

insects. It continues to be an adventurous journey, full of surprises about how cleverly plants hone in on these mechanisms and utilise them to their advantage.

REFERENCES

- Baker, H.G. (1977). Non-sugar chemical constituents of nectar. *Apidologie* 8, 349–356.
- Nepi, M., Grasso, D.A., and Mancuso, S. (2018). Nectar in plant–insect mutualistic relationships: from food reward to partner manipulation. *Front. Plant Sci.* 9, 1063.
- Stevenson, P.C., Nicolson, S.W., and Wright, G.A. (2017). Plant secondary metabolites in nectar: impacts on pollinators and ecological functions. *Funct. Ecol.* 31, 65–75.
- Mustard, J.A. (2020). Neuroactive nectar: compounds in nectar that interact with neurons. *Arthropod-Plant Inte.* 14, 151–159.
- Naef, R., Jaquier, A., Velluz, A., and Bachofen, B. (2004). From the linden flower to linden honey – volatile constituents of linden nectar, the extract of bee-stomach and ripe honey. *Chem. Biodivers.* 7, 1870–1879.
- Wright, G., Baker, D., Palmer, M., Stabler, D., Mustard, J., Power, E., Borland, A., and Stevenson, P. (2013). Caffeine in floral nectar enhances a pollinator's memory of reward. *Science* 339, 1202–1204.
- Singaravelan, N., Nee'man, G., Inbar, M., and Izhaki, I. (2005). Feeding responses of free-flying honeybees to secondary compounds mimicking floral nectars. *J. Chem. Ecol.* 31, 2791–2804.
- Arnold, S.E.J., Dudenhöffer, J.-H., Fountain, M.T., James, K.L., Hall, D.R., Farman, D.I., Wäckers, F.L., and Stevenson, P.C. (2021). Bumble bees show an induced preference for flowers when primed with caffeinated nectar and a target floral odor. *Curr. Biol.* 31, 4127–4131.
- Rands, S.A., and Whitney, H.M. (2010). Effects of pollinator density-dependent preferences on field margin visitations in the midst of agricultural monocultures: A modelling approach. *Ecol. Model.* 221, 1310–1316.
- Greenleaf, S.S., Williams, N.M., Winfree, R., and Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596.
- Frasnelli, E., Robert, T., Chow, P.K.Y., Scales, B., Gibson, S., Manning, N., Philippides, A.O., Collett, T.S., and Hempel de Ibarra, N. (2021). Small and large bumblebees invest differently when learning about flowers. *Curr. Biol.* 31, 1058–1064.e3.
- Harrap, M.J., Hempel de Ibarra, N., Whitney, H.M., and Rands, S.A. (2020). Floral temperature patterns can function as floral guides. *Arthropod-Plant Inte.* 14, 193–206.
- Clarke, D., Whitney, H., Sutton, G., and Robert, D. (2013). Detection and learning of floral electric fields by bumblebees. *Science* 340, 66–69.
- Harrap, M.J., Hempel de Ibarra, N., Knowles, H.D., Whitney, H.M., and Rands, S.A. (2021). Bumblebees can detect floral humidity. *J. Exp. Biol.* 224, jeb240861.
- Kevan, P.G., and Lane, M.A. (1985). Flower petal microtexture is a tactile cue for bees. *Proc. Natl. Acad. Sci. USA* 82, 4750–4752.
- Leonard, A.S., and Masek, P. (2014). Multisensory integration of colors and scents: insights from bees and flowers. *J. Comp. Physiol. A* 200, 463–474.
- Raguso, R.A. (2004). Flowers as sensory billboards: progress towards an integrated understanding of floral advertisement. *Curr. Opin. Plant Biol.* 7, 434–440.
- Si, A., Zhang, S.-W., and Maleszka, R. (2005). Effects of caffeine on olfactory and visual learning in the honey bee (*Apis mellifera*). *Pharmacol. Biochem. Behav.* 82, 664–672.
- Harrap, M.J., Rands, S.A., Hempel de Ibarra, N., and Whitney, H.M. (2017). The diversity of floral temperature patterns, and their use by pollinators. *eLife* 6, e31262.
- Hempel de Ibarra, N., and Vorobyev, M. (2009). Flower patterns are adapted for detection by bees. *J. Comp. Physiol. A* 195, 319–323.

Evolution: Natural selection, sexual selection, and the jaws of death

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<https://doi.org/10.1016/j.cub.2021.07.077>

Traits that increase reproductive success in males can have negative fitness consequences in females. A new study shows that natural selection by a predator that targets males with larger secondary sexual traits drives an evolutionary increase in female fitness.

Charles Darwin and Alfred Russel Wallace are regarded as co-discoverers of natural selection¹. They were both astute observers of nature and familiar with Malthusian arithmetic, which had led them to independently deduce that checks on population growth

created an intense and ubiquitous “struggle for existence”, the fuel of natural selection^{2,3}. As this phrase implies, there was a tendency to treat natural selection as arising from differences in survival, and both men emphasized ecological factors such

as competition and predation as vital forces in this regard. Darwin installed another pillar of evolutionary biology with *Descent of Man* in 1871⁴, in which he expounded his theory of sexual selection, where differences in reproduction took center stage. Sexual selection is

differential reproduction arising from competition for mates, leading to the evolution of spectacular ornamentation and weaponry, typically in males, called ‘secondary sexual characters’. Natural selection can have pronounced effects on such traits as well, contributing to the evolution of their structural design and ultimately acting as a brake on their continued exaggeration (Figure 1). The tension that can develop between natural and sexual selection is central to sexual conflict theory⁵.

Because there can be fundamentally different selection pressures on males and females⁶, a sexual character, say the leg spurs or colorful plumes in a bird, may provide a benefit to males through sexual selection, but the same trait when expressed in females may be opposed by natural selection, through reducing fecundity or making females more apparent to predators. In this way, when the direction of net selection on a trait depends on the sex in which it is expressed, there will be selection for sex-specific expression, and the result may be sexual dimorphism⁷. Darwin recognized that countervailing pressures can tug on secondary sexual characters in opposite directions⁴, and although hamstrung by his unsound theory of heredity, he anticipated intralocus sexual conflict. Quantifying costs of secondary sexual character expression in the light of natural selection and understanding the full ramifications of sexual conflict are major challenges facing evolutionary biology today^{5,8,9}. A recent study by Kensuke Okada and colleagues¹⁰ offers novel insight into the tug-of-war between natural and sexual selection, and how the evolutionary outcomes of this interplay are more far-reaching than at first might appear.

Working with a beetle, Okada and colleagues¹⁰ demonstrate how predation pressure opposes sexual selection on mandible size, a male-limited secondary sexual character, reducing the size of this trait over multiple generations of experimental exposure to predation. Intriguingly, this reduction in mandible size had the striking correlated outcome of increasing female lifetime fitness, even though females had never been exposed to the predator. The authors paint a fascinating picture of

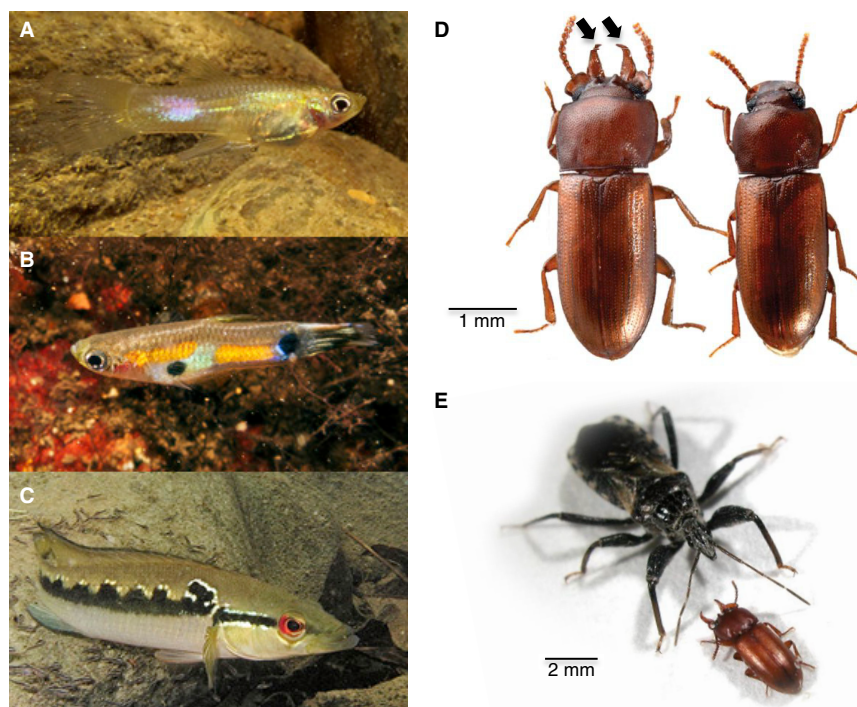


Figure 1. Male traits in the crosshairs of sex and death.

(A) In guppies, *Poecilia reticulata*, females are less attracted to relatively drab males¹⁶. In contrast, colorful males (B) reap sexual benefits from their flamboyant displays, but which are not cost-free — flashy pigments also catch the eye of natural enemies, such as a fish predator (C)¹⁷. (Fishes here are not to scale; photos: Paul Bentzen.) In a paradigmatic field transfer experiment¹⁸, guppies evolved to be more colorful in the absence of predators, providing a notable corollary to a recent laboratory evolution study of a beetle, *Gnatocerus cornutus* (D; image adapted from¹⁹). In this species, the male mandibles (arrowed in D; female on right), which are deployed in male-male combat and positively sexually selected¹⁴, decreased evolutionarily in size in response to the depredations of an assassin bug, *Amphilobus venator* (E; image by Kensuke Okada).

just how pervasive the effects of male-specific predation in nature might be: on the one hand, male-specific predation opposes the forces of sexual selection in males, and on the other hand it surprisingly boosts female fitness as a result of durable intersexual genetic correlations.

Gnatocerus cornutus is a 4–5 mm long tan-brown tenebrionid beetle that infests stored grains around the world. Sexual dimorphism is pronounced, with males sporting enlarged heads and jaws that they deploy in fights with one another for access to mates¹¹, while females possess no such mandibles at all (Figure 1D). To test the effects of predation on sexual trait elaboration, Okada and colleagues¹⁰ used a replicated evolution experiment where they exposed either only males or only females to predation over multiple generations in the laboratory, while also maintaining a predator-free

control. Predation involved beetles running the gauntlet of their natural assassins, reduviid bugs, *Amphilobus venator* (Figure 1E); this beast hunts by capturing adult beetles with its forelegs. Okada and colleagues¹⁰ show that males bearing enlarged jaws are killed more often than smaller-jawed rivals, but there is a twist to the story: the bugs attack in such a way that the larger mandibles of their prey themselves are actually not the focus of their predatory gaze. Rather, smaller-jawed beetles can move more quickly, outmaneuvering their would-be assassins to survive: be quick or be dead. Because the predators preferentially feast on slower-moving beetles, and because movement is negatively genetically correlated with mandible size^{12,13}, the predator imposed indirect selection on the Darwinian sexual trait.

In each generation of their experiment, Okada and colleagues¹⁰ allowed beetles

that survived the ravages of predation to enjoy the splendors of parenthood. By the 6th and 7th generations, all lineages subject to male-only predation had smaller jaws than control and female-only predation treatments. Furthermore, evolving in response to the predator left these males only half as likely to win fights with a rival than males from the other treatments. Thus, both a secondary sexual character and a key determinant of male fitness had been evolutionarily reduced through the depredations of a naturally occurring bug.

The females of the male-predation treatment never encountered the assassins, and yet changes to their morphology and life-history traits were remarkable. Here, the genetic correlation, which can arise when genes that affect the expression of one trait influence other traits as well (pleiotropy), is again central to the discussion. In the beetle, the genes that make smaller jaws in males increase abdomen size in males and also indirectly increase abdomen size in females. The abdomen is the province of female fecundity, with larger females producing more eggs, a general pattern seen in insects. One can envision, therefore, that in grain stores throughout the world without predators, the body plan of females is pulled away from its fitness optimum by sexual selection acting on males, fueling sexual conflict. In this trade-off, male and female fitnesses see-saw, depending upon the selection pressures each sex experiences; when predators appear on the seedy scene, viability selection now begins to tug favorably, though indirectly, upon female abdomen size.

Without a doubt, one of the most intriguing aspects of the study is the observed increase in female lifetime reproductive success as a correlated response to male-specific predation. A key question raised by this result is what might be the cause of the increased lifetime reproductive success. One reasonable possibility the authors suggest is that female 'quality' was increased, presumably as a function of boosted egg production capacity (fecundity). The authors were right not to press this possibility too strongly, however, as differences

between the selection treatments in traits (e.g., egg production or ovary size) that would have conferred the increased fecundity were not confirmed.

An alternative is suggested by the details of the experimental design. In their assay, lifetime reproductive success was measured by pairing individual females from the different treatments with males from the baseline stock. After copulation, females were each isolated and allowed to lay eggs for two months. Lifetime reproductive success was quantified as the total number of adult progeny produced from this single copulation. Now, we know from previous selection experiments that when males evolve smaller mandibles, they evolve larger testes as a correlated response, and larger testes means that more sperm are transferred to the female sperm storage organs (the spermathecae)¹³. Thus, perhaps females in the male-predation treatment had greater lifetime reproductive success not because of an increase in quality *per se*, as Okada and colleagues¹⁰ suggest, but because they had co-evolved increased sperm storage capacity (larger spermathecae). Spermathecal volume could have increased in the male-predation treatment as a response to directional selection imposed by increasing ejaculate size, or as a pleiotropic effect. Either way, a female able to store more sperm from a single mating could have produced more offspring over her lifetime independently of her intrinsic quality, in so far as the meaning of quality is generally conceived.

Okada and colleagues¹⁰ conducted a quantitative genetics experiment that confirms previously shown genetic relationships between the important traits¹⁴. This not only set up the expectation for a significant outcome to the introduction of a predator, it also put quantitative genetics theory through its paces. The authors predicted what should happen when they introduced the assassin bugs based on genetic information, and it did. This is powerful science. Their paper also highlights how the interplay between natural and sexual selection is ripe for study through experimental evolutionary approaches; however, the challenge of

multi-species evolution experiments is evident in their scarcity beyond those using micro-organisms¹⁵. The study provides a compelling demonstration of the manifold consequences of tension that can develop between natural selection and sexual selection, rooted in sexual differences theory⁶, and explicitly cast in an ecological light.

REFERENCES

1. Bowler, P.J. (2003). *Evolution: The History of an Idea*, 3rd Edition (University of California Press).
2. Darwin, C., and Wallace, A. (1858). On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *Proc. Linn. Soc. Zool.* 3, 45–62.
3. Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray).
4. Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex* (John Murray).
5. Arnqvist, G., and Rowe, L. (2005). *Sexual Conflict* (Princeton University Press).
6. Trivers, R.L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871–1971*, B. Campbell, ed. (Aldine), pp. 136–179.
7. Parker, G.A., and Partridge, L. (1998). Sexual conflict and speciation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 261–274.
8. Parker, G.A. (1970). Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects*, M.S. Blum, and N.A. Blum, eds. (Academic Press), pp. 123–166.
9. Wedell, N., Kvarnemo, C., Lessells, C.M., and Tregenza, T. (2006). Sexual conflict and life histories. *Anim. Behav.* 71, 999–1011.
10. Okada, K., Katsuki, M., Sharma, M.D., Kiyose, K., Seko, T., Okada, Y., Wilson, A.J., and Hosken, D.J. (2021). Natural selection increases female fitness by reversing the exaggeration of a male sexually selected trait. *Nat. Commun.* 12, 3420.
11. Okada, K., Miyanoshita, A., and Miyatake, T. (2006). Intra-sexual dimorphism in male mandibles and male aggressive behavior in the broad-horned flour beetle *Gnathocerus cornutus* (Coleoptera: Tenebrionidae). *J. Insect Behav.* 19, 457–467.
12. Fuchikawa, T., and Okada, K. (2013). Inter- and intrasexual genetic correlations of exaggerated traits and locomotor activity. *J. Evol. Biol.* 26, 1979–1987.

13. Yamane, T., Okada, K., Nakayama, S., and Miyatake, T. (2010). Dispersal and ejaculatory strategies associated with exaggeration of weapon in an armed beetle. *Proc. R. Soc. Lond. B Biol. Sci.* 277, 1705–1710.
14. Harano, T., Okada, K., Nakayama, S., Miyatake, T., and Hosken, D.J. (2010). Intralocus sexual conflict unresolved by sex-limited trait expression. *Curr. Biol.* 20, 2036–2039.
15. Brockhurst, M.A., and Koskella, B. (2013). Experimental coevolution of species interactions. *Trends Ecol. Evol.* 28, 367–375.
16. Houde, A.E. (1997). *Sex, Color and Mate Choice in Guppies* (Princeton University Press).
17. Magurran, A.E. (2005). *Evolutionary Ecology: The Trinidadian Guppy* (Oxford University Press).
18. Endler, J.A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34, 76–91.
19. Demuth, J.P., Naidu, A., and Mydlarz, L.D. (2012). Sex, war, and disease: the role of parasite infection on weapon development and mating success in a horned beetle (*Gnatocerus cornutus*). *PLoS One* 7, e28690.

Visual processing: Systematic variation in light–dark bias across visual space

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<https://doi.org/10.1016/j.cub.2021.07.057>

Detecting changes in luminance is a fundamental property of the visual system. A new study shows that lights and darks are represented differently across visual space, with strong OFF bias in central vision and balanced ON/OFF in the periphery.

Change is everywhere, and our brains have evolved to be excellent detectors of changes in our environment. For the visual system, the most fundamental change is that of luminance, where local increases or decreases in luminance activate distinct ON or OFF pathways, respectively. In recent years, a number of studies have demonstrated that these seemingly equivalent and parallel pathways are not in fact treated equally^{1–7}, and that biases in the processing of ON and OFF in the visual system may mirror the statistical patterns of the natural world^{8,9}. This idea is not without controversy, however, as multiple studies across different species have reported conflicting results regarding the direction and magnitude of ON/OFF biases^{1,10–14}. In new work reported in this issue of *Current Biology*, Williams *et al.*¹⁵ reconcile these apparent discrepancies by showing that OFF responses dominate central visual space, with more balanced ON/OFF responses in the periphery, thereby providing a coherent explanation for how biases in luminance representation are mapped across visual space.

In the visual system, luminance processing begins in the retina, where

retinal ganglion cells have ON-center or OFF-center receptive fields that preferentially respond when the center of their receptive field is brighter (ON) or darker (OFF) than its surroundings. These distinct ON and OFF pathways remain segregated through the lateral geniculate nucleus (LGN) before converging in primary visual cortex to generate orientation selective simple cells¹⁶. Importantly, specific ON and OFF information remains present and tightly integrated with orientation selectivity even after this convergence¹⁰, thereby maintaining extensive ON/OFF information for further processing in both primary visual cortex and downstream visual areas.

Notably, differences in the processing of ON and OFF information are present at the earliest stages of the visual system, with differences in the number of responsive neurons, their receptive field size, and the speed of response already present in the retina¹⁷. These differences are propagated and enhanced in the visual cortex, where OFF responses to luminance changes are both faster and more linear, while exhibiting smaller receptive fields and more spatially

constrained cortical responses than ON responses^{1–3,7,18}. This greater spatio-temporal precision leads to an OFF pathway with high acuity, well suited for detecting small, fast and local changes, in contrast to an ON pathway specialized for large and slow stimuli^{5,6}.

A number of studies across species have identified biases in the relative strength of ON versus OFF responses in the cortex; however, there are discrepancies in the direction and extent of those biases. Strongly OFF-dominant responses have been found in non-human primate¹¹ and carnivore¹ visual cortices, whereas slight ON-biased responses were observed in the ferret¹⁰. In the mouse, multiple contradictory findings have emerged, ranging from strong OFF dominance¹², to balanced responses¹³, to strong ON dominance¹⁴. These contrasting findings may be due to differences across species or visual stimuli⁵; however, it has also been suggested that variation in ON/OFF dominance across retinotopic position may be a potential mechanism to reconcile and unify these results¹⁰. Indeed, most studies in cats or primates that report OFF dominance focused on

