

Gene Drive Development in Non-Insect Targets – including Vertebrates, Snails, Fungi and Plants

A Horizon Scanning Survey up to end 2023

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Summary of findings:

Screening and analysis of the scientific literature for gene drive development in non-insect targets up to 31 December 2023,¹ showed:

- There are 46 current or proposed non-insect targets².
- Proposals span a wide range of species and taxonomic groups: from mammals and fish to snails, arachnids, fungi and plants (see Table 1).
- In the vast majority of cases the aim is to suppress or eradicate the target.
- Compared to gene drive systems in insects, the systems in other taxonomic groups are further away from releases into the environment.
- A significant amount of research has focussed on developing gene drives in mice, so far with limited success, though efforts are ongoing.
- Development of gene drives in mice is seen by many as a pathway to applying the technology in other mammals.
- There appear to be significant obstacles in applying homing CRISPR gene drive technology in new species and taxonomic groups.

Context

In 2016, the National Academy of Sciences Engineering and Medicine (NASEM) published their report ‘Gene Drives on the Horizon’. This was two years after Esvelt and colleagues first published their conceptual paper on utilising the then new CRISPR/Cas system to build a functional gene drive for the modification or eradication of wild populations (Esvelt *et al.* 2014). At the same time both publications highlighted the dangers and risks of this approach.

Within a year the first proof of concept was published, at that time in the fruit fly *Drosophila melanogaster*, a major model organism for insects (Gantz & Bier 2015). Other proofs of concept followed.

Where is research and development of gene drives now? What is on the horizon? What are the trends? Where has research advanced and where has it hit obstacles? Which species are being focused on and why? And which gene drive systems are being proposed and for which purposes?

To answer these questions, we have undertaken a survey of the scientific literature up until 31 December 2023. Whilst there was a slow steady stream of publications related to “gene drives” in the 10 years up to 2015, a steep rise occurred in 2016 and 2017 (see Figure 1). This started to plateau by 2018, with an average of 120 publications per year since, covering a wide range of disciplines, also including ethics, social sciences, and regulatory issues.

¹ A preliminary version of this survey was published in November 2023.

² The vast majority of the targets identified in the literature are single species, however some early stage proposals relate to broader taxonomic groups, the *Cervid* family (entry 11), the *Tetranychidae* (20), snail genera hosting schistosome parasites (22.1 -22.3), two species from the *Schistosoma* genus (24) and the *Myrtaceae* family (32).

This survey focuses on non-insect targets only. A separate horizon scanning survey for insect targets was published in November 2023 (Wells and Steinbrecher 2023).

This survey does not cover issues regarding risks, difficulties in performing robust risk assessments, or the lack of proven methods to confine, halt or reverse engineered gene drives.

This survey gives an overview of:

- What research has taken place or is ongoing.
- Which species and taxa are current or proposed targets for gene drive development, and which types of gene drives are being put forward.
- How far developments have progressed and what the next stages of experimentation might be.

KINGDOM	PHYLUM or SUB-PHYLUM	CLASS or SUPERCLASS or INFRAPHYLUM	ORDER		Entry number(s)	
Animals						
	Vertebrates	Mammals	<i>Rodentia</i> (Rodents)	House mice	 1.1.1 - 1.9	
					Other rodents	 2.1 - 6.2
				<i>Carnivora</i> (cats, dogs and related mammals)		 7.1 - 9
				<i>Diprotodontia</i> (Possums and related marsupials)		 10
				<i>Artiodactyla</i> (Deer, pigs and related mammals)		 11-12
				<i>Lagomorpha</i> (Rabbits and hares)		 13.1-13.4
			Birds		 14	
			Amphibians		 15.1-16	
			Bony fish		 17-18	
			Jawless fish		 19.1-19.2	
		Arthropods	Arachnids		 20-21	
			Insects		 See separate table	
		Molluscs			 22.1-22.3	
		Nematodes			 23	
		Flatworms			 24	
Fungi				 25-28		
Plants				 29-32		

Table 1: Overview of current gene drive targets.

Overview of gene drive survey data in taxonomic order. Entry numbers correspond to rows in the main data table.

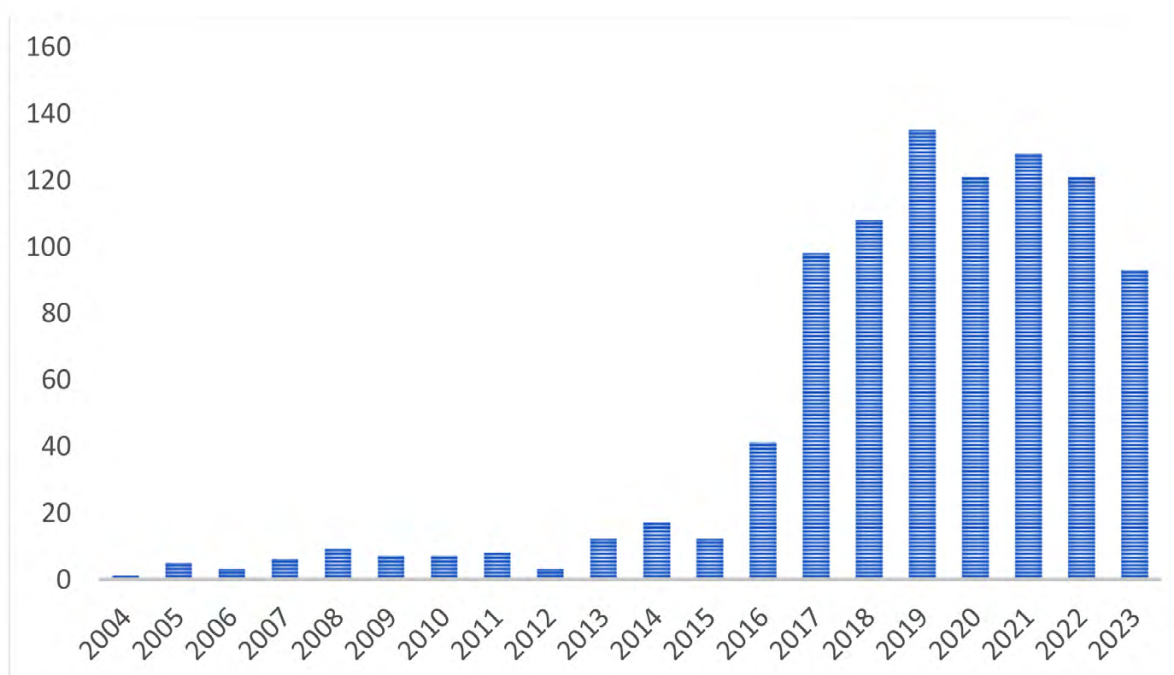


Figure 1: Number of publications per year related to gene drives

Findings

1. **There are proposals in a wide range of species and taxonomic groups:** showing there is momentum and ambition that goes far beyond mosquitoes and mice.
2. **In the vast majority of cases the aim is to suppress or eradicate the target²** (36 out of 41 target species or groups³), in some cases by modifying the target to render it susceptible to suppression.⁴
3. **Compared to gene drive systems in insects, the systems in other taxonomic groups are further away from releases in the environment.** The two most advanced systems - where there is an intention to target the organism in the wild - are both being developed in house mice (entries 1.1.1 and 1.7 in table). Neither of these systems have yet reached full proof of concept in the laboratory.
4. **A significant amount of research has focussed on developing gene drives in mice, so far with limited success, though efforts are ongoing.**
5. **Development of gene drives in mice is seen as a pathway to applying the technology in other mammals.** While this intention is often stated in general terms, an example that names a specific eventual target is the study from Castle *et al.* (2022) who use mice as a model organism with the ultimate aim of modifying deer (entries 1.6 and 11 in table).
6. **No functional gene drive system has been constructed in plants** up to December 2023. A homing CRISPR gene drive was reported in *Arabidopsis* (29) but the publication was later retracted. A 'gene drive like' system has been reported in *Nicotiana tabacum* (30), however the functionality of this system is limited, namely to produce point mutations in the mitochondrial genome. *Please note that subsequent to the cut-off date for this survey, two groups have reported laboratory proof of concept for gene drives in plants (Oberhofer et al. 2024 and Liu et al. 2024), both of which use toxin-antidote based designs rather than homing CRISPR.*

3 Five species that are model organisms where there is no intention to apply the technology in the wild are excluded from this total - these are entries 23 and 27-30 in the table

4 Targets where aim is suppression/eradication: 1, 3-10, 12-22, 24 (this entry comprises two species), 31 (this entry encompasses 14 invasive plant species). Targets where the aim is modification: 2, 11, 15, 22 (but suppression also proposed for *B. marinus* and *B. glabrata*), 25, 32. In one case - 26- the intention has not yet been specified.

7. **There appear to be significant obstacles in applying homing CRISPR gene drive technology in new species and taxonomic groups.** While homing CRISPR gene drives appear to be functional in laboratory settings in dipteran insects (i.e. flies and mosquitoes)⁵ and some fungi (*S. cerevisiae* and *C. albicans*: 27.1-28), the technology is so far only partially functional in mice (1.1.1 – 1.6). Despite efforts to apply this technology more widely, it is not yet functional in plants (29), nematodes (23), flatworms (24) or in the fungi *Fusarium graminearum* (25.2).
8. **It is possible that gene drive designs not based on homing CRISPR technology may be more effective in some species and taxonomic groups.** Development of designs based on the T-haplotype in mice (1.7) and Spok1 in *F. graminearum* (25.1), appears to have made some progress in the laboratory.
9. **Seventeen of the vertebrate targets relate to controlling or eliminating invasive species for conservation purposes, especially mammals.**
10. **While many proposals relate to eliminating invasive mammals on islands, there is ambition to apply gene drive technology for eradications at continental scale in Australia** (e.g. see Birand, Cassey, Ross, Thomas, *et al.* (2022)). There is ongoing interest in Australia in a number of mammalian targets including house mice, black rats, rabbits, cats, and foxes, with a body of work published from 2017 through to the present day relating to some or all of these species.
11. **A number of target species are integral and important species within ecosystems in their native range,** for example the red fox, the possum or the rabbit. Other targets are able to cross-breed with endangered species, such as feral house cats with the European wild cat. Significantly Thresher (2022) argues that employing a gene drive that carries the risk of causing complete global extinction of the European rabbit would be justifiable because ‘...the species seriously threatens agriculture, and native flora and fauna in almost all its extensive invasive ranges, and its loss, however serious, would still in turn damage only a limited ecosystem and set of economies.’
12. Genetic modification systems described as ‘gene drives’ have been developed in bacteria (Valderrama *et al.* 2019) and in viruses (Walter and Verdin, 2020). While these systems share some features with homing gene drives, for example employing CRISPR-Cas9, we do not include such systems in this survey because neither bacteria or viruses reproduce sexually, and they therefore do not meet the established definition of a gene drive.

Please see main table (pp.6-29) for details of findings.

Concluding remarks

Undertaking a broad survey of the research in this field makes the bigger picture clearer, allowing one to perceive trends, as well as obstacles. The wide-ranging ambition for gene drive technology is remarkable, and yet the survey also reveals that homing CRISPR gene drives may not be as broadly applicable across different species and taxonomic groups as originally hoped. A prevalence of proposals to suppress and potentially eradicate species or populations, as opposed to modifying them, is evident. While the reasons for this are not completely clear - it is possible that gene drives are starting to be perceived as a form of species-specific pesticide.

A key outcome of the survey is to raise questions: How might deployment of gene drive technology develop in the medium and long term? Is it going to become the go-to technology to tackle invasive species and ‘pests’? From vertebrates to insects to plants, be it for agriculture, conservation, or forestry, will gene drives be used as pesticides have been in the past? If the technology develops on this trajectory – and we observe that many agencies and academics do appear to view it this way – then serious reflection and analysis will be required. Who will model the deployment as a whole and analyse or assess the consequences, especially with regards to cumulative effects? What would this mean for biodiversity, and what for risk assessment, regulation, and governance, especially on an international and global level? And could the technology be used for purposes other than those currently discussed in the literature?

Methodology

Please see end of document.

Key to technology levels

- 1 Gene drive proposed
- 2 Gene drive proposed with supporting modelling work, or preliminary laboratory work funded
- 3 Preliminary laboratory work published
- 4 Research on gene drive construction funded
- 5 Limited proof of concept
- 6 Laboratory proof of concept
- 7 Non-insects- scaled up trials
Insects - large cage trials
- 8 Potential further contained trials
- 9 Experimental releases in natural environment
- X Abandoned project

Please see page 26 for a complete explanation of the technology levels

Colouring/symbols for progress of technology

	Evidence shows this approach doesn't work
	System is not intended for release
	No publications in three years up to December 2023
???	Uncertain if research has progressed to this stage
M	Modelling work has been done
G	Genome sequenced (with intention/possibility of constructing gene drive stated)

Key to geographic distribution maps

	Species is not present
	Species native range
	Species invasive range

Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?					Project leader(s)	Funders
Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system							Institution	

Kingdom: ANIMALS Subphylum: Vertebrates Class: Mammals Order: (Rodentia) Rodents Species: House mice



1.1 *Mus musculus* Homing CRISPR – proof of concept only

1.1.1	<i>Mus musculus</i> House mouse  After Musser <i>et al.</i> 2021	NA – intention is proof of concept of homing CRISPR gene drive in mammals Initial aims: 1) using gene drive technology to create lab mouse strains carrying multiple modifications (with otherwise impractical genotypes) for laboratory studies 2) finding a way to eliminate invasive rodent species or addressing rodent-borne diseases	Homing CRISPR CRISPR-Cas9 mediated gene drive	Grunwald <i>et al.</i> 2019 Weitzel <i>et al.</i> 2021 Grunwald, Weitzel and Cooper 2022	1	2	3	4	5	6	7	8	9	K.L. Cooper University of California San Diego, USA	Kinship Pew Packard NIH Allen TATA UCSD
1.1.2		Population suppression Suppressing/eradicating invasive rodents on islands, and reducing impacts of rodents on agriculture	Split homing CRISPR CRISPR-Cas9 based gene drive (test both 'zygotic' and 'germline' forms)	Pfützner <i>et al.</i> 2020	1	2	3	4	5	6	7	8	9	P.Q. Thomas University of Adelaide, Australia	DARPA

1.2 *Mus musculus* Homing CRISPR – targetting female fertility

1.2.1		Population suppression The 2017 press release says the aim is to improve pest control methods	Homing CRISPR (targeting 'haplosufficient female fertility gene') 'Homing gene drive targeting female fertility' (2018 paper) 'CRISPR-Cas9 split gene drive which disrupts an essential female fertility gene' (2019 poster)	RoslinInstitute 2017 McFarlane, Whitelaw, and Lillico 2018 – theoretical explanation of proposed GD designs McFarlane <i>et al.</i> 2020 – poster abstract No results published except poster abstract	1	2	3	4	5	6	7	8	9	C.B.A. Whitelaw S.G. Lillico Roslin Institute, University of Edinburgh, UK	CSC BBSRC
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	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9	Institution	
1.2.2		Population suppression	Homing CRISPR (targeting 'haplosufficient female fertility gene')	Brown 2021 - press release	1	2	3	4	5	6	7	8	9	T.A.A. Prowse P.Q. Thomas University of Adelaide, Australia	ARC New South Wales Government South Australia Government
		'eradicating mice from islands' or at continental scale [presumably Australia] to address their impacts on biodiversity	Homing gene drive	Birand, Cassey, Ross, Russell, <i>et al.</i> 2022 Birand, Cassey, Ross, Thomas, <i>et al.</i> 2022		M									
1.2.3		Population suppression	Homing CRISPR (targeting locally ¹ fixed alleles of female fertility genes)	Sudweeks <i>et al.</i> 2019 Oh <i>et al.</i> 2021	1	2	3	4	5	6	7	8	9	A.L. Lloyd North Carolina State University, USA + A.J. Piaggio USDA APHIS Wildlife Services, USA	DARPA
		'Suppressing' invasive rodents on islands to reduce impacts on biodiversity, agriculture and human health	Localized synthetic gene drive			M	G								
1.2.4		Population suppression	Homing CRISPR – four ² designs modelled	Prowse <i>et al.</i> 2017 (see also entries 1.3.3 and 1.5)	1	2	3	4	5	6	7	8	9	T.A.A. Prowse University of Adelaide, Australia	University of Adelaide
		'eradication of alien rodents on islands' to address impacts on bio-diversity The impacts of rodents on agriculture are also noted as a driver	'CRISPR gene drive' 'Homozygotic XX sterility'			M									

¹ Locally fixed alleles refers to alleles found in specific geographic locations - sometimes also referred to as 'private alleles'

² The designs modelled in this publication are covered in entries 1.2.4, 1.3.3 and 1.5

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
1.3	Mus musculus Homing CRISPR sex ratio distorter – Sox9 cargo³														
1.3.1		Population suppression	CRISPR based gene drive involving <i>Sox9</i> – probably a homing CRISPR drive with <i>Sox9</i> cargo	Campbell <i>et al.</i> 2019 No results published despite substantial funding (the work described in entry 1.3.3 may have informed this project)	1	2	3	4	5	6	7	8	9	Probably P.Q. Thomas University of Adelaide, Australia	DARPA
		'eradicating invasive rodent populations on islands' to address impacts on biodiversity	Paper describes development of 'CRISPR/Cas9 and CRISPR/Cpf1 ⁴ gene drives with <i>Sox9</i> and Y-shredder'				?								
1.3.2		Population suppression	Homing CRISPR (with <i>Sox9</i> cargo)	Brown, Eikenbary, and Landis 2022	1	2	3	4	5	6	7	8	9	W.G. Landis Western Washington University, USA	Funders not stated
		Eradicating invasive mouse populations on islands to address biodiversity impacts - with the Southeast Farallon island used as a case study	' <i>sox9</i> CRISPR cas9 gene drive'			M									
1.3.3		Population suppression	Homing CRISPR - four designs modelled ²	Prowse <i>et al.</i> 2017 (see also entries 1.2.4 and 1.5)	1	2	3	4	5	6	7	8	9	P.Q. Thomas University of Adelaide, Australia	University of Adelaide
		'eradication of alien rodents on islands' to address impacts on bio-diversity Aim ultimately is also to address impacts of alien rodents (esp. mice and rabbits) on agricultural production	'CRISPR gene drive' Variants named: 'Heterozygotic XX sterility' 'Heterozygotic XX sex reversal'			M									

³ *Sox9* is an autosomal gene that codes for a developmental transcription factor crucial for sex determination.

⁴ Cpf1 is the old term for what is now named Cas12a

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
1.4	<i>Mus musculus</i> Homing CRISPR sex ratio distorter – ‘Y-shredder’ cargo														
1.4		Population suppression	Homing CRISPR (with ‘Y shredder’ cargo)	Prowse <i>et al.</i> 2019 Campbell <i>et al.</i> 2019	1	2	3	4	5	6	7	8	9	J.V. Ross University of Adelaide, Australia	DARPA
		‘Suppression or eradication’ of rodent populations to reduce impacts on biodiversity and agriculture	Y chromosome shredding gene drive (Campbell <i>et al.</i> 2019) ‘Y-Chromosome deletion using Orthogonal Programmable Endonucleases (Y-CHOPE)’ (Prowse <i>et al.</i> 2019)	No results regarding gene drive construction published		M		?							
								?							
								?							
1.5	<i>Mus musculus</i> Homing CRISPR causing recessive embryonic lethality														
1.5		Population suppression	Homing CRISPR – four designs modelled ²	Prowse <i>et al.</i> 2017 (see also entries 1.2.4 and 1.3.3)	1	2	3	4	5	6	7	8	9	P.Q. Thomas University of Adelaide, Australia	University of Adelaide
		‘eradication of alien rodents on islands’ to address impacts on bio-diversity The impacts of rodents on agriculture are also noted as a driver	‘CRISPR gene drive’ ‘Homozygotic embryonic non- viability’			M									
1.6	<i>Mus musculus</i> Feasibility study for homing CRISPR for population modification in deer (see entry number 11)														
1.6		Population modification	Homing CRISPR	Castle <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	D. Westaway University of Alberta, Canada	Alberta Prion Research Institute CFI University of Alberta
		To demonstrate feasibility of a gene drive rendering wild deer immune to chronic wasting disease [by spreading <i>PRNP</i> null alleles]	CRISPR/Cas9 gene drive												

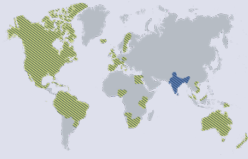
	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9		
1.7	<i>Mus musculus</i> T-haplotype⁵ targetting female fertility														
1.7		Population suppression	Split drive: a) <i>T</i> -haplotype element with gRNA cargo targeting 'haplosufficient female fertility gene' (<i>Prl</i>) b) Cas9 expressed separately (in male germline)	Gierus <i>et al.</i> 2022	1	2 M	3	4	5	6	7	8	9	P.Q. Thomas University of Adelaide, Australia	Funders not stated in pre-print publication
		Aim is to explore the potential of an engineered form of the <i>T</i> -haplotype for 'mouse population suppression or even eradication on islands'	tCRISPR split drive												
1.8	<i>Mus musculus</i> T-haplotype sex ratio distorter -<i>Sry</i>⁶ cargo (T-<i>Sry</i>)														
1.8.1		Population suppression	<i>T</i> -haplotype sex ratio distorter (carrying <i>Sry</i> cargo)	Leitschuh <i>et al.</i> 2018 Campbell <i>et al.</i> 2019 No results published despite substantial funding	1	2	3	4	5	6	7	8	9	J. Godwin North Carolina State University, USA	NSF DARPA
		Eradicating invasive populations on islands to address biodiversity impacts	<i>T</i> -complex drive												
1.8.2			<i>T</i> -haplotype sex ratio distorter (carrying <i>SRY</i> cargo)	Backus and Gross 2016	1	2 M	3	4	5	6	7	8	9	K. Gross North Carolina State University, USA	North Carolina State University NSF
			<i>t-Sry</i>												

5 *T*-haplotype or *t*-complex is a selfish genetic element functioning as a meiotic drive and sex-ratio distorter that naturally occurs in mice, though does not spread widely. It is a form of a toxin-antidote system and allows for the insertion of 'cargo' genes into the *t*-complex, for example female infertility genes such as *Sry*. The *t*-haplotype is linked to the occurrence of taillessness (gene symbol *T*), which gave it its name.

6 *Sry* is a Y-chromosomal gene responsible for sex determination (sex-determining region *Y*) and is required for initiating male development. It is also described as the *male phenotype control gene*. In females it will result in infertility due to partial male development.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9		
1.8.3			T-haplotype sex ratio distorter (carrying <i>Sry</i> cargo)	Manser <i>et al.</i> 2019	1	2 M	3	4	5	6	7	8	9	T.A.R. Price University of Liverpool, UK	SNSF NERC
			synthetic sperm-killing gene drive: 't-Sry'												
1.9	<i>Mus musculus</i> Y linked 'X-shredder' gene drive														
1.9		Population suppression	CRISPR based X-shredder gene drive (‘driving Y’)	Brown 2021 Birand, Cassey, Ross, Russell, <i>et al.</i> 2022	1	2 M	3	4	5	6	7	8	9	T.A.A. Prowse P.Q. Thomas University of Adelaide, Australia	ARC New South Wales Government South Australia Government
		‘eradicating mice from islands’ or at continental scale [presumably Australia] to address their impacts on biodiversity	X chromosome shredding gene drive	Birand, Cassey, Ross, Thomas, <i>et al.</i> 2022											
Kingdom: ANIMALS Class: Mammals Order: (Rodentia) Rodents Species: Other rodents 															
2.1	<i>Peromyscus leucopus</i> White footed mouse	Population modification	Not specified	Long <i>et al.</i> 2019	1	2	3 G	4	5	6	7	8	9	A.G. Barbour University of California Irvine, USA	NIH Bay Area Lyme Foundation UCI USC DoD
	 After Cassola <i>et al.</i> 2016	To modify wild populations of this species to render them resistant to the bacteria causing Lyme’s disease, and thus reduce spread of this disease to humans	Not specified												
2.2			CRISPR daisy drive	Buchthal <i>et al.</i> 2019	1	2	3	4	5	6	7	8	9	K.M. Esvelt MIT, USA	Greenwall Rainwater CDMRP - DoD Sloan Burroughs Wellcome Fund NIH MIT Media Lab
			localized ‘daisy drive’ system												

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9	Institution	
3.1	<i>Rattus norvegicus</i> Brown rat	Population suppression	Homing CRISPR (targeting 'haplosufficient female fertility gene' or 'haplosufficient zygote viability gene') and 'Y-shredder' (located on X-chromosome)	Champer <i>et al.</i> 2021	1	2 M	3	4	5	6	7	8	9	P.W. Messer Cornell University, USA	Predator Free NZ NIH Bio-heritage NZ UK NERC
	 After Khlyap 2012, appended after Hulme- Beaman 2021.	Eradicating invasive rat populations on islands to address their impacts on biodiversity	Three drives modelled: 'homing drive' targeting either female fertility or zygote viability; and 'Y-shredder located on the X-chromosome'												
3.2		Population suppression	Homing CRISPR (targeting 'haplosufficient female fertility gene')	RoslinInstitute 2017	1	2	3	4	5	6	7	8	9	C.B.A. Whitelaw S.G. Lillico Roslin Institute, University of Edinburgh, UK	CSC BBSRC
		'to curb pest rodent populations'	Homing gene drive targeting female fertility	McFarlane, Whitelaw, and Lillico 2018											
3.3		Population suppression	T-haplotype sex ratio distorter (carrying SRY cargo)	Manser <i>et al.</i> 2019	1	2	3	4	5	6	7	8	9	T.A.R. Price University of Liverpool, UK	SNSF UK NERC
		To eradicate invasive populations on islands	synthetic sperm-killing gene drive: 't-Sry'												
3.4		Population suppression	Homing CRISPR or not specified	Dearden <i>et al.</i> 2018										Various institutions	Funder not stated for Dearden <i>et al.</i> Godwin <i>et al.</i> funded by DARPA
		To control or eradicate invasive populations in New-Zealand or on islands	NA – proposal only	Godwin <i>et al.</i> 2019 These papers make similar proposals so have been combined in one entry											

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9	Institution	
4.1	<i>Rattus rattus</i> Common rat or black rat  Shiels & Veitch, 2023 ⁷	Population suppression 'eradication of alien rodents on islands' to address impacts on bio-diversity. The impacts of rodents on agriculture are also noted as a driver.	Homing CRISPR – two variants modelled 'CRISPR gene drive' Two variants modelled: 'Homozygotic embryonic non-viability' 'Homozygotic XX sterility'	Prowse <i>et al.</i> 2017		M								P.Q. Thomas University of Adelaide, Australia	University of Adelaide
4.2		Population suppression Eradicating invasive rat populations on islands to address their impacts on biodiversity	Homing CRISPR (targeting 'haplosufficient female fertility gene' or 'haplosufficient zygote viability gene') or 'Y-shredder' located on X-chromosome Three drives modelled: 'homing drive' targeting either female fertility or zygote viability 'Y-shredder located on the X-chromosome'	Champer <i>et al.</i> 2021		M								P.W. Messer Cornell University, USA	Predator Free NZ NIH Bio-heritage NZ UK NERC
4.3		Population suppression Eradication of this species at continental scale, presumably in Australia, to address impacts on biodiversity	Homing CRISPR or 'Y-linked X shredder' - Y-chromosome-linked X-shredder 'CRISPR homing drive targeting female fertility' or shredding drive ('driving-Y')	Birand, Cassey, Ross, Thomas, <i>et al.</i> 2022		M								T.A.A. Prowse University of Adelaide, Australia	ARC New South Wales Government South Australia Government

⁷ This map shows countries and regions where this species is present, and so does not show the true geographic range. It may be that the species is not present in the whole territory of a country, for example it is probably absent from Arctic areas of Canada.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9		
4.4		Population suppression	T-haplotype sex ratio distorter (carrying SRY cargo)	Manser <i>et al.</i> 2019	1	2	3	4	5	6	7	8	9	T.A.R. Price University of Liverpool, UK	SNSF UK NERC
		To eradicate invasive populations on islands	synthetic sperm-killing gene drive: 't-Sry'												
4.5		Population suppression	Homing CRISPR or not specified	Dearden <i>et al.</i> 2018 Moro <i>et al.</i> 2018										Various institutions	Funder not stated in most cases.
		To control or eradicate invasive populations in Australia, New-Zealand or on islands	NA – proposal only	Godwin <i>et al.</i> 2019 Thresher 2022 These papers make similar proposals so have been combined in one entry											Godwin <i>et al.</i> funded by DARPA
5	<i>Sciurus carolinensis</i> Grey squirrel	Population suppression	Homing CRISPR + Cleave and Rescue [Toxin Antidote] CRISPR combination, with 'daisy-field'	Faber <i>et al.</i> 2021	1	2	3	4	5	6	7	8	9	G. Gorjanc Roslin Institute, University of Edinburgh, UK	BBSRC
		To 'control a targeted grey squirrel population' to reduce impacts on biodiversity and damage to property in the UK (where it is invasive)	HD-CIvR: 'composed of homing (H), daisyfield (D), and cleave-and-rescue (CIvR) gene drives' (a highly speculative and complex drive)												
6.1	<i>Rattus exulans</i> Polynesian rat	Population suppression	Homing CRISPR or not specified	Dearden <i>et al.</i> 2018 Godwin <i>et al.</i> 2019	1	2	3	4	5	6	7	8	9	Various institutions	Funder not stated for Dearden <i>et al.</i>
	 After Ruedas <i>et al.</i> 2016	To control or eradicate invasive populations in New-Zealand or on islands	NA – proposal only	These papers make similar proposals so have been combined in one entry											Godwin <i>et al.</i> funded by DARPA

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?										Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system													
Kingdom: ANIMALS		Class: Mammals	Order: <i>Carnivora</i> (Cats, dogs and related mammals)													
7.1	<i>Felis catus</i> House cat & feral cat	Population suppression	Not stated	Australian Wildlife Conservancy 2022	1	2	3	4	5	6	7	8	9	Not known	AWC and/or CSIRO	
	 After Bengsen <i>et al.</i> 2015	To eradicate or control feral cats in Australia to reduce predation of native species	Not stated													
7.2	 <i>Felis silvestris</i> (wild cat). After Yamaguchi <i>et al.</i> 2015 ⁸	Population suppression	Homing CRISPR or 'Y-linked X shredder' - Y-chromosome- linked X-chromosome shredding drive	Birand, Cassey, Ross, Thomas, <i>et al.</i> 2022	1	2 M	3	4	5	6	7	8	9	T.A.A. Prowse University of Adelaide, Australia	ARC New South Wales Government South Australia Government	
		Eradication at continental scale, presumably in Australia, to address impacts on biodiversity	'CRISPR homing drive targeting female fertility' or ('driving-Y')													
7.3		Population suppression	Homing CRISPR	Moro <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	M. Tizard Australian Animal Health Laboratory, Australia	No specific funder acknowledged All authors appear to be Australian Government employees	
		Eradication or control of feral cats in Australia to address their impact on biodiversity, i.e. native fauna.	RNA-guided gene drive													

⁸ We have included the range of the wild cat, *Felis silvestris*, which can readily hybridise with the domestic cat, *Felis catus*.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9	Institution	
8.1	<i>Vulpes vulpes</i> European red fox	Population suppression	Homing CRISPR or 'Y-linked X shredder' Y-chromosome-linked X-chromosome- shredding drive	Birand, Cassey, Ross, Thomas, <i>et al.</i> 2022	1	2 M	3	4	5	6	7	8	9	T.A.A. Prowse University of Adelaide, Australia	ARC New South Wales Government South Australia Government
	 After Hoffman & Sillero- Zubri, 2021	Eradication at continental scale, presumably in Australia, to address impacts on biodiversity	'CRISPR homing drive targeting female fertility' or 'driving-Y'												
8.2		Population suppression	Homing CRISPR	Moro <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	M. Tizard Australian Animal Health Laboratory, Australia	No specific funder acknowledged All authors appear to be Australian Government employees
		Suppression/eradication to address decline in 'Australia's terrestrial mammal fauna' caused by predation by foxes. The paper also states '...foxes are a serious agricultural pest'.	RNA-guided gene drive												
9	<i>Mustela erminea</i> Stoats	Population suppression	Homing CRISPR	Dearden <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	D.R. Penman Lincoln University, New Zealand	Funder not stated
		To control or eradicate this invasive species in New Zealand to reduce predation of native birds including kiwis	NA – proposal only												

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
Kingdom: ANIMALS		Class: Mammals	Order: <i>Diprotodontia</i> (Possums and related marsupials)												
10	<i>Trichosurus vulpecula</i> Brushtail possum	Population suppression	Homing CRISPR	Dearden <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	D.R. Penman Lincoln University, New Zealand	Funder not stated
		To control or eradicate this invasive species in New Zealand to reduce damage to native trees and the spread of bovine tuberculosis	NA – proposal only												
Kingdom: ANIMALS		Class: Mammals	Order: <i>Artiodactyla</i> (Deer, Pigs and related mammals)	 											
11	<i>Cervid family</i> Deer	Population suppression	Homing CRISPR	Castle <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	D. Westaway University of Alberta, Canada	Alberta Prian Research Institute CFI University of Alberta
		To render the wild population immune to chronic wasting disease [by spreading <i>PRNP</i> null alleles] > see entry 1.6	CRISPR/Cas9 gene drive initial work on rabbit and mouse cell lines only												
12	<i>Sus scrofa</i> Feral pigs	Population suppression	Not specified	Carter <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	T Strive Centre for Invasive Species Solutions, Australia	Not stated Probably CSIRO
		To address the 'social, economic and environmental burden' of this non-native species in Australia	NA – proposal only												

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
Kingdom: ANIMALS		Class: Mammals	Order: <i>Lagomorpha</i> (Rabbits and hares)	Theoretical studies only											
13.1	<i>Oryctolagus cuniculus</i> European rabbit	Population suppression	Homing CRISPR – two variants modelled	Prowse <i>et al.</i> 2017	1	2 M	3	4	5	6	7	8	9	P.Q. Thomas University of Adelaide, Australia	University of Adelaide
	 After Tablado <i>et al.</i> 2009	Eradication of invasive rabbit populations on islands to address biodiversity impacts Impacts of rabbits on agriculture are also noted	CRISPR gene drive Two variants modelled: 'Homozygotic embryonic non- viability' 'Homozygotic XX sterility'												
13.2		Population suppression	Homing CRISPR or 'Y-linked X shredder'- Y-chromosome- linked X-chromosome shredding drive	Birand, Cassey, Ross, Thomas, <i>et al.</i> 2022	1	2 M	3	4	5	6	7	8	9	T.A.A. Prowse University of Adelaide, Australia	ARC New South Wales Government South Australia Government
		Eradication at continental scale, presumably in Australia, to address impacts on biodiversity	'CRISPR homing drive targeting female fertility' or 'driving-Y'												
13.3		Population suppression	Homing CRISPR or not specified	Moro <i>et al.</i> 2018 Thresher 2022	1	2	3	4	5	6	7	8	9	Various institutions	Funder not stated in both cases.
		To control or eradicate invasive populations in Australia or New-Zealand	NA – proposal only	These papers make similar proposals so have been combined in one entry											

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
Kingdom: ANIMALS		Class: Birds	Theoretical studies only												
14	<i>Sturnus vulgaris</i> Common starling	Population suppression	Homing CRISPR	Moro <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	M. Tizard Australian Animal Health Laboratory, Australia	No specific funder acknowledged
		Suppression to address 'impacts to biodiversity and agriculture', however this species is noted for the damage it causes to crops so this is likely the primary driver	RNA-guided gene drive												All authors appear to be Australian Government employees
Kingdom: ANIMALS		Class: Amphibians													
15.1	<i>Bufo marinus</i> or <i>Rhinella marina</i> Cane toad	Population modification	Homing CRISPR	Tingley <i>et al.</i> 2017	1	2	3	4	5	6	7	8	9	R Shine University of Sydney, Australia	Not stated
	 After Solis <i>et al.</i> , 2009	To 'detoxify' toads in Australia to address impacts on native species which are poisoned by eating them.	NA – proposal only												
15.2		Population suppression	Homing CRISPR	Moro <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	M. Tizard Australian Animal Health Laboratory, Australia	No specific funder acknowledged
		Suppression to address impacts on native species in Australia, which are either predated by toads or poisoned by eating them.	RNA-guided gene drive	Cooper <i>et al.</i> 2020 – conference abstract											All authors appear to be Australian Government employees
15.3		Population suppression	Z linked W-shredder, with variable parameters <i>(to control species with ZW sex determination)</i>	Holman 2019	1	2	3	4	5	6	7	8	9	L. Holman University of Melbourne, Australia	ESEB SNSF
		Suppressing 'invasive populations of cane toads'	Z linked 'W-shredder' (analogue to Y linked X-shredder)												

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9		
16	<i>Eleuthero-dactylus coqui</i> Caribbean tree frog	Population suppression	Homing CRISPR	Thresher 2022 Feasibility study										A.C. Thresher University of California San Diego, USA	Funder not stated
		Eradication or suppression of this species, (accepting risk of global extinction), to address biodiversity impacts of invasive populations	'CRISPR/Cas suppression-drive'												
Kingdom: ANIMALS Super-class: Bony fish 															
17	<i>Cyprinus carpio</i> European carp ⁹	Population suppression	Not specified	Minnesota Aquatic Invasive Species Research Centre 2022										M. Smanski University of Minnesota, USA	ENRTF
		Control of invasive populations of this species	Not specified												
18	<i>Pterois volitans</i> Red lionfish	Population suppression	Homing CRISPR	Vacura <i>et al.</i> 2018										P. Venturelli Ball State University, USA	Funder not stated
		To control or eradicate this invasive species to address damaging impacts to native reef communities in Caribbean and Western Atlantic	NA -preliminary theoretical study												

⁹ Kopf *et al.* 2019 raised the possibility of using a gene drive to suppress invasive populations of carp but do not recommend this approach.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders		
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system														
Kingdom: ANIMALS		Infraphylum: Jawless fish														Theoretical studies only	
19.1	<i>Petromyzon marinus</i> Sea lamprey	Population suppression or population modification to enable suppression	Options proposed include: Split homing CRISPR 'Y-Linked X-shredder' Homing CRISPR Toxin Antidote	Ferreira-Martins <i>et al.</i> 2021	1	2	3	4	5	6	7	8	9	M.S. Docker University of Manitoba, Canada	Funders not stated		
	 After NatureServe, 2013 ¹⁰	Suppression or eradication of the lamprey from the North American Great Lakes to prevent this parasitic species damaging fish stocks	Options proposed include: 'Split gene drive' 'Driving y' 'Homing suppression gene drive' 'Toxin-antidote gene drive'														
19.2		Population suppression	Homing CRISPR or not specified	York, Thresher, and McCauley 2021 Lampman <i>et al.</i> 2019 These papers make similar proposals so have been combined in one entry										Various institutions	Funders not stated		
		Suppression or eradication of the lamprey from the North American Great Lakes to prevent this parasitic species damaging fish stocks	NA - proposal only														
Kingdom: ANIMALS		Phylum: Arthropods	Class: Arachnids														
20	<i>Tetranychidae family</i> Spider mites	Propose population replacement (to render them more susceptible to insecticides)	Homing CRISPR	Li <i>et al.</i> 2020	1	2	3	4	5	6	7	8	9	B.E. Tabashnik University of Arizona, USA	BARD		
		Reduction of damage to agricultural and horticultural crops	NA -preliminary theoretical study														

¹⁰ This map shows only the inland range for this species, that is watersheds and freshwater lakes where it is present. The species lives part of its life in saltwater and its native range also 'includes the Atlantic coast of North America from Newfoundland to northern Florida, the Atlantic coast of Europe, and the Baltic, western Mediterranean and Adriatic seas.' (Government of Ontario, 2018). In the great lakes, where it is invasive, it has adapted to live entirely in freshwater conditions (Government of Ontario, 2018).

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?											Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system													Institution	
21	<i>Varroa destructor</i> Varroa mite	Population modification to enable suppression	Homing CRISPR	Faber <i>et al.</i> 2021	1	2	3	4	5	6	7	8	9			B.A. Harpur Purdue University, USA	BBSRC University of Edinburgh Purdue University Project Apis M.
		Suppression or eradication of varroa mites from honeybee colonies to prevent harm to the colony and honey production	(homing) CRISPR Cas9 gene drive			M											

Kingdom:
ANIMALS

Phylum:
Arthropods

Class:
Insects



SEE SEPARATE TABLE

Kingdom:
ANIMALS

Phylum:
Molluscs

Class:
Gastropods



22.1	<i>Biomphalaria glabrata</i>	Population modification	Not specified but cites examples of homing CRISPR	Hambrook <i>et al.</i> 2020	1	2	3	4	5	6	7	8	9			P.C. Hannington University of Alberta, Canada	NSERC
	 After Habib <i>et al.</i> 2021 ¹¹	The aim is to modify snail populations to increase their immunity to schistosome infection, thereby disrupting the schistosome lifecycle and reducing transmission to humans	Not specified														

¹¹ This map show countries where this species is present and does not show the exact geographic range.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9	Institution	
22.2	<i>Biomphalaria glabrata</i> (and other snails of <i>Biomphalaria</i> , <i>Bulinus</i> , <i>Oncomelania</i> & <i>Neotricula</i> genera which host schistosome parasites) All <i>Biomphalaria</i> species susceptible to <i>Schistosoma mansoni</i> . After Habib <i>et al.</i> 2021 ¹² 	Population suppression and/or Population modification 'Modification of natural snail populations' to reduce 'schistosomiasis prevalence and transmission'	Several approaches proposed Several approaches proposed	Maier <i>et al.</i> 2019 - presentation	1	2	3	4	5	6	7	8	9	M. Zamanian University of Wisconsin, USA J. Reinhard-Rupp Global Health Institute of Merck, Switzerland	Global Health Institute of Merck
22.3	<i>Biomphalaria glabrata</i>	Population modification The aim is to modify snail populations to increase their immunity to schistosome infection, thereby disrupting the schistosome lifecycle and reducing transmission to humans	Homing CRISPR CRISPR gene drive	Grewelle <i>et al.</i> 2022	1	2 M	3	4	5	6	7	8	9	G.A. De Leo Stanford University, USA	Stanford University NSF
Kingdom: ANIMALS Phylum: Nematodes 															
23	<i>Caenorhabditis brenneri</i>	Proof of principle experiments – not intended for release to 'test and optimize daisy-chain, daisyfield, and daisy quorum drives—including for daisy restoration—in fast-reproducing laboratory populations of worms...'	daisy-chain drive, daisyfield drive, daisy quorum drive daisy-chain drive, daisyfield drive, daisy quorum drive	Esvelt 2017a Esvelt 2017b No results have been published despite substantial funding	1	2	3	4	5	6	7	8	9	K.M. Esvelt MIT, USA	DARPA This funding has now ended

12 This maps show countries where these species are present, and does not show the exact geographic range.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
Kingdom: ANIMALS		Phylum: Flatworms													
24	<i>Schistosoma mansoni</i> (<i>Schistosoma haematobium</i> also proposed) Blood flukes	Population suppression	Z linked W-shredder, with variable parameters (as described by Holman, 2019)	AAAS 2016 Iordanskiy <i>et al.</i> 2017 - conference abstract Holman 2019	1	2	3	4	5	6	7	8	9	K.M. Esvelt MIT, USA P. Brindley George Washington University, USA	MaxMind and probably others This funding has likely ended
		To suppress schistosome parasites to thereby reduce human morbidity and mortality from schistosomiasis	One proposal would be a Z linked 'W-shredder' (as described by Holman, 2019) 'all of the offspring will be born either female or male.' (AAAS 2016)	No results have been published											
Kingdom: FUNGI															
25.1	<i>Fusarium graminearum</i>	Population modification	Engineered gene drive employing <i>Spok1</i> (spore killer meiotic drive from <i>Podospora</i> spp.)	Gardiner <i>et al.</i> 2020 Urquhart and Gardiner, 2022 ¹³	1	2	3	4	5	6	7	8	9	K. Kazan CSIRO, Queensland, Australia D. M. Gardiner CSIRO, Queensland, Australia	CSIRO ARC Australian Government
		To modify populations of <i>F. graminearum</i> to disrupt virulence factors in this species, and so reduce head blight in wheat and barley	<i>Spok1</i>							?					
25.2		Population modification	Split homing CRISPR	Gardiner <i>et al.</i> 2020	1	2	3	4	5	6	7	8	9	K. Kazan Agriculture and Food, CSIRO, Australia	CSIRO
		To modify populations of the <i>F. graminearum</i> (presumably for same reasons as in 25)	Do not use any particular term – but give detailed description of design												

13 Urquhart and Gardiner (2022) report further experimental work to characterise *Spok1* using the model organisms *S. cerevisiae* and *E. coli*. The 'genetic control of plant-pathogenic fungi' is mentioned as a possible future goal, with *F. graminearum* mentioned specifically.

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9	Institution	
26	<i>Fusarium verticillioides</i>	To control this plant pathogen which causes 'ear and stalk rot of maize' and which can 'contaminate maize kernels with fumonisin mycotoxins'	Engineered gene drive employing Spore Killer Candidate-1 (<i>SKC1</i>) from <i>F. verticillioides</i>	Lohmar, Rhoades, Hammond, <i>et al.</i> 2022 Lohmar, Rhoades, Patel, <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	T. M. Hammond University of Illinois, USA Daren W Brown USDA, Agricultural research service, Illinois, USA	NSF USDA
		Not specified	'SKC1 based control practices' [which would 'require modifications to SKC1']												
27.1	<i>Saccharomyces cerevisiae</i> brewer's or baker's yeast	Population modification	Split homing CRISPR	DiCarlo <i>et al.</i> 2015	1	2	3	4	5	6	7	8	9	G.M. Church Harvard Medical School, USA	DOE NCI NIDDK Wyss Institute
		Proof of principle of population modification via a split homing gene drive in this model organism	'split CRISPR-Cas9 gene drive'							?	?	?			
27.2		Population modification	Split homing CRISPR	Roggenkamp <i>et al.</i> 2017	1	2	3	4	5	6	7	8	9	GC Finnigan Kansas State University, USA	NIH Kansas State University
		To generate homozygous diploid states in modified yeast	Cas9 gene drive system												
27.3		Population modification	Probably homing CRISPR (as team had used this technology in other work)	Aguilera 2017 - press release No results published	1	2	3	4	5	6	7	8	9	S. Kryazhmsky J. Meyer University of California San Diego, USA	DARPA
		To study gene drives over many generations to understand the emergence of resistance	NA – no publications												
27.4		Population modification	Split homing CRISPR	Roggenkamp <i>et al.</i> 2018	1	2	3	4	5	6	7	8	9	G.C. Finnigan Kansas State University, USA	NIH USDA Kansas State University
		To test various methods to modulate gene drive activity, e.g. Cas9 expression level (Roggenkamp <i>et al.</i> 2018), expression of anti-CRISPR proteins (Basgall <i>et al.</i> 2018) and Cas9 nuclear localisation (Goeckel <i>et al.</i> 2019).	CRISPR-Cas9 gene drive / CRISPR gene drive	Basgall <i>et al.</i> 2018 Goeckel <i>et al.</i> 2019						?	?	?			

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s)	
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system											Institution	Funders
27.5		Population modification	Multi-locus split homing CRISPR	Yan and Finnigan 2018	1	2	3	4	5	6	7	8	9	G.C. Finnigan Kansas State University, USA	NIH USDA
		To test a split gene drive system to simultaneously propagate gene drives at three different loci	multi-locus CRISPR gene drive							?					
27.6		Population modification	Split homing CRISPR employing Cas12a	Lewis, Yan, and Finnigan 2021	1	2	3	4	5	6	7	8	9	G.C. Finnigan Kansas State University, USA	Kansas State University USDA
		Proof of principle of population modification via a split homing gene drive based on Cas12a	'Cas12a-based gene-drive system'							?					
27.7		Population modification	Split homing CRISPR	Bakerlee <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	M.M. Desai Harvard University, USA	DoD NSERC Canada NIH NSF
		To generate a library of 'all combinations of 10 missense mutations from across the genome' to study interactions between these mutations (epistasis)	'hierarchical' CRISPR gene drive							?					
27.8		Population modification	Homing CRISPR variant	Abdullah <i>et al.</i> 2023	1	2	3	4	5	6	7	8	9	A H Kachroo Concordia University, Montreal, Canada	NSERC Canada CFI Québec Ministère de l'Économie, de la Science et de l'Innovation Concordia University Welch Foundation Army Research Office NIH
		'[T]o readily combine genetically engineered loci' in yeast	marker-less enrichment and recombination of genetically engineered loci (MERGE)												

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system		1	2	3	4	5	6	7	8	9		
28	<i>Candida albicans</i>	Population modification	Split homing CRISPR	Shapiro <i>et al.</i> 2018 Halder <i>et al.</i> 2019										J. Collins MIT & Harvard University, USA R.S. Shapiro University of Guelph, Canada	Allen CIHR NIH Wyss Institute NSERC Canada Banting Burroughs Wellcome Fund
		To create single and double deletion mutants in this species for laboratory studies	CRISPR-Cas9 based gene drive								?	?	?		
Kingdom:  PLANTS															
29	<i>Arabidopsis thaliana</i> Thale cress	Population modification	Homing CRISPR	Zhang, Mudgett, <i>et al.</i> 2021 Zhang <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	Y. Zhao University of California San Diego, USA	TIGS UCSD NIH
		The intention was to demonstrate a gene drive system in a plant model species. The authors state this technology could 'accelerate crop breeding'	CRISPR/Cas9-based gene drive	paper WITHDRAWN after a year											
30	<i>Nicotiana tabacum</i> Tobacco	Population modification	TALEN gene-drive mutagenesis	Forner <i>et al.</i> 2022	1	2	3	4	5	6	7	8	9	R. Bock Max Planck Institute for Molecular Plant Physiology, Germany	Max Planck Society ERC
		The aim is to demonstrate a technology for modifying the plant mitochondrial genome for laboratory experiments and to 'enable the exploitation of mitochondria in biotechnology and synthetic biology'	transcription activator- like effector nuclease (TALEN) gene-drive mutagenesis (GDM), or TALEN-GDM												

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?									Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system												
PLANTS															
31	Various weed and invasive species: <i>Alopecurus myosuroides</i> ¹⁴ Black grass <i>Amaranthus palmeri</i> ¹⁴ Palmer amaranth <i>Amaranthus tuberculatus</i> ¹⁴ Rough fruited water hemp <i>Ambrosia artemisiifolia</i> ¹⁴ Common ragweed <i>Cynodon dactylon</i> ¹⁴ Bermuda grass <i>Cyperus rotundus</i> ¹⁴ Purple nut sedge <i>Eichhornia crassipes</i> Water hyacinth <i>Kochia scoparia</i> ¹⁴ Kochia <i>Lantana camara</i> ¹⁴ Common lantana <i>Lolium rigidum</i> ¹⁴ Rigid rye grass <i>Lupinus arboreus</i> Yellow bush lupin/tree lupin <i>Lychnis coronia 'Alba'</i> Rose campion <i>Tanacetum vulgare</i> ¹⁴ Common tansy <i>Setaria glauca</i> ¹⁴ Yellow foxtail	Population modification to enable suppression To reduce the presence and impact of weed species on agricultural production by modifying them, potentially to render them less competitive, or more sensitive to herbicide. The technology might also be used to tackle other invasive plant species.	Homing CRISPR is most common proposed technology NA - Proposals only	Neve 2018 Chen <i>et al.</i> 2019 Kumaran <i>et al.</i> 2020 Perotti <i>et al.</i> 2020 Tek and Budak 2022 Wong <i>et al.</i> 2022 Croghan <i>et al.</i> 2023 Kumam <i>et al.</i> 2023 All the above papers make similar proposals so have been combined into one entry Mitchell and Bartsch (2020) suggest common ragweed as a target	1	2	3	4	5	6	7	8	9	Proposals from several funded CSIRO researchers including at the University of Queensland, Australia, and researchers at Rothamsted Research UK	Various funders including BBSRC and CSIRO

	Species	Intended direct effect	Type of gene drive (our categories)	Publication(s) where research is described	How close is strain/system to experimental releases in the wild?										Project leader(s) Institution	Funders
	Geographic range	Intended use (as stated by authors)	Developer's name for gene drive system													
32	<i>Myrtaceae</i> family (including <i>Eucalyptus</i> <i>spp.</i>)	Population modification	NA	Barrett <i>et al.</i> 2019	1	2	3	4	5	6	7	8	9	D.M. Gardiner CSIRO Agriculture and Food, Australia	CSIRO	
		To modify wild populations in Australia to render them resistant to the fungal pathogen <i>Puccinia psidii</i>	The proposals do not focus on any particular type of gene drive													

Key to technology levels

- 1 **Gene drive proposed:** a proposal has been put forward in the scientific literature or from another academic source (e.g. funding body)
- 2 **Gene drive proposed with supporting modelling work, or preliminary laboratory work funded:** a proposal has been made in the scientific literature supported by modelling work, or preliminary laboratory work has been funded but has not yet been published
- 3 **Preliminary laboratory work published:** laboratory research relevant to gene drive construction published (e.g. developing molecular biology methods) with possibility or intention to construct gene drive stated
- 4 **Research on gene drive construction funded:** research on gene drive construction has been funded, but no results yet published OR results published showing non-functional gene drives, or similar very limited progress
- 5 **Limited proof of concept:** Published results show a gene drive is to some extent functional, however there are outstanding technical issues such as resistance or low efficiency
- 6 **Laboratory proof of concept:** Taking published results at face value, the system works effectively in the laboratory
- 7 **Scaled up trials:** Data published from scaled up trials in contained environments, offering a more accurate simulation of conditions in natural environment
- 8 **Potential further contained trials:** After large cage trials (or other scaled up trials), it is not currently clear what further trials may take place prior to experimental releases. One possibility is trials in outdoor cages
- 9 **Experimental releases in natural environment:** Field trials are underway with releases in the natural environment. This does not indicate that the technology has been shown to be effective or safe
- X **Abandoned project:** Research to construct a gene drive has been carried out, but has been unsuccessful and to our knowledge is no longer active

Abbreviations for funders and other organisations

Allen	Allen Frontiers Group
ARC	Australian Research Council
AWC	Australian Wildlife Conservancy
Banting	Banting Research Foundation
BARD	United States—Israel Binational Agricultural Research and Development Fund
BBSRC	UK Biotechnology and Biological Sciences Research Council
Bioheritage NZ	New Zealand Bio-heritage National Science Challenge
CDMRP - DoD	Congressionally Directed Medical Research Programs Department of Defense
CFI	Canada Foundation for Innovation
CIHR	Canadian Institutes of Health Research
CSC	Commonwealth Scholarship Commission
CSIRO	Commonwealth Scientific and Industrial Research Organisation
DARPA	US Defense Advanced Research Projects Agency
DoD	US Department of Defense
DOE	US Department of Energy
ERC	European Research Council
ESEB	European Society for Evolutionary Biology
Greenwall	Greenwall foundation
Kinship	Kinship foundation
NCI	US National Cancer Institute
NERC	UK Natural Environment Research Council
NIDDK	US National Institute of Diabetes and Digestive and Kidney Diseases
NIH	US National Institutes of Health
NSERC Canada	Natural Sciences and Engineering Research Council of Canada
NSF	US National Science Foundation
Packard	David and Lucile Packard Foundation
Pew	Pew Charitable Trust
Predator Free NZ	New Zealand Predator Free Program
Rainwater	Rainwater Foundation
Sloan	Sloan Foundation
SNSF	Swiss National Science Foundation
TATA	TATA trusts
TIGS UCSD	Tata Institute for Genetics and Society University of California San Diego
UCI	University of California Irvine
UCSD	University of California San Diego
USC	University of South Carolina
USDA	US Department of Agriculture
Wyss Institute	Wyss Institute for Biologically Inspired Engineering

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Methodology

Literature searches

Literature searches for 2004 through to the 31 December 2023 were carried out using the advanced search function in the Web of Science Core Collection database, with the search term TS= (“gene drive” or “gene drives”). Relevant journal articles were identified by systematically screening titles and abstracts from the search outputs. Press releases from academic institutions and other relevant materials on the web were identified using appropriate web searches (e.g. searching for the names of group leaders, target species, and the term ‘gene drive’). We recognise that all relevant material on the web may not have been identified.

Criteria for inclusion

Laboratory research and modelling on gene drives in non-insect species as reported in the academic literature and other sources such as press releases from funders and universities, has been included. This includes ‘preliminary research’ – i.e. research that states it could potentially support gene drive construction – for example genome sequencing or identification of target genes.

Proposals for gene drives which do not include any modelling or laboratory research are included if they are the first such proposal, and if no more advanced work has taken place for this target. Additional proposals are included at our discretion, for example if they contain novel ideas for gene drive technology (e.g. the Z-linked W-shredder), novel applications, or indicate wide interest in a particular target species.

Basis for generating entries in table

Broadly, each entry in the table describes development of a particular gene drive concept in a specific target species or group, as described in the relevant literature. In some cases where multiple options are considered in a single publication, multiple proposed gene drives are described in a single row (generally these are early-stage proposals or modelling studies). Where similar proposals to target a particular species have been made in different publications without any supporting modelling or laboratory work, these are also combined into one entry. The ‘project leader’ is identified as the last author on the publications describing the research or proposals.