risk in high-investment species. Sexual selection may also indirectly increase extinction risk by pulling male and female phenotypes away from their natural selection optima[2] or by lowering the effective population size through skewed reproductive success[3].

Palaeontologists have documented a variety of factors that can contribute to lineage extinction[21]. The most consistent finding in these studies is that widespread and abundant taxa tend to have a lower extinction risk[21], and indeed, we also find that our proxy for these characteristics, occupancy, is an important predictor of extinction risk, with high occupancy protecting against extinction (Table 1). Other palaeontological studies have reported that extinction and origination rates can vary markedly across taxa[34] and we also find that these rates differ across taxonomic families (Table 1). The capture–mark–recapture approach accounts for these substantial contributions to extinction risk, but shows that these factors on their own cannot explain the data as well as models that also include sexual dimorphism (Table 1).

We have assessed still other potential predictors of extinction risk, but none of these predictors can account for the relationship between extinction and sexual dimorphism that we document here. Carapace size and shape are only weakly related to sexual dimorphism[26], and substituting these factors for dimorphism in the best supported model greatly reduces support ($\Delta\mathrm{AICc} = 9.64$). Stratigraphic architecture can have a strong effect on the distribution of observed extinctions[35], but there is no reason to expect it to differently affect species according to their sexual dimorphism. Moreover, we have repeated the analyses here using occurrence data from a different composite reference section several hundred kilometres away in central Alabama (Extended Data Fig. 1) and obtained similar results (Extended Data Table 1).

Current extinction risks are heavily shaped by human impacts and their drivers may differ from extinctions in pre-human ecosystems[36]. Nevertheless, if costly male traits increase extinction risk by decreasing the capacity of populations to respond to changing conditions, this mechanism should also operate in present-day populations and thus compound risks from habitat destruction, invasive species, climate change and other anthropogenic causes. Moreover, if the effect of sexual dimorphism on extinction is as strong in other taxa as what we document here for cytheroid ostracods, intense sexual selection may be important for attempts to evaluate extinction risk and design management plans of extant species.

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at https://doi.org/10.1038/s41586-018-0020-7.

Received: 6 November 2017; Accepted: 16 February 2018.

1. Höglund, J. & Sheldon, B. C. The cost of reproduction and sexual selection. *Oikos* **83**, 478–483 (1998).
2. Lande, R. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305 (1980).
3. Kokko, H. & Brooks, R. Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fenn.* **40**, 207–219 (2003).
4. Tanaka, Y. Sexual selection enhances population extinction in a changing environment. *J. Theor. Biol.* **180**, 197–206 (1996).
5. Lumley, A. J. et al. Sexual selection protects against extinction. *Nature* **522**, 470–473 (2015).
6. Lorch, P. D., Proulx, S., Rowe, L. & Day, T. Condition-dependent sexual selection can accelerate adaptation. *Evol. Ecol. Res.* **5**, 867–881 (2003).
7. Darwin, C. *The Descent of Man, and Selection in Relation to Sex*. (John Murray, London, 1871).
8. Andersson, M. *Sexual Selection*. (Princeton Univ. Press, Princeton, 1994).
9. Martínez-Ruiz, C. & Knell, R. J. Sexual selection can both increase and decrease extinction probability: reconciling demographic and evolutionary factors. *J. Anim. Ecol.* **86**, 117–127 (2017).
10. Jacomb, F., Marsh, J. & Holman, L. Sexual selection expedites the evolution of pesticide resistance. *Evolution* **70**, 2746–2751 (2016).
11. Reding, L. P., Swaddle, J. P. & Murphy, H. A. Sexual selection hinders adaptation in experimental populations of yeast. *Biol. Lett.* **9**, 20121202 (2013).
12. Doherty, P. F. Jr et al. Sexual selection affects local extinction and turnover in bird communities. *Proc. Natl Acad. Sci. USA* **100**, 5858–5862 (2003).
13. Bro-Jørgensen, J. Will their armaments be their downfall? Large horn size increases extinction risk in bovids. *Anim. Conserv.* **17**, 80–87 (2014).
14. Sorci, G., Møller, A. P. & Clobert, J. Plumage dichromatism of birds predicts introduction success in New Zealand. *J. Anim. Ecol.* **67**, 263–269 (1998).
15. McLain, D. K., Moulton, M. P. & Sanderson, J. G. Sexual selection and extinction: the fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evol. Ecol. Res.* **1**, 549–565 (1999).
16. Morrow, E. H. & Fricke, C. Sexual selection and the risk of extinction in mammals. *Proc. R. Soc. B* **271**, 2395–2401 (2004).
17. Prinzing, A., Brändle, M., Pfeifer, R. & Brandl, R. Does sexual selection influence population trends in European birds? *Evol. Ecol. Res.* **4**, 49–60 (2002).
18. Thomas, G. H., Lanctot, R. B. & Székely, T. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Anim. Conserv.* **9**, 252–258 (2006).
19. McLain, D. K., Moulton, M. P. & Redfearn, T. P. Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos* **74**, 27–34 (1995).
20. Payne, J. L. et al. Extinction intensity, selectivity and their combined macroevolutionary influence in the fossil record. *Biol. Lett.* **12**, 20160202 (2016).
21. Orzechowski, E. A. et al. Marine extinction risk shaped by trait–environment interactions over 500 million years. *Glob. Change Biol.* **21**, 3595–3607 (2015).
22. Knell, R. J., Naish, D., Tomkins, J. L. & Hone, D. W. E. Sexual selection in prehistoric animals: detection and implications. *Trends Ecol. Evol.* **28**, 38–47 (2013).
23. Cohen, A. C. & Morin, J. G. Patterns of reproduction in ostracodes: a review. J. Crustac. *Biol.* **10**, 184–212 (1990).
24. Martins, M. J. F., Hunt, G., Lockwood, R., Swaddle, J. P. & Horne, D. J. Correlation between investment in sexual traits and valve sexual dimorphism in *Cyprideis* species (Ostracoda). *PLoS ONE* **12**, e0177791 (2017).
25. Kamiya, T. Heterochronic dimorphism of *Loxoconcha uranouchiensis* (Ostracoda) and its implications for speciation. *Paleobiology* **18**, 221–236 (1992).
26. Hunt, G. et al. Sexual dimorphism and sexual selection in cytheroidean ostracodes from the Late Cretaceous of the U.S. coastal plain. *Paleobiology* **43**, 620–641 (2017).
27. Puckett, T. M. Santonian–Maastrichtian planktonic foraminiferal and ostracode biostratigraphy of the northern Gulf Coastal Plain, USA. *Stratigraphy* **2**, 117–146 (2005).
28. Liow, L. H. & Nichols, J. D. in *Quantitative Methods in Paleobiology* The Paleontological Society Papers Vol. 16 (eds Alroy, J. & Hunt, G.) 81–94 (The Paleontological Society, New Haven, 2010).
29. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference*. 2nd edn (Springer, New York, 2010).
30. Servedio, M. R. & Boughman, J. W. The role of sexual selection in local adaptation and speciation. *Annu. Rev. Ecol. Evol. Syst.* **48**, 85–109 (2017).

31. Horne, D. J., Danielopol, D. L. & Martens, K. in *Sex and Parthenogenesis. Evolutionary Ecology of Reproductive Modes in Non-marine Ostracods* (ed. Martens, K.) 157–195 (Backhuys Publishers, Leiden, 1998).
32. Lüpold, S. et al. How sexual selection can drive the evolution of costly sperm ornamentation. *Nature* **533**, 535–538 (2016).
33. Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F. & Partridge, L. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373**, 241–244 (1995).
34. Stanley, S. M. An analysis of the history of marine animal diversity. *Paleobiology* **33**, 1–55 (2007).
35. Holland, S. M. The stratigraphic distribution of fossils. *Paleobiology* **21**, 92–109 (1995).
36. Payne, J. L., Bush, A. M., Heim, N. A., Knope, M. L. & McCauley, D. J. Ecological selectivity of the emerging mass extinction in the oceans. *Science* **353**, 1284–1286 (2016).

Acknowledgements We thank L. Smith (LSU) and C. Sanford (NMNH) for help with access to museum specimens and C. Hall, C. Sweeney, J. Shaw, and J. Stedman for assistance in data collection. This research was supported by NSF-EAR 1424906 and the National Museum of Natural History, Smithsonian Institution.

Reviewer information *Nature* thanks M. Gage, R. Knell and the other anonymous reviewer(s) for their contribution to the peer review of this work.

Author contributions G.H. and M.J.F.M. collected the sexual dimorphism data and performed the analyses; T.M.P. collected the stratigraphic data and helped with the collection of dimorphism data. R.L., J.P.S. and G.H. designed the project and M.J.F.M. and G.H. primarily wrote the paper.

Competing interests The authors declare no competing interests.

Additional information
Extended data is available for this paper at https://doi.org/10.1038/s41586-018-0020-7.
Supplementary information is available for this paper at https://doi.org/10.1038/s41586-018-0020-7.
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METHODS

Dimorphism data. Procedures for measuring sexual dimorphism in valve size and shape have been described previousl[26]. In brief, we photographed individual ostracods from field and museum collections and computed body size (area) and shape (length-to-height ratio, L/H) from their digitized outlines. Sex clusters were recognized from the log-transformed size and shape data using finite mixture models, with the more elongated (higher L/H) cluster interpreted to be male similar to living cytheroids (Fig. 1). We computed magnitudes of size and shape dimorphism as male minus female means in log(area) and log(L/H), respectively. Because males are the more elongated sex in cytheroids, shape dimorphism is always positive. By contrast, size dimorphism can vary in magnitude and direction: it is positive when males are larger than females and negative when females are the larger sex.

Stratigraphic data. We analysed stratigraphic occurrence data for 93 ostracod species from a composite reference section in eastern Mississippi[27] (Extended Data Fig. 1), omitting non-cytheroid ostracods and taxa that have not been resolved to species level. We recorded the presence or absence of these species for 88 samples for which the stratigraphic position relative to several marker beds was measured. We combined some adjacent samples with low abundances to yield 71 samples for analysis and converted stratigraphic heights to absolute ages using an age model with tiepoints from the range endpoints of several planktonic foraminifera (*Dicarinalla asymetrica* (last appearance) 83.64 million years ago (Ma), *Radotruncana calcarata* (first appearance) 76.18 Ma, *Radotruncana calcarata* (last appearance) 75.71 Ma, *Globotruncana aegyptiaca* (first appearance) 74 Ma) and setting the youngest Cretaceous sediments in the section to be 66.3 Ma, following a previously published study[37]. The resulting 71 samples spanned over 200 m of section and 17.5 Myr with a mean spacing between consecutive samples of 250 thousand years (median = 122 thousand years) (Extended Data Fig. 1).

Of the 93 species analysed, we had direct estimates of sexual dimorphism for 69. The remaining species were found too rarely to infer sex clusters and were assigned dimorphism values equal to the mean of their congeneric species (17 species); if no data were available from a genus, we used family means instead (7 species). These substitutions are reasonable, because there is phylogenetic signal in sexual dimorphism in this fauna[26].

We also analysed stratigraphic occurrence data from an additional composite reference section in central Alabama (Extended Data Fig. 1) as a replicate to assess the robustness of the results from the eastern Mississippi section (Extended Data Table 1).

Modelling extinction, speciation and preservation. In order to model speciation, extinction and preservation probabilities of species, we used capture–mark–recapture (CMR) methods implemented in the program MARK[38] using the interface provided by the R package RMark[39]. The input data for CMR are the set of encounter histories for all species. Each encounter history is represented by a vector with an entry for each sample, with '1' indicating that the focal species was sampled and '0' indicating that it was not (for example, 001101000 for a species that was absent in the first two samples, present in the third, fourth and sixth samples, and then not encountered thereafter). Such encounter histories allow calculation of probabilities of preservation, origination and extinction using the Pradel seniority model (following a previously published study[40]). MARK uses maximum likelihood to estimate origination and extinction from first and last occurrences in encounter histories while allowing for incomplete sampling.

The CMR approach has several strengths for the present study compared to alternative approaches. First is the fact that one does not need to observe the entire temporal range of species to fit the models. Some species existed before our window of observation and others persisted after, but this is handled without issue in the CMR framework. Second, CMR approaches estimate speciation and extinction probabilities while accounting for incomplete and potentially variable preservation. Some alternatives, such as survival analysis or the analysis of raw stratigraphic ranges do not have these benefits.

The third advantage of CMR is perhaps the most important for the present study: it allows for parameters to be functions of covariates, which can be attributes of either samples or taxa. We modelled speciation and extinction probabilities as functions of size dimorphism, shape dimorphism or both. As alternatives, we also considered models in which these probabilities were constant (the same for all species and time intervals) and variable over time (estimated separately for each time interval). Preservation probabilities were similarly modelled as constant, variable with time, variable across each geological formation and member, and as a function of log-sample size.

In addition, we considered two additional variables that are known to influence speciation and extinction in other palaeontological studies: occupancy and family membership. Occupancy is a common measurement of how widespread a taxon is[41], here calculated as the proportion of samples in which a species was found to occur, excluding samples from formations for which a taxon has never been found in order to omit samples from before it originated or after it went extinct. We also excluded samples from the focal composite reference section so that the occupancy data would be independent of the observations used for CMR modelling. Taxonomic family was considered to capture variation in speciation and extinction across broader clades; phylogenetic relationships are not known for the included taxa, which prevents a more nuanced approach. Only two families in this study were diverse enough to be treated as separate factors: Trachyleberididae (56 species) and Cytherideidae (12 species). All remaining families were lumped together as a background family rate (25 species). We considered models in which speciation, extinction and preservation probabilities depended on occupancy and taxonomic family individually and combined. Because sexual dimorphism, occupancy and family membership were all individually predictive of extinction risk, we also fit additional models in which extinction depended on these variables in combination. Finally, we also assessed whether sexual size dimorphism was more predictive of extinction when computed as the absolute value of the size difference between sexes, rather than the signed difference, male minus female, as described above. Model support was modestly lower (ΔAICc $\approx$ 1) when using absolute size differences, indicating that our results are more consistent with extinction risk being influenced by male reproductive investment rather than the absolute size difference between the sexes.

In total, we fit 576 different model configurations: 12 extinction models × 8 speciation models × 6 preservation models. We used ΔAICc and Akaike weights to summarize model support, and used model averaging[29] to compute coefficient estimates and confidence limits that account for model uncertainty. Continuous covariates were related to probabilities through logit link functions and differing time spans between samples were accounted for in the analysis using the 'time.intervals' argument in the 'process.data' function of RMark. MARK parameterizes models in terms of survivorship, rather than extinction. To present the results more intuitively, we computed extinction probabilities as 1 – survivorship probabilities, and reversed the signs of coefficients so that higher, positive numbers reflecting increasing extinction risk. We also converted probabilities of extinction over a 1-Myr time span to the more commonly reported extinction rates per Myr using equation A1 from the study by Raup[42].

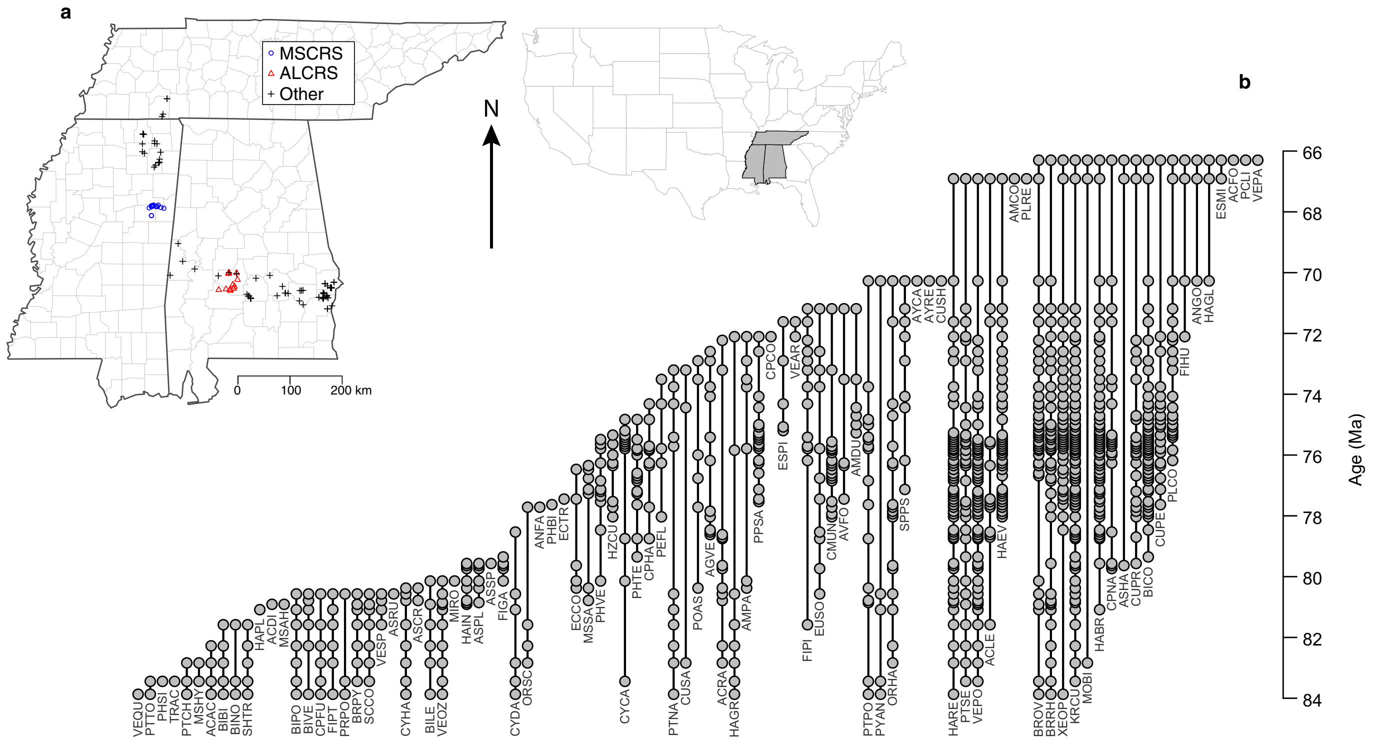
Figure 2 visualizes extinction rates with respect to size and shape dimorphism, as predicted by the model. These predictions were generated by an extinction model that included terms for these two variables, plus occupancy and family membership, using model-averaged coefficients for all terms. Plotted ranges for size and shape dimorphism were chosen to span the values in the observed data. Computing predicted extinction rate from the full model requires values for occupancy and family membership (in addition to size and shape dimorphism). The former was set as the mean occupancy across all species, and the latter, family membership, was set as Trachyleberididae, the most diverse family in the fauna. This figure thus shows predicted extinction for trachyleberidid species with average occupancy, but the patterns discussed are the same under other visualization choices.

Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

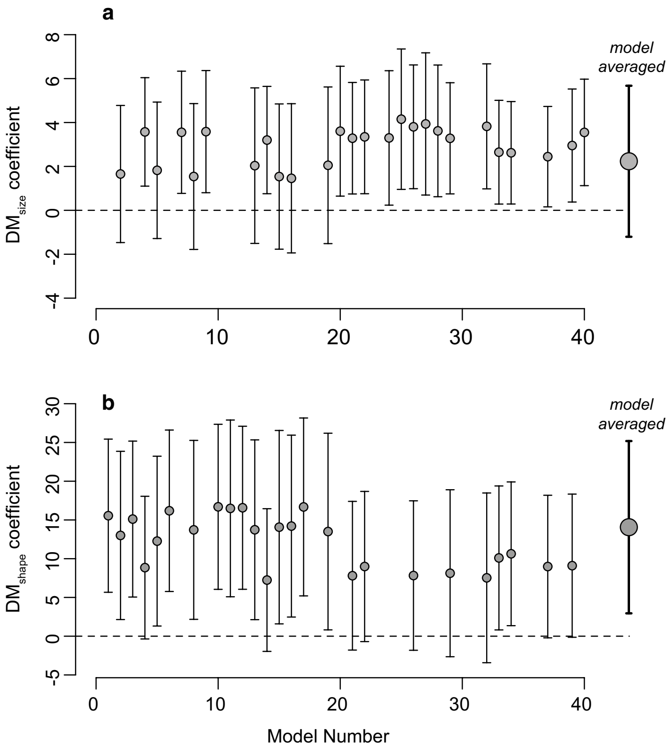
Code availability. The R script to perform the CMR analyses is provided in the Supplementary Information.

Data availability. Sexual dimorphism data were published previously[26] and are shown in Supplementary Table 2. Input files for CMR analyses, which include stratigraphic occurrence (Supplementary Data) and related sample information (Supplementary Table 3), are provided in the Supplementary Information.

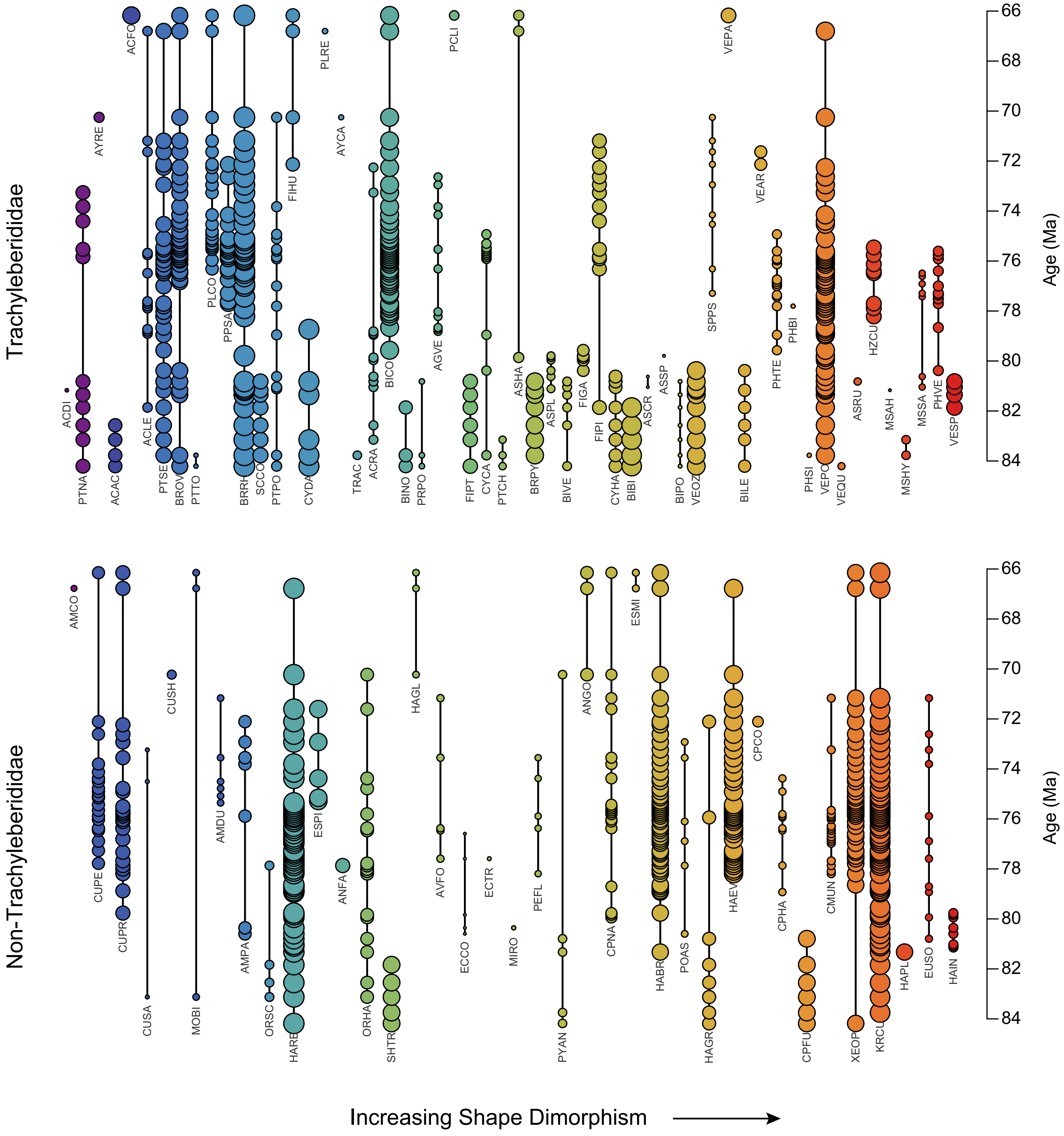
37. Larina, E. et al. Upper Maastrichtian ammonite biostratigraphy of the Gulf Coastal Plain (Mississippi Embayment, southern USA). *Cretac. Res.* **60**, 128–151 (2016).
38. White, G. C. & Burnham, K. P. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139 (1999).
39. Laake, J. L. *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK*. AFSC Processed Report No. 2013-01 (Alaska Fisheries Science Center, 2013).
40. Liow, L. H. & Finarelli, J. A. A dynamic global equilibrium in carnivoran diversification over 20 million years. *Proc. R. Soc. B* **281**, 20132312 (2014).
41. Foote, M. et al. Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science* **318**, 1131–1134 (2007).
42. Raup, D. M. Mathematical models of cladogenesis. *Paleobiology* **11**, 42–52 (1985).



Extended Data Fig. 1 | Stratigraphic section showing the occurrence of 93 species over time. a, Location map of Tennessee, Mississippi and Alabama. The locations of samples that were collected from the focal composite reference section in Mississippi (MSCRS, blue circles) and the composite section in Alabama, which were treated as a replicate (ALCRS, red triangles), are shown along with the additional samples in the database that were used to compute occupancy (crosses). **b**, Stratigraphic occurrences for the MSCRS are shown. Each grey circle represents the occurrence of a species in a sample, with each species labelled according to four-letter abbreviations given in Supplementary Table 4. The map was made using the R package ‘maps’.



Extended Data Fig. 2 | Estimated model coefficients relating sexual size and shape dimorphism to extinction. a, Sexual size dimorphism (DM_{size}). **b**, Shape dimorphism (DM_{shape}). The best 40 models are shown, sorted in order of decreasing support. The model-averaged coefficients are shown on the far right as larger circles. These estimates integrate over all models, weighted by their support, appropriately accounting for uncertainty in model selection. Error bars are 95% confidence intervals generated by MARK software.



Extended Data Fig. 3 | Stratigraphic occurrences of species plotted with respect to shape dimorphism. Top, species in the family Trachyleberididae; bottom, all other species. Species are sorted left to right based on shape dimorphism, with more extreme dimorphism plotted towards the right and in warmer colours. Symbol size is proportional to occupancy (larger indicates more broadly distributed). In the Trachyleberididae, there is a clear visual indication that more strongly dimorphic species have shorter stratigraphic durations.

Extended Data Table 1 | Best supported models for extinction and speciation using occurrence data from a replicate reference section in central Alabama

Rank	Extinction	Speciation	ΔAICc
1	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + Occupancy	time	0.00
2	$\mathrm{DM}_{\mathrm{shape}}$ + Occupancy + Family	time	3.27
3	$\mathrm{DM}_{\mathrm{size}}$ + Occupancy + Family	time	3.57
4	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + Occupancy + Family	time	3.73
5	Occupancy	time	4.88
6	Occupancy + Family	time	5.28
7	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$ + Occupancy	time	5.29
8	$\mathrm{DM}_{\mathrm{size}}$	time	6.48
9	$\mathrm{DM}_{\mathrm{size}}$ + $\mathrm{DM}_{\mathrm{shape}}$	time	6.96
10	$\mathrm{DM}_{\mathrm{shape}}$	time	7.85
11	$\mathrm{DM}_{\mathrm{shape}}$ + Occupancy + Family	time	8.39
12	$\mathrm{DM}_{\mathrm{size}}$ + Occupancy + Family	time	8.64
13	$\mathrm{DM}_{\mathrm{size}}$ + DMshape + Occupancy + Family	time	8.78
14	constant	time	9.24
15	Family	time	9.51

Models are listed in order of decreasing model support as measured by ΔAICc; all models with non-negligible support ($\Delta\mathrm{AICc} < 10$) are shown. The next two columns list the covariates that influence extinction and speciation, respectively, under each model. $\mathrm{DM}_{\mathrm{size}}$, sexual size dimorphism; $\mathrm{DM}_{\mathrm{shape}}$, sexual shape dimorphism. Occupancy measures how widespread a species is and family indicates the taxonomic family. Constant indicates that speciation or extinction probabilities are the same in each time interval and do not depend on sexual dimorphism or any other covariate. Similar to the Mississippi reference section, the best supported model in which extinction does not depend on sexual dimorphism (model 5) has substantially less support than the best model. Preservation probabilities for these models are a function of occupancy, and in some cases, also include a factor for geological formation/member.

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Experimental design

1. Sample size

Describe how sample size was determined.	Sample sizes were not predetermined. We measured and used sexual dimorphism data from all species for which we could obtain reliable estimates.

2. Data exclusions

Describe any data exclusions.	No data were excluded from the analyses.

3. Replication

Describe the measures taken to verify the reproducibility of the experimental findings.	This is not an experimental study, so there are no true replicates. However, as we report in Extended Data Table 2, we performed the same analyses on an additional stratigraphic section and obtained similar results.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.	No samples were allocated into experimental groups.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.	There were no experimental/control groups, so blinding was not possible.

Note: all in vivo studies must report how sample size was determined and whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	Test values indicating whether an effect is present *Provide confidence intervals or give results of significance tests (e.g. P values) as exact values whenever appropriate and with effect sizes noted.*
☐	☒	A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars in all relevant figure captions (with explicit mention of central tendency and variation)

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	All analyses were done using R (https://www.r-project.org), relying on the RMark package as an interface to the MARK software; MARK performs the CMR analysis. The custom analysis script and input files are provided in Supplementary Information.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a third party.	No unique materials were used

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	No eukaryotic cell lines were used
b. Describe the method of cell line authentication used.	No eukaryotic cell lines were used
c. Report whether the cell lines were tested for mycoplasma contamination.	No eukaryotic cell lines were used
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No eukaryotic cell lines were used

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide all relevant details on animals and/or animal-derived materials used in the study.	No animals were used

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	No human research participants used