Naturally clonal vertebrates are an untapped resource in ecology and evolution research

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Naturally clonal vertebrates are an untapped resource in ecology and evolution research

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Abstract |

Science requires replication. The development of many cloned or isogenic model organisms is a testament to this. But researchers are reluctant to use these traditional animal model systems for certain questions in evolution or ecology research because of concerns over relevance or inbreeding. It has largely been overlooked that there are a substantial number of vertebrate species that reproduce clonally in nature. This review highlights how use of these naturally evolved, phenotypically complex animals can push the boundaries of traditional experimental design and contribute to answering fundamental questions in the fields of ecology and evolution.

Introduction

The ability to reliably generate genetically identical animals revolutionized science. Among vertebrates, mice, rats, zebrafish and frogs have been bred into numerous isogenic lines and even more species have successfully been cloned or genetically manipulated through sophisticated molecular methods[1]. Use of these animals as replicate individuals has allowed us to investigate and disentangle the relative influences of genetic and environmental variation on the expression of key phenotypic traits ranging from molecular patterns to behavior. This level of precision, however, comes at a cost: the genotypes of these engineered vertebrates are not products of natural selection raising concerns about the potential ecological relevance and generalizability of the expressed phenotypes[2]. Because of this, many researchers in ecology and evolution have been reluctant to use isogenic or cloned model systems.

To date, however, it has largely been overlooked that there are a substantial number of vertebrate species that reproduce clonally, naturally. Since the identification of the first naturally clonal, or unisexual, vertebrate in 1932, the Amazon molly (*Poecilia formosa*)[3], researchers have identified roughly 100 species, or 'biotypes' of unisexual vertebrates across at least 22 genera of fish, amphibians and reptiles (Fig. 1)[4-6]. The common characteristic among these animals is that they reproduce without genetic recombination thus producing broods or clutches of genetically identical offspring. Much of the previous research on unisexual vertebrates has focused on questions relating to their unisexual nature (Box 1).

Here, we argue that unisexual vertebrate animals offer a unique combination of traits making them ideal systems for tackling many long-standing and emerging questions in ecology and evolution[7,8]. As with traditional isogenic and cloned model systems they provide the opportunity to generate genetically identical replicate individuals within lineages and exploit the genetic variation that is present among lineages (within a biotype). And in contrast to many traditional vertebrate model systems like mammals, many unisexual vertebrates require no parental care after birth, so in combination with their clonality, researchers have an unparalleled ability to disentangle genetic from environmental influences, including during very early life. These animals thus combine the highly desirable experimental control of genes and environment with the phenotypic complexity of vertebrates that have evolved under natural selection. Additionally, these animals are geographically widespread both within and between biotypes, ecologically diverse, and can often be studied under field conditions (Table 1). This enormous potential stands in sharp contrast to the fact that unisexual vertebrates currently play at best a marginal role for research in ecology and evolution.

Below we first outline basics of unisexual vertebrate reproductive biology; and then our main goal in this review is to highlight how unisexual vertebrates can be used to push the boundaries of classic experimental design, promoting novel insights into a range of fundamental questions in ecology and evolution. We focus on four key areas where we see the greatest potential 1) to better understand the genotype-phenotype link; 2) to better investigate how animals integrate cues from multiple sources over ontogeny; 3) to test theories about the processes generating phenotypic variation within populations and 4) to generate replicate animal groups to investigate social and collective dynamics.

Basics of unisexual reproductive biology

There are a number of common characteristics shared by all unisexual vertebrates. First, unisexuality appears to be limited to ectothermic animals, namely lizards, fish and amphibians[4]. Second, these animals are all-female lineages, hence the name ‘unisexual’[9]. Finally, most if not all biotypes evolved as a result of a hybridization event between two relatively closely related species[9,] but see[10]. A major advantage of their hybrid origin is that these animals are often nearly completely heterozygous across their entire genome[5,11], helping to limit concerns about inbreeding depression that are typically raised with cloned or isogenic animals. Additionally, recent work in the unisexual Amazon molly demonstrated that the structure and continued evolution of its genome appears to match the processes occurring in the genomes of its sexual ancestors in terms of gene conversion rates, patterns of gene evolution and transposable element activity[11]. So while these animals employ unique reproductive modes, their biology, ecology and molecular processes can likely be generalized (to some extent) beyond this one species group.

Unisexual verterbrates reproduce using three main reproductive strategies: parthenogenesis, gynogenesis and hybridogenesis (Fig. 2) [5,6,9]. These modes differ in whether the eggs are reduced or not in chromosome number and whether they need sperm to stimulate development. Parthenogenic animals are truly clonal in that they generate unreduced eggs with no recombination and without external input (i.e. sperm) from another animal, though in some biotypes, pseudo-copulation with another female appears to enhance reproductive success[12]. This mode of reproduction is (in vertebrates) only found in Squamate lizards and snakes[13]. Gynogenetic vertebrates also produce unreduced eggs, but require sperm from a related species to stimulate embryonic development, though this genetic material is generally not incorporated into the egg[14]. Hybridogenetic animals retain some hallmarks of sexual reproduction: they produce reduced eggs without recombination containing just one parental genome, generally the maternal genome, discarding the other. The egg is fertilized with sperm, producing a diploid offspring. As such, one genome (the maternal) is inherited clonally through the lineage, and the other (the paternal) is inherited sexually anew each generation[9]. This reproductive mode has also been called hemiclonality[9]. Unisexual biotypes can arise either through a single hybridization event (e.g. the gynogenetic fish *P. formosa*[15,16]), where all genetic variation among lineages is a result of subsequent mutations or introgression, or through multiple hybridizations and backcrossings (e.g. the parthenogenetic gecko *Heteronotia binoei*[17]) resulting in extensive genetic variation among lineages. As such, all biotypes exhibit some level of clonal diversity offering the opportunity for researchers to investigate their questions across multiple genetic backgrounds.

We note that at least two other modes of reproduction exist among vertebrates that result in genetically identical offspring: polyembryony and constitutive self-fertilization. Polyembryony occurs through the splitting of a single embryo such as in monozygotic twins (or triplets, etc). However, each embryo is the result of sexual reproduction so while siblings are clones within a generation, there is no maintenance of a clonal lineage across generations[18]. While common in plants and invertebrates, especially parasitoid wasps, polyembryony is confined to *Dasypus* armadillos in vertebrates[18]. Constitutive self-fertiliziation is a form of inbreeding that over many generations results in essentially homozygous clones. The only vertebrates known (so far) to constitutively self-fertilize are the mangrove killifish (*Kryptolebias marmoratus*) and possibly the closely related *Kryptolebias ocellatus*[19]. These modes are not strictly unisexual as recombination still occurs, and are relatively rare among vertebrates but could still be utilized in much the same way as we advocate for unisexual vertebrates.

The different unisexual reproductive modes can be advantageous for different research questions and designs: parthenogenetic animals produce truly clonal offspring enabling powerful replicate individual approaches in vertebrates; so do gynogenetic animals but here researchers can control when reproduction occurs by controlling females' access to sperm. Hybridogenetic animals can be used to test the effects of one genomic complement in multiple different genetic backgrounds which is especially useful for questions on the causes and consequences of epistasis[20]. And so depending the desired level of genetic control researchers could chose the species that exhibits the most appropriate reproductive biology for their question of interest.

The link from genotype to phenotype

Advances in –omics technologies (e.g. genomics, transcriptomics, proteomics) have provided major breakthroughs in understanding the pathways from genotype to phenotype. These techniques have now been applied across a variety of animal systems[21-23] but there are still a number of limitations that can make it difficult to disentangle the molecular underpinnings of ecologically and evolutionarily important traits. First, studies of differential gene (or protein or metabolite) expression can be very noisy often because allelic variation overshadows any treatment effects[24-26]. Second, a major goal is to understand the temporal changes of expression profiles, but again, allelic variation among individuals often clouds these dynamics. Third, the use of only a limited number of vertebrate models, such as mice and rats, has biased gene discovery and annotation to often focus on loci with human medical implications[27]. So from a methodological point of view, unisexual vertebrates can provide serious advantages as model organisms in –omics studies. Researchers can more precisely pinpoint expression differences by comparing groups of these genetically identical animals. And sampling from groups of identically treated unisexual vertebrates would offer a more intimate look into expression dynamics over time.

A practical benefit is that researchers can likely reduce the number of biological replicates as they will be able to capture the level of natural variation in expression with fewer animals[28].

At the forefront of this field is the study of how epigenetic mechanisms can give rise to heritable phenotypic variation. Heritable changes in gene expression patterns can occur through at least three pathways: DNA methylation, chemical changes to DNA-binding proteins (e.g. histones) and regulation by small RNA molecules[29]. Importantly, these mechanisms are themselves influenced by genetic variation and are inherently dynamic, changing both within and between generations[29]. And so, a full understanding of what ultimately generates differential gene expression requires model systems where genetic and epigenetic variation can be studied independently[21,30]. Indeed, the use of naturally inbred lines of plants (accessions) such as *Arabidopsis,* or asexual lineages of invertebrates such as *Daphnia* has highlighted the important role of epigenetic processes in generating ecologically relevant phenotypic variation[31]. For example, recent work on corals demonstrates the power of taking rigorous replicate individual approaches into an ecological context. Corals can reproduce asexually through budding so parts of a single colony (clone) can be separated and used as replicate ‘individuals’. Using a reciprocal transplant design, Kenkel and Matz[24] tested how plasticity in gene expression mediates local adaptation in a coral (*Porites astreoides*) across different environments. Because they used genetically identical replicate individuals, they confirmed that a large part of these expression differences must be due to epigenetic mechanisms. Oldach et al.[32] also took advantage of the clonal nature of coral to understand the molecular basis of reproductive timing in *Acropora gemmifera.* They were able to repeatedly take tissue samples from the same (clonal) coral over several weeks to precisely follow how gene expression in a given genotype responded to the lunar cycle. So far, such work has lagged behind in vertebrate systems, likely because of the technical and logistical constraints imposed by most (sexually reproducing) vertebrate animals. Here unisexual vertebrates offer the experimental rigor typically associated with plant and invertebrate studies, opening up new opportunities to investigate the molecular basis, particularly the epigenetic basis, of ecologically relevant phenotypic traits across the animal kingdom.

Despite their genetic similarity there is still considerable phenotypic variation within unisexual vertebrate lineages in many traits including behaviour[33], life-history[34] and morphology[35,36], suggesting epigenetic processes may be of particular biological importance in these animals. DNA methylation is perhaps the best studied epigenetic mechanism to date and unisexual vertebrates offer the ideal opportunity to disentangle its role from that of genetic variation in producing phenotypic variation. This has been exemplified with work done on *Chrosomus eos-neogaeus*, a diploid gynogenetic unisexual fish from the hybridization of the finescale dace (*C. neogaeus*) and the northern redbelly dace (*C. eos*)[37]. This species exhibits high levels of variation in methylation patterns (i.e. epi-mutations or epi-alleles) across its genome[38] and these methylation patterns correlate with environmental variables among different populations[39,40] suggesting such epi-mutations may provide a mechanism to facilitate local adaptation in the absence of genetic variation. An exciting area for future research would be to directly compare differences in epigenetic mechanisms between unisexual biotypes and their sexual counterparts to test the role of epigenetics in population persistence and adaptation. Here, gynogenetic unisexuals will be especially powerful as they must co-exist with their sexual ancestors to acquire sperm. For example, the unisexual Amazon molly (*P. formosa*) can utilize sperm from at least three other sexual molly species (*P. latipinna, P. mexicana, P. latipunctata*)[41] and thus is completely sympatric with at least one of these species across its entire range[41]. This opens up the possibility for powerful comparisons between closely related species that share half of their genome and occupy the same environments but differ in reproductive mode. One might predict that unisexual vertebrates exhibit epigenetic mechanisms that are more responsive to environmental cues compared to sexual species. Indeed, despite asexual organisms generally being considered 'evolutionary dead-ends', multiple unisexual vertebrate biotypes have persisted for hundreds of thousands[16], or even millions of years[42] suggesting that these animals may exhibit particularly flexible and sensitive epigenetic mechanisms[43,44]. Taken together epigenetic mechanisms may be especially relevant within unisexual vertebrates offering the next major step forward in understanding how animals can respond to environmental change in the absence of allelic variation.

Cue integration and development in labile traits

A key aim in developmental and evolutionary biology is to understand how animals integrate information from their genes, parents and environment to shape their phenotypes over ontogeny[45-47]. The classic quantitative genetics view is that phenotypic variation develops as a result of the combined influence of genetic and environmental variation[48]. However, a limitation of this framework is that it is largely descriptive, being unable to make mechanistic predictions about how different sources of variation result in changes to an animal's phenotype. Such a mechanistic understanding is especially important for labile traits, such as behavioral or physiological traits, which are repeatedly expressed and modulated throughout an animal's lifetime. Because of this, recent authors suggest that a complementary framework is needed that explicitly takes into account the path-dependent and iterative nature of ontogeny[46,49,50]. Indeed, there is accumulating evidence using unisexual and other isogenic vertebrates showing that even genetically identical individuals reared under essentially identical environments still exhibit considerable phenotypic variation [33,51-53]. These findings highlight how our explanations of phenotypic variation will remain incomplete if we do not explicitly consider developmental processes. In particular, models incorporating Bayesian updating mechanisms and dynamic stochastic and/or chaotic processes are well suited to explain and make predictions about how different cues should be integrated over time[45-47]. Bayesian updating models generally have three main components[46,54,55]: first, an individual's prior information, which is their naïve assessment of the environment before any experience with it; this is likely informed by cues it receives from its genes and parents. Second, the likelihood function describes the likely state of the environment given a particular cue, e.g. predator olfactory cues generally signal an increased likelihood of a risky environment. These two components are then integrated to generate the animal's posterior expectations, which can be considered their labile phenotype. This dynamic framework can therefore explain and predict how an animal's phenotype should develop dependent on genetic, parental and environmental cues.

Recent work has shown the potential of these theoretical-conceptual models in explaining and predicting development in labile traits. Stein and colleagues used threespined sticklebacks, *Gasterosteus aculeatus*, to manipulate two sources of cues: parental and personal experience with predator cues[56]. They found that sticklebacks adjust their behavior and gene expression in response to these cues non-additively with the presentation of cues as either parental or personal information generating similar phenotypic responses in the offspring[56]. Other work using *Drosophila* instead manipulated genetic and environmental cues to show that different genotypes respond to different environments in predictable ways[57]. Both studies provide support for key predictions from information integration theory but were limited in manipulating only two cue sources. Unisexual vertebrates would offer the next step forward by providing unparalleled control over all cues in three main ways. First, in addition to providing replicate individuals of the same genotype, these animals also provide the opportunity to manipulate genetic cues as all biotypes of unisexual vertebrates contain multiple lineages (genotypes). Second, unisexual vertebrates offer the opportunity to disentangle potential pre- and post-birth maternal influences. This is because all unisexual vertebrates are either egg-laying or live-bearing but with typically no parental care after birth. This means mothers have ample opportunity to interact with their young pre-birth potentially providing maternal cues to their offspring through manipulations to their offspring's gene expression (see above) and/or variation in hormonal or resource deposition[58]. Third, once the offspring are born, researchers have near complete control over early life personal experiences, which are known to be especially foundational to phenotypic development[59]. Taken together, these characteristics of unisexual vertebrates will allow researchers to substantially advance our understanding of how individuals use, value and integrate information coming from multiple sources to shape their phenotypes.

Evolutionary emergence of individual variation

A major goal in both ecology and evolution is to uncover the factors that drive and maintain between-individual phenotypic variation within populations, particularly in behavior, foraging specializations and cognition[60-63]. Much of the research in this field has been theoretical-conceptual in nature[60], and empirical evidence suggests a relationship between patterns of variation and several ecological factors such as predation risk[64,65] and social dynamics[66,67]. At least three (non-exclusive) classes of mechanisms have been proposed to translate these ecological pressures into between-individual phenotypic variation: (epi)genetic variation, cue integration over development and state-dependent feedbacks[68-70]. Unisexual vertebrates offer a step forward by allowing us to adopt a highly controlled replicate individual approach to rigorously test many of the specific hypotheses associated with these mechanisms. We have discussed above why and how unisexual vertebrates are uniquely suited for the study of (epi-)genetic variation and cue integration. Here we elaborate on how they can be leveraged to test the hypotheses associated with the idea that state-dependent feedbacks are a major mechanism underlying individual variation.

A major body of theoretical-conceptual work has been developed on understanding individual behavioral variation (i.e. animal personalities, or behavioral types) in terms of how feedbacks between behavior and state variables (e.g. metabolic rate, residual reproductive value, social positions) can generate and/or exaggerate consistent individual behavioral variation[60,71]. While correlational studies of these ideas are common, rigorous manipulative experimental tests are still rare – unisexual vertebrates are ideally suited to make such tests. For example, while not strictly unisexual, the mangrove killifish (*Kryptolebias marmoratus*) is a self-fertilizing hermaphroditic fish with multiple nearly genetically identical lineages. Edenbrow & Croft[34,72] found that different genetic lineages of this species exhibited differences in life-history traits[34] and that these traits were also influenced by environmental cues such as predation threat as predicted[72]. However, somewhat unexpectedly they found that this natural variation in life-history traits did not explain any variation in behavioral traits. This study highlights how the important next step in this research area is to firmly test for causal links between state and behavior. Testing the assumptions, and then predictions of these theories is critical: for example, whereas state variables are generally predicted to cause variation in behavior, Bijleveld and colleagues[73] used an experimental approach to show that the opposite may also be true. They manipulated the gizzard size, a major metabolic organ, of red knot birds and found no resulting impacts on individual behavior. Rather, the animal's behavior seemed to predict their gizzard size. This suggests there is a more complex interplay between state and behavior than previously expected. These relationships can be rigorously disentangled using unisexual vertebrates, for example, by experimentally manipulating individual states (e.g. body condition, early-life experience) within the same clonal lineage and then following any resulting impacts on behavior. Unisexual vertebrates are ectothermic animals, and so researchers could manipulate body size by varying the thermal regime or body fat by altering the lipid content in the animal's food, for example. Additionally, the strength and direction of feedback loops are predicted to vary based on the fitness landscape and species ecology. And so another experimental option would be to systematically vary the costs and benefits of different behaviors and/or states by presenting animals with predator cues or higher competition, for example, and investigate whether this results in increased or decreased levels of individual behavioral variation as predicted by the various theories. For example, if animals exhibit asset protection this is generally predicted to result in negative feedbacks eroding behavioral variation, though some models also suggest positive feedbacks can occur that would exaggerate individual differences[74,75]. Alternatively, state-dependent safety or starvation avoidance should increase variation among individuals through positive feedback loops[76,77]. The use of unisexual vertebrates and replicate individual approaches has the potential to revolutionize the study of individual behavioral variation by pushing it from being a field that mainly documents the presence of this variation, to one that can predict when, how and why it emerges.

Social behavior and network structure

Many animal species need to regularly interact with conspecifics and so understanding social behavior and group dynamics is of central importance in animal biology. Questions in this area relate to understanding the mechanisms that generate social behavior and social structure, and then the consequences of these collective and group dynamics on individual fitness[78,79]. A major limitation to testing these questions however is that when using non-isogenic organisms, the individuals are always (genetically) different from each other making true replication at the group level difficult. Similarly, any consequences of group dynamics and social structure on the individual will be modulated by (genetic) variation among individuals. As unisexual vertebrates exhibit a large diversity of social structures ranging from highly social and schooling fish such as the Amazon molly, to more solitary and territorial reptiles such as the whiptail lizards, *Aspidoscelis* biotypes[9], these animals provide a broad range of excellent model systems in which to study the interplay between individual phenotypes and group dynamics in a true replicate individual and group fashion.

Social networks describe and quantify the pattern of social interactions among members of a group. A major question is to understand how and why the component parts (i.e. individuals) give rise to key features of the group phenotype[80,81]? To this end, there is recent work showing the long-lasting consequences of early life experiences on later adult behavior in unisexual animals. Using the unisexual Amazon molly, Laskowski et al.[82] gave genetically identical individuals different social experiences of either winning or losing aggressive encounters in the first few months of their lives. This early-life experience nearly perfectly predicted their ability to achieve a high dominance rank in a group setting over six months later after sexual maturity. As such, these genetically identical and size-matched adult fish exhibited a reliable phenotype (dominance behavior) based exclusively on their early life experience. This raises the possibility that researchers can generate individuals with particular phenotypes allowing strong tests of how individual phenotypes and group composition affect social dynamics and network structures. Indeed, the first major test will be whether networks can be replicated and if this depends on the phenotypes of the component individuals, or on external environmental influences. Work in great tits (*Parus major*) suggest that social networks might be quite robust across contexts: Firth & Sheldon[83] were able to manipulate the social network by altering which birds could access particular feeding stations. The resulting changes in how individuals associated in a foraging context carried over to how individuals associated in a mating context. Using unisexual vertebrates, researchers could build on this to more closely investigate the mechanisms generating particular network structures. One might predict that within a given environment, a group of genetically identical individuals should reliably exhibit the same network structure. The next step would be to test how the external environment, such as threat of predation or resource availability modulates the network structure and how persistent these changes are. Using a replicate individual (and group) approach would also allow researchers to disentangle between effects driven purely by group size versus by phenotypic composition of the group. For example, in collective decision making, larger groups frequently perform better but it is often unclear whether this is caused by the group size, per se, or the fact that larger groups are more likely to harbor a high performing individual[84].

Once groups are created, the next step is to test how different network structures feedback to influence individual and group success. Social network structure is predicted to influence such processes as information (or disease) transfer and collective behaviours[78,79]. For example, Aplin and colleagues[85] tracked the spread of information through flocks of great tits by teaching only particular individuals a novel way to access food from an experimental feeder. They were then able to follow how these feeding strategies spread through the network. Unisexual vertebrates provide the opportunity to build on this work by allowing researchers to replicate and manipulate social networks, a persistent challenge in most (sexually reproducing) species. For example, testing disease transmission dynamics could be especially fruitful in unisexual vertebrates as their genetic similarity removes the possibility that some individuals may be more or less susceptible to the disease or parasite of interest. In addition, researchers could manipulate lineage (genotypic) composition within groups to explicitly test the role of genetic variation in transmission dynamics. Understanding how group structure influences individual fitness could provide valuable insights into other social dynamics such as partner choice, predator avoidance and social cohesion. Taken together, the ability to replicate groups and potentially generate individuals with desired phenotypes through careful breeding make unisexual vertebrates ideally suited for investigating questions about the causes and consequences of network structures.

Summary & conclusions

Unisexual vertebrates offer the experimental control of the traditional isogenic and cloned animal model systems with the ecological realism of a phenotypically complex naturally evolved vertebrate (Box 2). This group of animals is biologically diverse containing at least

100 biotypes exhibiting different reproductive modes, social structures and life-history strategies. Many of these species can be easily kept and bred in the lab, and can also studied under field conditions making them highly desirable as study organisms for questions in ecology and evolution. Of course, no system is without some drawbacks and unisexual vertebrates will not be appropriate for every question. The biology and ecology of the animal will ultimately determine their suitability for a specific research question and this should be carefully considered before adopting any new study system. Nevertheless, we urge researchers to consider the suitability of these amazing animals to help them rigorously test hypotheses about fundamental questions in ecology and evolution in creative and novel ways.

Table 1. General ecological characteristics of selected unisexual vertebrates. Under "Repro. Mode", H stands for hybridogenesis, G stands for gynogenesis and P stands for parthenogenesis. More complete lists of known unisexual vertebrates can be found in[6,9]

Species	**Repro. mode**	**Ploidy & ancestral species**	**Range & ecological notes**	**Ref**
Amazon molly *Poecilia formosa*	G	Diploid *P.mexicana,* *P.latipinna*	Southern Texas and Gulf coast of Mexico. Occupies small, slow-moving freshwater bodies. Highly gregarious live-bearer. Produces broods (~10-50 offspring) 2-4 times per year.	[41,86]
Topminnows and livebearers *Poeciliopsis spp.*	G, H	Diploid & triploid biotypes *P. lucida,* *P. monacha,* *P. latidens,* *P. occidentalis*	Baja coast of Mexico. Occupies small freshwater bodies in desert habitats. Likely experiences high competition during dry seasons. Highly gregarious live-bearer.	[87,88]
Spined loaches *Cobitis spp.*	G	Triploid and tetraploid biotypes *C. taenia,* *C. elongatoides,* *C. tanaitica,* *C. taurica,* *C. strumicae,* *C. melanoleuca*	Widespread across non-Mediterranean Europe. Bottom-dwelling and often buries itself in the substrate of rivers. Mostly nocturnal. Mostly solitary egg-layer. Spawns once per year.	[89-91]
Mole salamanders *Ambystoma spp.*	G, H	Several polyploid biotypes *A. laterale,* *A. texanum,* *A. jeffersonianum,* *A. tigrinum*	Around the Great Lakes region and Northeastern North America. Terrestrial in wooded areas but lays eggs in (often ephemeral) ponds. Generally solitary. Likely the oldest unisexual vertebrates (~2-4 mya)	[42,92]
Edible water frogs *Pelophylax esculentus* (formerly *Rana esculenta*)	H	Diploid & triploid biotypes *P.lessonae,* *P.ridibunda*	Widespread across non-Mediterranean Europe. Occupies (sometimes ephemeral) freshwater bodies where they lay their eggs. Biotypes often contain males (which also reproduce hybridogenetically)	[93,94]
Whiptail lizards *Aspidoscelis tesselatus* (formerly *Cnemidophorus*)	P	Diploid *A. tigris marmorata,* *A. gularis septemvittata*	Common across the southwestern US and central-northern Mexico. Occupies dry, scrublands and seems to prefer human-disturbed areas. Egg-laying. Generally solitary and diurnal.	[95,96]
Caucasian rock lizard *Lacerta armeniaca*	P	Diploid *L. mixta,* *L. valentini*	Between Black and Caspian seas (Turkey, Georgia, Armenia). Occurs in rocky forests and seems to prefer drier areas. Generally solitary. Egg-laying.	[97,98]

Figure Captions

Figure 1: Three examples of unisexual vertebrates. There are over 100 known biotypes of unisexual vertebrates, all of which are reptiles, fish and amphibians.

Figure 2: Modes of unisexual reproduction. All unisexual vertebrates reproduce without genetic recombination. Parthenogenic and gynogenetic animals produce unreduced eggs containing the complete genome of the mother; gynogenetic eggs must be stimulated with the sperm of another species (usually one of the sexual ancestral species) to begin development though the genetic material from the sperm is discarded. Hybriogenetic animals produce reduced eggs containing only half of the mother's genome, usually the maternal half. The egg is then fertilized with the sperm of another species producing a diploid offspring with a new paternal half of its genome.

Box 1 | **Examples of previous research with unisexual vertebrates**

Research on unisexual vertebrates has addressed a wealth of questions but often focusing on questions related to their nature – that is, how does (a)sexuality emerge and persist and what are its consequences for the species' ecology and evolution? To illustrate some of this breadth, here we highlight research surrounding three different unisexual vertebrates.

Aspidoscelis* whiptail lizards (formerly *Cnemidophorus)

While the phylogeny of this genus is still not fully resolved, it appears that many, perhaps up to half, of the species in this group are parthenogenic[99,100]. Previous work on this group generated the 'Balance Hypothesis' whereby successful hybridization between two sexual species requires them to be phylogenetically distant enough that normal meiosis is disrupted, but not so distant as to lead to aberrant development[101]. Many of the resulting biotypes are triploid[13], generally with two genomic complements from one ancestral species and just one from the other, though at least one biotype has genomic complements from three different ancestral species (*Aspidoscelis exsanguis*[102]). And so these lizards have been particularly useful for investigating how they resolve the genomic conflict between their different genomic complements[13]. At least one sexual species pair has been successfully bred in the lab to generate a new parthenogenetic biotype in an example of instantaneous speciation[103] offering key insights into the molecular mechanisms underlying (the lack of) recombination during meiosis[13].

***Poecilia formosa,* the Amazon molly**

As a gynogenetic animal, the Amazon molly requires sperm from one of her two ancestral species, the sailfin or Atlantic mollies (*P. latipinna, P. mexicana*) or a third closely related species (*P. latipunctata*) to stimulate embryonic development [15,41]. As such, it is completely sympatric with at least one of its host species across its entire range and has been used to investigate how species interactions can stabilize the co-existence of such asexual/sexual complexes. These sympatric species differ little in dietary preferences[104] and parasitism rates[105], and while males of *P. latipinna* and *P. mexicana* prefer to mate with their own conspecific females they will mate with the unisexual *P.formosa* especially as this appears to increase their attractiveness to their own females through mate-choice copying[106].

***Poeciliopsis monacha-lucida-occidentalis* complex**

This group consists of several hybridogenetic or gynogenetic biotypes[107]. The recurrent hybridizations between the unisexual biotypes and sexual ancestral species has resulted in considerable standing clonal diversity[108]. Vrijenhoek[109] developed the ‘Frozen Niche Variation’ hypothesis to explain how each clonal variant ‘freezes’ a combination of traits in a lineage and those lineages within the least ecological overlap with the parental species are most likely persist. This type of ‘inter-clonal selection’ or ‘clonal sorting’ offers a mechanism to explain the persistence of these asexual lineages with the sexual ancestral species and is supported from evidence from this[110] and other unisexual species[111].

Box 2 | **Potential of unisexual vertebrates in ecology & evolution research**

Unisexual vertebrates have a number of characteristics that make them ideal systems to address long-standing and emerging questions of importance in ecology and evolution: 1) individuals are genetically identical within lineages, 2) offspring typically do not require parental care after birth, 3) their genotypes are ecologically relevant as products of natural selection and 4) they are geographically, ecologically and phenotypically diverse species. In our review, we highlight how these animals can be used to break new ground in four key research areas.

Molecular mechanisms

Key advantage: Disentangle genetic from epigenetic variation

- How do epigenetic processes shape local adaptation?
- What are the temporal dynamics in expression profiles?
- Are epigenetic mechanisms more environmentally responsive in unisexual vertebrates?

Developmental processes

Key advantage: Control and manipulate sources of variation

- How do individuals integrate genetic, parental and environmental information over ontogeny?
- When and why do individuals value some types of information more than others?
- What are the mechanisms through which non-genetic maternal information transfer ccurs?

Individual variation

Key advantage: Replicate individuals

- When and how do differences in state variables generate individual differences?

- What environmental factors modulate the strength and direction of feedbacks between state and behavior?

Group dynamics

Key advantage: Replicate groups

- Do groups of genetically identical animals in identical environments develop similar social networks?
- How do environmental factors modulate network structure?
- How does network structure influence individual fitness and group performance?

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Competing interests

We declare no competing interests.

Contributions

KLL, MW and JK conceived the idea for the manuscript. KLL wrote the initital draft. All authors substantially contributed to revisions and editing of manuscript.

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