

are low, a strategy that can ensure long-term survival of the wasp and, by extension, the symbiont. Finally, parasitoid microbes may also decrease hybrid viability and further promote speciation, but studies are limited. Which of these or other processes explains wasp biodiversity remains to be discovered, and likely all of the above mechanisms have contributed to the astounding diversity of parasitoid wasps.

Conclusions

Despite their diversity, ubiquitous nature, and beneficial status, parasitoid wasps have received far less attention than more charismatic insects such as butterflies and bees. Understanding how and why these wasps have come to be so diverse informs evolutionary theory, patterns of speciation and extinction, and community-interaction dynamics. Further, as we understand parasitoids better, including how they locate and overcome host defenses, we can better use these wasps to help control pests within our gardens, field crops, forests, and greenhouses. By conserving and enhancing our native parasitoid populations, pest populations are less likely to spiral out of control causing devastating crop losses or the need for excessive chemical control. But these tactics require detailed knowledge on which species exist and which specific hosts they attack - foundational science that is still deficient for most parasitoid wasps. But beyond their beneficial use to humans, parasitoid wasps are truly fascinating creatures that display a wide array of strategies to locate, attack, live-off of, and eventually kill their hosts. The most current research seeks to understand the evolution of these traits that are uniquely adapted for efficient utilization of other organisms. From venoms to developing teratocytes to harnessing viruses within their own genomes, parasitoid wasps have truly mastered host exploitation. Meanwhile, the number and diversity of symbionts and pathogenic microbes that are helping or exploiting parasitoid wasps is little known - leaving the field of parasitoid research a fertile arena for scientific discovery for decades to come.

DECLARATION OF INTERESTS

The authors declare no competing interests.

FURTHER READING

- Asgari, S., and Rivers, D.B. (2011). Venom proteins from endoparasitoid wasps and their role in host-parasite interactions. Annu. Rev. Entomol. *56*, 313–335. https://doi.org/10.1146/ annurev-ento-120709-144849.
- Austin, A., and Dowton, M., eds. (2000). Hymenoptera: Evolution, Biodiversity and Biological Control (Victoria, Australia: CSIRO Publishing).
- Blaimer, B.B., Santos, B.F., Cruaud, A., Gates, M.W., Kula, R.R., Mikó, I., Rasplus, J.Y., Smith, D.R., Talamas, E.J., Brady, S.G., and Buffington, M.L. (2023). Key innovations and the diversification of Hymenoptera. Nat. Commun. 14, 1212. https://doi.org/10.1038/ s41467-023-36868-4.
- Burke, G.R., Hines, H.M., and Sharanowski, B.J. (2021). The presence of ancient core genes reveals endogenization from diverse viral ancestors in parasitoid wasps. Genome Biol. Evol. 13, evab105. https://doi.org/10.1093/ dbe/evab105.
- Charnov, E.L., Los-den Hartogh, R.L., Jones, W.T., and van den Assem, J. (1981). Sex ratio evolution in a variable environment. Nature 289, 27–33. https://doi.org/10.1038/289027a0.
- Dicke, M., Cusumano, A., and Poelman, E.H. (2020). Microbial symbionts of parasitoids. Annu. Rev. Entomol. *65*, 171–190. https://doi. org/10.1146/annurev-ento-011019-024939.
- Drezen, J.-M., Bezier, A., Burke, G.R., and Strand, M.R. (2022). Bracoviruses, ichnoviruses, and virus-like particles from parasitoid wasps retain many features of their virus ancestors. Curr. Opin. Insect Sci. 49, 93–100. https://doi. org/10.1016/j.cois.2021.12.003.
- Forbes, A.A., Bagley, R.K., Beer, M.A., Hippee, A.C., and Widmayer, H.A. (2018). Quantifying the unquantifiable: Why Hymenoptera, not Coleoptera, is the most speciose animal order. BMC Ecol. 18, 21. https://doi.org/10.1186/ s12898-018-0176-x.
- Hawkins, B.A. (1993). Refuges, host population dynamics and the genesis of parasitoid diversity. In Hymenoptera and Biodiversity, J. LaSalle and I.D. Gauld, eds. (Wallingford, Oxford, UK: C.A.B. International), pp. 235–256.
- Memmot, J., and Godfray, H.C.J. (1994). The structure of a tropical host-parasitoid community. J. Anim. Ecol. 3, 521–540. https:// doi.org/10.2307/5219.
- Pennacchio, F., and Strand, M.R. (2006). Evolution of developmental strategies in parasitic Hymenoptera. Annu. Rev. Entomol. 51, 233–258. https://doi.org/10.1146/annurev. ento.51.110104.151029.
- Quicke, D.J.L. (1997). Parasitic Wasps (London: Chapman and Hall).
- Strand, M.R. (2014). Teratocytes and their functions in parasitoids. Curr. Opin. Insect Sci. 6, 68–73. https://doi.org/10.1016/j. cois.2014.09.005.
- Tumlinson, J.H. (2023). Complex and beautiful: Unraveling the intricate communication systems among plants and insects. Annu. Rev. Entomol. 68, 1–12. https://doi.org/10.1146/ annurev-ento-021622-111028.

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Trajectory of increased iceberg kill-off in West Antarctica's shallows

Current Biology

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Compared with low latitude coasts, many polar latitudes are still little impacted by intense and direct anthropogenic stressors. Climate forcing is now bringing rapid physical change to nearshore polar realms. In the shallow coastal waters adjacent to the United Kingdom's Rothera Research Station in the West Antarctic Peninsula (WAP), 225 seabed markers at 5-25 m depth have been surveyed and replaced every year from 2002-2023 (75 markers at each of 5, 10 and 25 m). This is one of the longest continuously running marine disturbance experiments in the world, in one of Earth's fastest changing environments. Different categories of sea ice are recorded (including when the sea surface freezes into fast ice) at Rothera since the 1980s, and losses of marine ice in both polar regions are one of the striking responses to a warming planet¹. Five to ten years of seabed marker hit rate data (marker broken or moved) showed that reduced sea ice cover is correlated with disturbance and mortality on the seabed^{2,3}.

Now that this long-term monitoring has yielded 20 years of sea ice-iceberg hit data, it is clear that such a trend is robust enough to hindcast and forecast. Sea ice duration was recorded from the 1980s to present and hindcasting seabed disturbance rates to correspond to these values suggests that more than twice the area of shallow coastal seabed is now catastrophically scoured by icebergs (Figure 1). Projecting the trend forward suggests that in just two decades there may be little or no seasonal fast ice in this area and that on average half the seabed may be hit by icebergs every year.

Iceberg collisions with the seabed (scour) are one of the most frequent natural catastrophic events⁴. Iceberg scour rate is influenced by the duration

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of seasonal sea surface freezing ('fast ice', which 'locks' icebergs stationary), the generation of icebergs by calving from glaciers or ice-shelves, and weather (wind) and tide (current). Seasonal sea ice has been recorded daily by an observer and remote sea ice cameras at Rothera and other research stations from the 1980s to the present day. It is also undertaken at larger scale by Earth observation (satellite-derived data). The timing of formation of seasonal sea ice and its duration are highly variable. Over the last few decades, West Antarctica, and particularly the Bellingshausen Sea, has shown intense and sustained seasonal sea ice losses, much like most of the Arctic¹. The NOAA's climate.gov open access map shows 2022 and 2023 successively became the lowest winter sea ice maximum extents on record so the Arctic/West Antarctic trend has begun to manifest throughout most of the Southern Ocean⁵. Thus, although the Rothera study site is in a sea-ice loss hotspot, it could be argued to be increasingly relevant as an early warning system for much broader coastal Antarctic environments. Sea ice losses are likely to have many influences on biota, through loss of habitat for pagophiles, including under-ice algae and crucially krill⁶, influences on light-climate, albedo, gas exchange and near-surface oceanography altering the mobility of icebergs.

Measuring direct seabed impacts by icebergs is much more difficult and time-consuming than measuring sea surface ice extent. The seabed cannot be seen by satellites beyond the shallows, nor at the sub-metre resolution required. Seabed depth can be repeatedly mapped by multibeam sonar to indicate the frequency of scours but research ship time is sparse and expensive. Autonomous Underwater Vehicles may ultimately begin to have this capacity but to date scouring has been easiest to measure manually by SCUBA divers. Few other bases or research stations have SCUBA capabilities, which are required to replace seabed markers hit by icebergs each year. One of those that does use SCUBA, the Argentine station Carlini, also monitored both sea ice duration and seabed ice scour of markers by icebergs to reveal similar data to this study across a four-year period⁷. The effect of scouring by icebergs on the local biota is intense, killing up to 99% of biota

hit³⁻⁷. The severity of this is increased on hard substrata by the depressed recovery potential because of very slow growth, development and delayed maturity of most Antarctic benthos⁸. In deeper water (>100 m) the rate of ice scour in a given area is likely to occur at frequencies of once every tens to hundreds of years. This leaves time for denuded spaces to recover by larval settlement or adult immigration from surrounding mature communities⁴.

Seasonal sea ice losses are likely to be sustained and not recover but they are not the only driver of ice scouring rates. Circulation, seabed topography and iceberg frequency, and thus generation of icebergs, are also important. Ice shelves may be scarce along the WAP but marine terminating glaciers are common and likely to be the major source of regional and local icebergs. As most regional glaciers are retreating at an accelerating pace9, iceberg generation seems likely to also be sustained or even increasing. However, the size of icebergs is likely to decrease as glaciers approach grounding lines. The only trend in ice scour drivers that seems to be dampening an otherwise increasing and escalating pattern is surface wind weakening¹⁰. Projecting the trends of regional seasonal sea ice duration and ice scour rate forward (Figure 1) suggests that catastrophic disturbance of shallow (0–25 m) Antarctic benthos will increase to the point whereby 50% of the seabed may be hit annually by 2050. The effects will continue deeper than 25 m but at lower levels. Our impact forecast does assume that our area is representative of a very much wider whole, but not of all areas, and that the relation between climate, marine ice loss and icebergs we report here holds across the region. Our data show that, despite many factors and influences, iceberg scour is highly stochastic and that some places are more likely to be hit than others; if the trend continues, then the scouring rate of the seabed shallows will have tripled in half a century. This should provide reliable banquets for the few scavengers mobile enough to evade iceberg scour and repopulate scours from further afield but, as with elsewhere globally, it seems likely to be a case of few winners, many losers, at least in the shallows. It should be noted that the vast majority of continental shelf around Antarctica is deep and beyond the scouring range of most icebergs, but our data refer to the shallow areas



Figure 1. Sea ice duration and iceberg scouring.

(Top) Long-term coastal monitoring shows that iceberg scouring rate of the seabed is correlated with the duration of seasonal sea ice at Rothera station. Each point represents a year of observations over 22 years until 2023. (Bottom) Sea ice duration with time (decadal mean +/- SD) at Rothera in blue with projection shown as dashed line (significant decrease of sea ice with time since 1985 has associated ANOVA, F > 81, p < 0.001). Decade of 1980s includes five annual observations (1985-1989). Annual iceberg scour disturbance of 225 seabed markers (decadal mean +/- SD) at Rothera in red with hindcast in dark red and projection shown as dashed line (significant increase of iceberg scouring of seabed with time has associated ANOVA, F > 22, p < 0.02).

around the 15,200 km of non-ice bound coast. Since the start of our monitoring the number of seabed markers that have not been hit within the last decade is currently just 6%. This value is important because a decade is the approximate period that it takes community structure to recover from catastrophic disturbance. The very small proportion of local shallow (coastal) seabed with older, more mature communities with late successional or climax species seems set to shrink much further. Once glaciers retreat beyond their grounding lines then newly calved ice will fall on land rather than into the sea, but the freshening and sedimentation from those streams will add to the threats of warming, acidification and invasive species establishment.

SUPPLEMENTAL INFORMATION

Supplemental information including one table and methods can be found with this



article online at https://doi.org/10.1016/j. cub.2024.03.036.

ACKNOWLEDGEMENTS

We would like to thank the marine teams of Rothera Research Station across the last two decades for the work to annually survey and replace seabed markers as well as record daily sea ice presence. We thank Chuck Amsler and three anonymous referees for constructive comments leading to an improved manuscript. We dedicate this manuscript to Mr J.G. Potter and Mrs H.P. Potter, RIP.

AUTHOR CONTRIBUTIONS

D.K.A.B. and L.S.P. conceived the experimental design. All authors contributed to field data collection. D.K.A.B. analysed data and wrote the initial manuscript. All authors reviewed and revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

- Parkinson, C.L. (2019). A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. Proc. Natl. Acad. Sci. USA *116*, 14414–14423.
- Smale, D.A., Brown, K.M., Barnes, D.K.A., Fraser, K.P.P., and Clarke, A. (2008). Ice scour disturbance in Antarctic waters. Science 321, 371.
- Barnes, D., and Souster, T. (2011). Reduced survival of Antarctic benthos linked to climateinduced iceberg scouring. Nat. Clim. Change 1, 365–368. https://doi.org/10.1038/nclimate1232.
- Gutt, J., and Piepenburg, D. (2003). Scale dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. Mar. Ecol. Prog. Ser. 253, 77–83.
- Purich, A., and Doddridge, E.W. (2023). Record low Antarctic sea ice coverage indicates a new sea ice state. Commun. Earth Environ. 4, 314. https://doi. org/10.1038/s43247-023-00961-9.
- Atkinson, A., Siegel, V., Pakhomov, E.A., and Rothery, P. (2004). Long term decline in krill stock and increase in salps within the Southern Ocean. Nature 432, 100–103.
- Barnes, D.K.A., Fleming, A., Sands, C.J., Quartino, M.L., and Deregibus, D. (2018). Icebergs, sea ice, blue carbon and Antarctic climate feedbacks. Philos. Trans. Math. Phys. Eng. Sci. 376, 20170176. https://doi.org/10.1098/rsta.2017.0176.
- Peck, L.S. (2018). Antarctic marine biodiversity: Adaptations environments and responses to change. Oceanogr. Mar. Biol. Annu. Rev. 56, 105–236.
- Cook, A.J., Holland, P.R., Meredith, M.P., Murray, T., and Vaughan, D.G. (2016). Ocean forcing of glacier retreat in the western Antarctic Peninsula. Science 353, 283–286. https://doi.org/10.1126/ science.aae0017.
- Neme, J., England, M.H., and McC. Hogg, A. (2022). Projected changes of surface winds over the Antarctic continental margin. Geophys. Res. Let. 49, e2022GL098820. https://doi. org/10.1029/2022GL098820.

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Rapid spread of a vertically transmitted symbiont induces drastic shifts in butterfly sex ratio

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The causes and consequences of sex-ratio dynamics constitutes a pivotal subject in evolutionary biology¹. Under conditions of evolutionary equilibrium, the male-to-female ratio tends to be approximately 1:1; however, this equilibrium is susceptible to distortion by selfish genetic elements exemplified by driving sex chromosomes and cytoplasmic elements^{2,3}. Although previous studies have documented instances of these genetic elements distorting the sex ratio, studies specifically tracking the process with which these distorters spread within populations, leading to a transition from balanced parity to a skewed, female-biased state, are notably lacking. Herein, we present compelling evidence documenting the rapid spread of the cytoplasmic endosymbiont Wolbachia within a localized population of the pierid butterfly Eurema hecabe (Figure 1A). This spread resulted in a shift in the sex ratio from near parity to an exceedingly skewed state overwhelmingly biased toward females, reaching 93.1% within a remarkably brief period of 4 years.

Some E. hecabe females are infected with a strain of Wolbachia, wFem, that causes feminization (Figure 1B)⁴. wFem-infected females have a Z0 sex chromosome constitution. The mechanism of feminization is not known, but it is thought that wFem females do not transmit their Z chromosome to their offspring and that Wolbachia transforms Z0 individuals into females; a similar phenomenon has been demonstrated in the sister species Eurema mandarina⁵. All E. hecabe, including wFem-infected females, also carry a strain of Wolbachia, wCI, that causes cytoplasmic incompatibility.

Females carrying only *w*Cl produce an equal ratio of male and female offspring with ZZ and ZW genotypes, respectively. (Here we abbreviate females singly infected with wCl as "C", and those doubly infected with wCl and wFem as "CF").

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Based on a 2008 investigation, the frequency of CF females in an E. hecabe population on Ishigaki Island was recorded at a relatively low frequency of 8.0% (4 CF females and 46 C females)⁴. Subsequently, our comprehensive collection effort yielded a total of 1,392 individuals of E. hecabe comprising 853 females and 539 males. This sampling was conducted across 31 sites on Ishigaki Island during nine visits from 2015 to 2022. The observed proportion of females ranged from 35.6% to 47.6% during the period between 2015 and 2018. However, after 2019, a discernible increase in females occurred, elevating the proportion of females to 93.1% (Figure 1C,D). Furthermore, the infection frequency of wFem increased from 0.00-0.08 in 2015-2016 to 0.87 in 2022 (Figure 1E). Interestingly, the frequency of CF females and the female-to-male ratio tended to be lower during autumn; this was potentially attributed to heightened summer heat stress in the subtropical climate zone of Ishigaki Island (see Supplemental discussion). Under laboratory conditions, the offspring of 10 female butterflies gathered in April 2019 were reared to adulthood. Consistent with the findings of a previous study⁴, the offspring of seven CF females exhibited an exclusively or predominantly female composition (157 females and 1 male; Table S1). Conversely, the offspring of three C females comprised both males and females (87 females and 68 males). Thus, the rapid increase in the frequency of CF females appears to explain the prompt alteration observed in the sex ratio on Ishigaki Island.

An alteration in the population sex ratio has also been documented in the nymphalid butterfly *Acrea encedon*. The female ratio experienced a transition from 36.0% in 1909–1912 to an overwhelming 98.4% in 1963–1964 (estimated to have occurred within a span of 100–150 generations⁶). In subsequent research, the presence of male-killing *Wolbachia* was reported in

