Check for updates

WILEY

californicus

RESEARCH ARTICLE



Food deprivation exposes sex-specific trade-offs between stress tolerance and life span in the copepod Tigriopus Ning Li 💿 📔 Ben A. Flanagan 💿 📔 Suzanne Edmands 💿

Department of Biological Sciences, University of Southern California, Los Angeles, California, USA

Correspondence

Ning Li, Department of Biological Sciences, University of Southern California, 3616 Trousdale Parkway, AHF 130, Los Angeles, CA 90089, USA. Email: ningli@usc.edu

Funding information National Institute on Aging, Grant/Award Number: R21AG055873; National Science Foundation, Grant/Award Number: DEB-1656048

Abstract

Long life is standardly assumed to be associated with high stress tolerance. Previous work shows that the copepod Tigriopus californicus breaks this rule, with longer life span under benign conditions found in males, the sex with lower stress tolerance. Here, we extended this previous work, raising animals from the same families in foodreplete conditions until adulthood and then transferring them to food-limited conditions until all animals perished. As in previous work, survivorship under food-replete conditions favored males. However, under food deprivation life span strongly favored females in all crosses. Compared to benign conditions, average life span under nutritional stress was reduced by 47% in males but only 32% in females. Further, the sexspecific mitonuclear effects previously found under benign conditions were erased under food limited conditions. Results thus demonstrate that sex-specific life span, including mitonuclear interactions, are highly dependent on nutritional environment.

KEYWORDS

aging, food limitation, interpopulation hybrid, longevity

TAXONOMY CLASSIFICATION Evolutionary ecology

| INTRODUCTION 1

A long-standing dogma in biology is that the ability to withstand stress is associated with longer life (Kirkwood & Austad, 2000). This is supported by overlap in the genetic bases for these two traits, including the roles of molecular chaperones, antioxidants, and genes involved in repair of oxidative damage (Landis et al., 2004; Vermeulen & Loeschcke, 2007). More direct evidence comes from artificial selection experiments, in which selection for longer life span increases resistance to stressors such as starvation, desiccation, ethanol, and high temperature (Scannapieco et al., 2009; Service et al., 1985), and

selection for increased stress resistance (desiccation, starvation, and high temperature) also increases longevity (Lind et al., 2017; Pijpe et al., 2008; Rose et al., 1992).

The copepod Tigriopus californicus provides a counter example to the expected positive relationship between stress tolerance and life span. Females are more tolerant than males to a range of stressors (Foley et al., 2019; Kelly et al., 2012; Willett, 2010) and also exhibit a substantially muted transcriptomic response to oxidative stress (Li et al., 2019, 2020). While females might be expected to also have longer lives, the first large-scale study of longevity in this species (Flanagan et al., 2021) showed that life span under benign conditions

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. © 2022 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.

is either equivalent between sexes or longer in males. Further, comparisons of two parental lines and their reciprocal F1 hybrids revealed sex-specific mitonuclear effects on longevity. Such mitonuclear interactions are perhaps unsurprising, given that the two parental lines have widely divergent mitochondrial haplotypes (20.6%; Barreto et al., 2018) and that mitochondrial function is known to involve interactions with over 1000 proteins encoded by the nuclear genome (Bar-Yaacov et al., 2012). Because *T. californicus* does not have sex chromosomes (Alexander et al., 2015; Voordouw & Anholt, 2002), it offers a simpler system for testing sexually dimorphic mitochondrial effects, as asymmetric inheritance of mitochondria is not confounded with asymmetric inheritance of sex chromosomes.

Here, we extend previous work (Flanagan et al., 2021) to assess sex-specific effects of nutritional stress. By using the same parental and reciprocal crosses, we test how mitochondrial effects are altered by environment. Given that mitochondria are the location where dietary nutrients are converted to ATP, mitochondrial effects might be expected to highly dependent on nutritional environment. In this study, we use an additional clutch of offspring from the same families assayed in Flanagan et al. (2021), raising animals under benign conditions until adulthood, and then transferring them to culture medium without food. In this way, we test how nutritional stress impacts sex differences in longevity, including the role of mitochondrial effects.

2 | MATERIALS AND METHODS

Populations were collected from San Diego, CA (S: 32.75°N, 117.25°W), and Friday Harbor Laboratories, WA (F: 48.55°N, 123.01°W). They were kept in a 20°C incubator with a 12h:12h light:dark cycle. Isofemale lines from each population were established from single ovigerous females and inbred for a minimum of ten generations before experiments began. Lines were maintained in petri dishes (diameter × height = 100 mm × 15 mm) in natural filtered seawater (37 μ m) supplemented with a mixture of powdered Spirulina (Nutrex Hawaii) and ground Tetramin flakes (Tetra) at a concentration of 0.1 g of each food per L.

Tigriopus californicus mature males clasp virgin females using their antennae and remain clasped until the females become reproductively mature (Burton, 1985; Egloff, 1966; Vittor, 1971). Therefore, virgin females can be obtained by teasing apart the clasped pair on a moist filter paper under a dissecting microscope using fine probes. This technique has been tested to be satisfactory with few individuals injured and no impaired brood production during the handling procedure (Burton, 1985; Vittor, 1971). As described in Figure 1, within-population crosses (FF cross: F female mated with F male, and SS cross: S female mated with S male) and reciprocal, betweenpopulation crosses (FS cross: F female mated with S male, and SF cross: S female mated with F male) were set up by combining virgin females with mature males from the designated populations. Only one female and one male were allowed in one petri dish, and they usually form a pair within one day. The culture medium was



FIGURE 1 Crossing design using inbred lines from San Diego, CA (SD/S), and Friday Harbor Laboratories, WA (FHL/F). SD nuclear and mitochondrial (mt) genomes are indicated in black, and FHL nuclear and mitochondrial genomes are indicated in gray. Solid bars indicate nuclear alleles contributed by the mother, and dotted bars indicate nuclear alleles contributed by the father. F1 generation cohorts were named as dam × sire

the same as the original population cultures. This experiment used the fourth clutch of the crosses generated in Flanagan et al., 2021 for direct comparisons with the survival and longevity under benign conditions. Briefly, males were removed to avoid further harassment after the females were released from the pair. New crosses were set up to replace the ones whose individuals died or whose females were not successfully fertilized. Petri dishes were checked every day until the fertilized egg sacs hatched. The offspring from the first three egg clutches were collected and assayed under benign conditions (Flanagan et al., 2021), while the offspring from the fourth clutch were then counted and transferred to a new petri dish for this study. The estimated effect of clutch number on survival was minimal during the previous experiment for the first three clutches under benign conditions (coxph, z = -1.94, p = .052) (Flanagan et al., 2021). Further, prior work in T. californicus failed to detect an effect of clutch number on the proportion of surviving individuals fourteen days after hatching, although later clutches had fewer offspring and smaller body size (Powers et al., 2020).

The larvae were fed and rehydrated once every week until 28 days post-hatching, at which time the females and males could be distinguished from the structure of antennae (Egloff, 1966). The two sexes were counted and if animals had formed pairs, they were separated using fine probes as described above. At day 28 post-hatching, the food limitation treatment was initiated by transferring males and females into separate petri dishes with filtered seawater only. We characterize this as a food limitation treatment rather than a starvation treatment since the coarsely filtered seawater (37 μ m) is expected to contain microbes and also support some algal growth. To measure survivorship and maximum life span under food limitation, animals were counted every day beginning on day 28 and dead individuals were removed until all individuals died.

In total, 15 FF families, 8 FS families, 12 SF families, and 13 SS families were used for this study. Survival analysis was conducted

Ecology and Evolution

3 | RESULTS AND DISCUSSION

In this study, we used an additional clutch of offspring from the same families used in Flanagan et al. (2021), raising them in the same benign conditions until day 28 posthatching. At this time point, sex ratios in Flanagan et al. (2021) and the current study were similar (Figure 2). In both cases, ratios in the four crosses were either equivalent or male-biased.

After day 28, copepods were sexed and either maintained in benign conditions (Flanagan et al., 2021) or transferred to foodlimited conditions (current study) until all animals perished. Here, results of the two studies were dramatically different. Under benign conditions (Table 1), combined results show increased male longevity, with males having longer average life span, longer average maximum life span, and higher overall survival (coxme, $\chi^2 = 14.23$, p = 1.62 e-4). Sex-specific life span differs between the four crosses, including higher overall survival for males in one F1 cross (FS) and sex-equivalent survival in the other F1 cross (SF). Because these reciprocal F1 have different mitochondrial haplotypes on a 50:50



TABLE 1 Life span comparisons between benign conditions and limited food conditions in each sex within each cross

		Benign conditions ^a			Limited food conditions		
Cross	Sex	Average life span	Maximum life span ^b	Overall survival ^c	Average life span	Maximum life span ^b	Overall survival ^c
FF	Female	52.7 ± 0.6	80.5 ± 6.4	No difference	41.8 ± 0.4	48.6 ± 2.1	Female > Male*
	Male	56.9 ± 0.7	90.7 ± 7.7		40.4 ± 0.3	44.3 ± 2.0	
FS	Female	78.0 ± 2.5	107.8 ± 9.6	Male > Female*	60.8 ± 2.3	73.0 ± 4.3	Female > Male*
	Male	89.6 ± 0.8	135.2 ± 8.3		45.7 ± 0.6	60.9 ± 4.9	
SF	Female	91.2 ± 1.3	131.0 ± 9.2	No difference	52.0 ± 0.8	62.4 ± 3.4	Female > Male*
	Male	88.3 ± 1.2	113.4 ± 7.4		47.5 ± 0.7	57.6 ± 4.1	
SS	Female	85.2 ± 2.2	111.4 ± 10.6	Male > Female*	51.7 ± 0.7	53.6 ± 2.8	Female > Male*
	Male	104.7 ± 1.9	140.9 ± 11.4		44.2 ± 0.7	51.1 ± 3.1	
Total	Female	71.5 ± 0.8	107.5 ± 5.0	Male > Female*	48.9 ± 0.5	57.8 ± 2.0	Female > Male*
	Male	84.0 ± 0.6	120.6 ± 4.8		44.3 ± 0.3	52.2 ± 1.9	

Note: Results are coded in red if higher in females and blue if higher in males. Data are shown as mean ± SEM. *p-value <.01.

Abbreviations: FF, F female mated with F male; FS, F female mated with S male; SF, S female mated with F male; SS, S female mated with S male. ^aData for benign conditions are from Flanagan et al., 2021.

^bMaximum life span is a family-based calculation and estimated from all families within each cross.

^cOverall survival is based on analyses from a cox-proportional hazard model with mixed effects.

3 of 6

VILEY



FIGURE 3 Kaplan-Meier curve with 95% confidence bands displaying the estimated survival probability for crosses FF (a), FS (b), SF (c), and SS (d) under limited food conditions. The number of female and male individuals used in this study was listed in each panel. Asterisks indicate significance level (**p-value <.01; *** p-value <.001) between sexes by a cox-proportional hazard model with mixed effects (coxme)

nuclear background, with nuclear contributions from different parental crosses, this suggests sex-specific mitochondrial effects. Results under limited food conditions (Table 1 and Figure 3) are strikingly different, revealing increased female longevity for nearly all metrics. Combined results showed females having longer average life span, longer average maximum life span and higher overall survival (coxme, $\chi^2 = 287.60$, p < 2.20 e-16). Overall survival also favored females in each of the four crosses, suggesting that higher female tolerance to nutritional stress overrides the sex-specific mitonuclear interactions inferred under benign conditions.

Importantly, the food deprivation treatment (no added food beginning at adulthood) was detrimental to both sexes, reducing average life span by 31.6% in females and 47.3% in males. In contrast, other studies found that less drastic food limitation commonly extends life span. Moderate diet restriction, typically 10%–60%, has been found to increase longevity across a remarkably diverse range of organisms including yeast (Gouspillou & Hepple, 2013), nematodes (Gouspillou & Hepple, 2013), fruitflies (Krittika & Yadav, 2019), rodents (Kane et al., 2018), fish (Terzibasi et al., 2009), non-human primates (Colman et al., 2009), *Daphnia* (Hearn et al., 2019), and copepods (Saiz et al., 2015), suggesting common underlying mechanisms. Such studies typically find that moderate diet restriction is more beneficial in females than males (Aw et al., 2017; Freire et al., 2020; Ingram & de Cabo, 2017; Magwere et al., 2004), paralleling our finding that food deprivation is less detrimental in females.

Higher female tolerance of food deprivation is a common pattern in arthropods in general (Gerofotis et al., 2019; Knapp, 2016; Matzkin et al., 2009) and copepods in particular (Finiguerra et al., 2013; Holm et al., 2018). A frequent explanation for the pattern is higher body size in females, a pattern found in many arthropods (e.g., Holm et al., 2018; Gerofotis et al., 2019) including *T. californicus* (Edmands & Harrison, 2003). Another contributing factor may be higher lipid reserves found in some females (e.g., Holm et al., 2018; Gerofotis et al., 2019), although sex differences in lipid content are not known for *Tigriopus*. A third contributing factor commonly cited for copepods is that males typically expend more energy on searching for mates (Finiguerra et al., 2013; Holm et al., 2018). This is likely the case in *T. californicus*, where males mate repeatedly while females mate only once (Burton, 1985). Higher female tolerance of food deprivation is so common in copepods that female-skewed ratios can be used

5 of 6

WILEY

as an indicator of food scarcity in the wild (Finiguerra et al., 2013). Female bias is less detrimental to population viability than male-bias (Edmands, 2021; Wedekind, 2002), but the extreme female bias found in some natural copepod populations can cause sperm limitation (Kiørboe, 2007).

In summary, under benign conditions *T. californicus* defies the expected positive relationship between stress tolerance and life span, with stress-sensitive males generally living longer than females. Exposure to food limitation beginning at adulthood restores the expected longer life of females. This is true for all crosses, thus overriding the sex-specific mitochondrial effects found under benign conditions. Importantly, food limitation may be the more common state for copepods in natural conditions. Results are consistent with work on *Drosophila* (Camus et al., 2012; Nagarajan-Radha et al., 2019) in which sex-specific life span, including effects of mitochondrial haplotype, are dependent on nutritional environment.

ACKNOWLEDGMENTS

This work was supported by the National Institute on Aging of the U.S. National Institutes of Health [grant R21AG055873 to S.E.] and the U.S. National Science Foundation [grant DEB-1656048 to S.E.]. Computation for the work described in this paper was supported by the University of Southern California's Center for High-Performance Computing (https://hpcc.usc.edu).

CONFLICT OF INTEREST

All authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Ning Li: Conceptualization (lead); Formal analysis (lead); Methodology (lead); Supervision (equal); Visualization (lead); Writing – original draft (lead); Writing – review & editing (equal). Ben A. Flanagan: Data curation (equal); Formal analysis (equal); Methodology (equal); Resources (lead); Writing – review & editing (equal). Suzanne Edmands: Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (equal); Writing – original draft (lead); Writing – review & editing (equal).

DATA AVAILABILITY STATEMENT

All the data and scripts are available at Dryad (https://doi. org/10.5061/dryad.h44j0zpn1).

ORCID

Ning Li [®] https://orcid.org/0000-0002-5080-5726 Ben A. Flanagan [®] https://orcid.org/0000-0002-0204-6139 Suzanne Edmands [®] https://orcid.org/0000-0002-2127-2684

REFERENCES

Alexander, H., Richardson, J., Edmands, S., & Anholt, B. (2015). Sex without sex chromosomes: Genetic architecture of multiple loci independently segregating to determine sex ratios in the copepod *Tigriopus californicus. Journal of Evolutionary Biology*, 28, 2196–2207. https://doi.org/10.1111/jeb.12743

- Aw, W. C., Garvin, M. R., Melvin, R. G., & Ballard, J. W. O. (2017). Sex-specific influences of mtDNA mitotype and diet on mitochondrial functions and physiological traits in *Drosophila melan*ogaster. PLoS One, 12, e0187554. https://doi.org/10.1371/journ al.pone.0187554
- Barreto, F. S., Watson, E. T., Lima, T. G., Willett, C. S., Edmands, S., Li, W., & Burton, R. S. (2018). Genomic signatures of mitonuclear coevolution across populations of *Tigriopus californicus*. *Nature Ecology* & *Evolution*, 2(8), 1250–1257. https://doi.org/10.1038/s4155 9-018-0588-1
- Bar-Yaacov, D., Blumberg, A., & Mishmar, D. (2012). Mitochondrialnuclear co-evolution and its effects on OXPHOS activity and regulation. *Biochimica et Biophysica Acta (BBA) - Gene Regulatory Mechanisms*, 1819(9-10), 1107–1111. https://doi.org/10.1016/j. bbagrm.2011.10.008
- Burton, R. (1985). Mating system of the intertidal copepod *Tigriopus* californicus. Marine Biology, 86, 247–252. https://doi.org/10.1007/ BF00397511
- Camus, M. F., Clancy, D. J., & Dowling, D. K. (2012). Mitochondria, maternal inheritance, and male aging. *Current Biology*, 22, 1717–1721. https://doi.org/10.1016/j.cub.2012.07.018
- Colman, R. K., Anderson, R. M., Johnson, S. C., Kastman, E. K., Kosmatka, K. J., Beasley, T. M., Allison, D. B., Cruzen, C., Simmons, H. A., Kemnitz, J. W., & Weindruck, R. (2009). Caloric restriction delays disease onset and mortality in rhesus monkeys. *Science*, 325(5937), 201–204. https://doi.org/10.1126/science.1173635
- Edmands, S. (2021). Sex ratios in a warming world: Thermal effects on sex-biased survival, sex determination, and sex reversal. *Journal of Heredity*, 112, 155–164. https://doi.org/10.1093/jhere d/esab006
- Edmands, S., & Harrison, J. S. (2003). Molecular and quantitative trait variation within and among populations of the intertidal copepod *Tigriopus californicus*. *Evolution*, *57*, 2277–2285. https://doi. org/10.1111/j.0014-3820.2003.tb00239.x
- Egloff, D. A. (1966). Ecological aspects of sex ratio and reproduction in experimental and field populations of the marine copepod Tigriopus californicus. Stanford University.
- Finiguerra, M. B., Dam, H. G., Avery, D. E., & Burris, Z. (2013). Sex-specific tolerance to starvation in the copepod Acartia tonsa. Journal of Experimental Marine Biology and Ecology, 446, 17–21. https://doi. org/10.1016/j.jembe.2013.04.018
- Flanagan, B. A., Li, N., & Edmands, S. (2021). Mitonuclear interactions alter sex-specific longevity in a species without sex chromosomes. Proceedings of the Royal Society B: Biological Sciences, 288, 20211813. https://doi.org/10.1098/rspb.2021.1813
- Foley, H. B., Sun, P. Y., Ramirez, R., So, B. K., Venkataraman, Y. R., Nixon, E. N., Davies, K. J. A., & Edmands, S. (2019). Sex-specific stress tolerance, proteolysis, and lifespan in the invertebrate *Tigriopus californicus*. *Experimental Gerontology*, 119, 146–156. https://doi. org/10.1016/j.exger.2019.02.006
- Freire, T., Senior, A. M., Perks, R., Pulpitel, T., Clark, X., Brandon, A. E., Wahl, D., Hatchwell, L., Le Couteur, D. G., Cooney, G. J., Larance, M., Simpson, S. J., & Solon-Biet, S. M. (2020). Sex-specific metabolic responses to 6 hours of fasting during the active phase in young mice. *Journal of Physiology*, *598*, 2081–2092. https://doi. org/10.1113/JP278806
- Gerofotis, C. D., Kouloussis, N. A., Koukougiannidou, C., Papadopoulos, N. T., Damos, P., Koveos, D. S., & Carey, J. R. (2019). Age, sex, adult and larval diet shape starvation resistance in the Mediterranean fruit fly: An ecological and gerontological perspective. *Scientific Reports*, 9, 1–12. https://doi.org/10.1038/s41598-019-47010-0
- Gouspillou, G., & Hepple, R. T. (2013). Facts and controversies in our understanding of how caloric restriction impacts the mitochondrion. *Experimental Gerontology*, 48, 1075–1084. https://doi. org/10.1016/j.exger.2013.03.004

- Hearn, J., Pearson, M., Blaxter, M., Wilson, P. J., & Little, T. J. (2019). Genome-wide methylation is modified by caloric restriction in Daphnia magna. BMC Genomics, 20, 197. https://doi.org/10.1186/ s12864-019-5578-4
- Holm, M. W., Rodríguez-Torres, R., van Someren Gréve, H., Hansen, B. W., & Almeda, R. (2018). Sex-specific starvation tolerance of copepods with different foraging strategies. *Journal of Plankton Research*, 40, 284–294. https://doi.org/10.1093/plankt/fby006
- Ingram, D. K., & de Cabo, R. (2017). Calorie restriction in rodents: Caveats to consider. Ageing Research Reviews, 39, 15–28. https:// doi.org/10.1016/j.arr.2017.05.008
- Kane, A. E., Sinclair, D. A., Mitchell, J. R., & Mitchell, S. J. (2018). Sex differences in the response to dietary restriction in rodents. *Current Opinion in Physiology*, *6*, 28–34. https://doi.org/10.1016/j. cophys.2018.03.008
- Kelly, M. W., Sanford, E., & Grosberg, R. K. (2012). Limited potential for adaptation to climate change in a broadly distributed marine crustacean. Proceedings of the Royal Society B: Biological Sciences, 279, 349–356. https://doi.org/10.1098/rspb.2011.0542
- Kiørboe, T. (2007). Mate finding, mating, and population dynamics in a planktonic copepod Oithona davisae: There are too few males. Limnology and Oceanography, 52, 1511–1522. https://doi. org/10.4319/lo.2007.52.4.1511
- Kirkwood, T. B., & Austad, S. N. (2000). Why do we age? *Nature*, 408, 233–238. https://doi.org/10.1038/35041682
- Knapp, M. (2016). Relative importance of sex, pre-starvation body mass and structural body size in the determination of exceptional starvation resistance of Anchomenus dorsalis (Coleoptera: Carabidae). PLoS One, 11, e0151459. https://doi.org/10.1371/ journal.pone.0151459
- Krittika, S., & Yadav, P. (2019). An overview of two decades of diet restriction studies using *Drosophila*. *Biogerontology*, 20, 723–740. https://doi.org/10.1007/s10522-019-09827-0
- Landis, G. N., Abdueva, D., Skvortsov, D., Yang, J., Rabin, B. E., Carrick, J., Tavaré, S., & Tower, J. (2004). Similar gene expression patterns characterize aging and oxidative stress in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States* of America, 101, 7663–7668. https://doi.org/10.1073/pnas.03076 05101
- Li, N., Arief, N., & Edmands, S. (2019). Effects of oxidative stress on sexspecific gene expression in the copepod Tigriopus californicus revealed by single individual RNA-seq. Comparative Biochemistry and Physiology Part D: Genomics and Proteomics, 31, 100608. https://doi. org/10.1016/j.cbd.2019.100608
- Li, N., Flanagan, B. A., Partridge, M., Huang, E. J., & Edmands, S. (2020). Sex differences in early transcriptomic responses to oxidative stress in the copepod *Tigriopus californicus*. *BMC Genomics*, 21, 1– 11. https://doi.org/10.1186/s12864-020-07179-5
- Lind, M. I., Chen, H. Y., Meurling, S., Guevara Gil, A. C., Carlsson, H., Zwoinska, M. K., Andersson, J., Larva, T., & Maklakov, A. A. (2017). Slow development as an evolutionary cost of long life. *Functional Ecology*, 31, 1252–1261. https://doi. org/10.1111/1365-2435.12840
- Magwere, T., Chapman, T., & Partridge, L. (2004). Sex differences in the effect of dietary restriction on life span and mortality rates in female and male Drosophila melanogaster. The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 59, 3–9. https:// doi.org/10.1093/gerona/59.1.B3
- Matzkin, L. M., Watts, T. D., & Markow, T. A. (2009). Evolution of stress resistance in *Drosophila*: Interspecific variation in tolerance to desiccation and starvation. *Functional Ecology*, *23*, 521–527. https://doi. org/10.1111/j.1365-2435.2008.01533.x

- Nagarajan-Radha, V., Rapkin, J., Hunt, J., & Dowling, D. K. (2019). Interactions between mitochondrial haplotype and dietary macronutrient ratios confer sex-specific effects on longevity in Drosophila melanogaster. The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 74, 1573–1581. https://doi.org/10.1093/ gerona/glz104
- Pijpe, J., Brakefield, P. M., & Zwaan, B. J. (2008). Increased life span in a polyphenic butterfly artificially selected for starvation resistance. *The American Naturalist*, 171, 81–90. https://doi. org/10.1086/524200
- Powers, M. J., Weaver, R. J., Heine, K. B., & Hill, G. E. (2020). Predicting adult lifespan and lifetime reproductive success from earlylife reproductive events. *Marine Biology*, 167(10), 147. https://doi. org/10.1007/s00227-020-03765-z
- Rose, M. R., Vu, L. N., Park, S. U., & Graves, J. L. Jr (1992). Selection on stress resistance increases longevity in *Drosophila melanogaster. Experimental Gerontology*, 27, 241–250. https://doi. org/10.1016/0531-5565(92)90048-5
- Saiz, E., Calbet, A., Griffel, K., Bersano, J. G. F., Isari, S., Solé, M., Peters, J., & Alcarez, M. (2015). Ageing and caloric restriction in a marine planktonic copepod. *Scientific Reports*, *5*, 14962. https://doi. org/10.1038/srep14962
- Scannapieco, A. C., Sambucetti, P., & Norry, F. M. (2009). Direct and correlated responses to selection for longevity in Drosophila buzzatii. Biological Journal of the Linnean Society, 97, 738–748. https://doi. org/10.1111/j.1095-8312.2009.01223.x
- Service, P. M., Hutchinson, E. W., MacKinley, M. D., & Rose, M. R. (1985). Resistance to environmental stress in *Drosophila melanogaster* selected for postponed senescence. *Physiological Zoology*, *58*, 380– 389. https://doi.org/10.1086/physzool.58.4.30156013
- Terzibasi, E., Lefrançois, C., Domenici, P., Hartmann, N., Graf, M., & Cellerino, A. (2009). Effects of dietary restriction on mortality and age-related phenotypes in the short-lived fish *Nothobranchius furzeri*. Aging Cell, 8, 88–99. https://doi. org/10.1111/j.1474-9726.2009.00455.x
- Therneau, T. M. (2020). Mixed effects cox models [R package coxme version 2.2-16].
- Vermeulen, C., & Loeschcke, V. (2007). Longevity and the stress response in Drosophila. Experimental Gerontology, 42, 153–159. https://doi. org/10.1016/j.exger.2006.09.014
- Vittor, B. A. (1971). Effects of the environment on fitness related life history characters in Tigriopus californicus. University of Oregon.
- Voordouw, M. J., & Anholt, B. R. (2002). Heritability of sex tendency in a harpacticoid copepod, *Tigriopus californicus*. Evolution, 56, 1754– 1763. https://doi.org/10.1111/j.0014-3820.2002.tb00189.x
- Wedekind, C. (2002). Manipulating sex ratios for conservation: Shortterm risks and long-term benefits. *Animal Conservation*, 5(1), 13–20. https://doi.org/10.1017/S1367943002001026
- Willett, C. S. (2010). Potential fitness trade-offs for thermal tolerance in the intertidal copepod *Tigriopus californicus*. *Evolution: International Journal of Organic Evolution*, 64, 2521–2534. https:// doi.org/10.1111/j.1558-5646.2010.01008.x

How to cite this article: Li, N., Flanagan, B. A., & Edmands, S. (2022). Food deprivation exposes sex-specific trade-offs between stress tolerance and life span in the copepod *Tigriopus californicus. Ecology and Evolution*, 12, e8822. https://doi.org/10.1002/ece3.8822

6 of 6