


Review

# Female alternative reproductive tactics: diversity and drivers

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It is often argued that anisogamy causes alternative reproductive tactics (ARTs) to be more common in males than females. We challenge this view by pointing out logical flaws in the argument. We then review recent work on the diversity of female ARTs, listing several understudied types such as solitary versus communal breeding and facultative parthenogenesis. We highlight an important difference between male and female ARTs that caused female ARTs to be overlooked: male ARTs tend to focus on successful fertilization, whereas female ARTs occur at many stages of reproduction and often form complex networks of decision points. We propose to study correlated female ARTs as a whole to better understand their drivers and eco-evolutionary dynamics.

## Do ARTs evolve more easily in males than in females?

**Alternative reproductive tactics (ARTs;** see [Glossary](#)) refer to discrete variations in a reproductive behavior that occur within the same sex in a population of the same species. The different variations must serve the same functional end and directly contribute to the production of offspring. Continuous behavioral variations (e.g., biased resource allocation to sons and daughters) and those that indirectly influence fitness (e.g., dispersal, infanticide, or reproductive suppression) are not considered to be ARTs. ARTs are often thought to evolve in response to intense reproductive competition and are a means for individuals who might not succeed through conventional tactics (e.g., fighting for territories or singing to attract partners) to reproduce [1]. Although in both sexes there are examples of ARTs, as well as less clear-cut variable reproductive tactics such as continuous offspring sex allocation by female ungulates [2] and different types of 'sneaker' tactics in male fish [3], the existing literature has focused on discrete ARTs in males. ARTs have been predicted to evolve more easily in males because **anisogamy** biases the intensity of sexual selection between the sexes [1]. Because there does not appear to be any theoretical work linking anisogamy to the evolution of ARTs, current literature generally relies on limited evidence to explain why ARTs may evolve more easily in males than in females [4,5]. The arguments generally follow two chains of logic: either through females investing more heavily in reproduction, leading them to have less opportunity to 'cheat', or through stronger intrasexual competition and consequent higher fitness variance in males, causing them to explore alternative ways to achieve fertilization (Figure 1, shaded arrows).

Does anisogamy necessarily lead to fewer ARTs in females because of their greater investment in reproduction? A closer examination of the proposed logic chain reveals several important caveats that undermine this common view (Figure 1, upper broken lines). For many species, egg production represents only a small proportion of the entire investment needed to produce independent offspring, and the relative contributions of the male and female parents can vary greatly across breeding stages [6]. In sex role-reversed species such as pipefishes and jacanas, males often invest more in reproduction than females. Although such cases are relatively rare in the animal

## Highlights

Alternative reproductive tactics (ARTs) are thought to be more abundant in males than in females owing to higher fitness variance in males and higher female investment in reproduction, but there are no strong empirical or theoretical studies that support this.

Whereas male ARTs tend to act pre-mating (focusing on fertilization), female ARTs can occur at various stages of reproduction (from mate finding to brood care) and form complex networks of decision points.

The evolutionary dynamics of female ARTs can be condition- and frequency-dependent, and can be influenced by factors including sexual antagonism and intralocus tactical conflict.

Evidence for female ARTs is abundant, and they are more common than is often appreciated. However, their eco-evolutionary drivers are not well understood, calling for future research.

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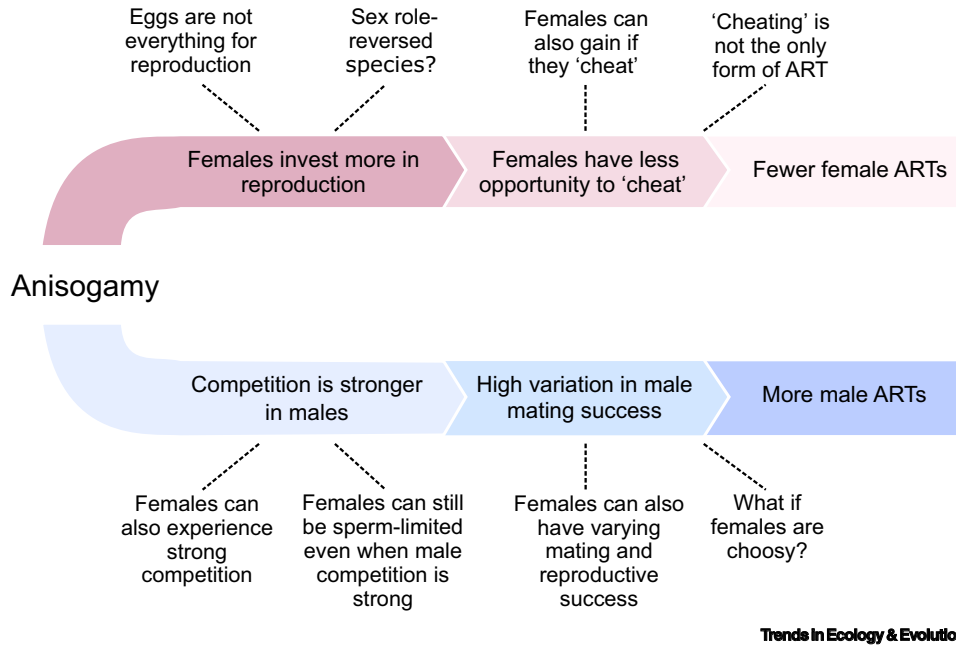
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Figure 1. An illustration of the commonly cited logic chains leading from anisogamy to fewer alternative reproductive tactics (ARTs) in females (top) than in males (bottom). We identify several caveats that deserve further investigation (indicated by broken lines and italics).

kingdom [7], it is still peculiar that we do not seem to have any examples of female ARTs in sex role-reversed species. Furthermore, because females usually invest heavily in reproduction, natural selection can favor a tactic that parasitizes the investment of others to reduce reproductive costs. Indeed, conspecific brood parasitism, where some females lay eggs in the nests of others, is abundant across taxa (e.g., the burying beetle *Nicrophorus vespilloides* [8] and many species of birds [9]) and is a well-recognized type of female ART. There are also ways other than 'cheating' that females could use to increase their reproductive fitness. For example, female striped mice *Rhabdomys pumilio* and house mice *Mus musculus domesticus* can breed solitarily or in groups [10,11].

Similarly, the argument that ARTs are more abundant in males because of stronger competition for fertilization between them does not always hold (Figure 1, lower broken lines). For example, in **lekking species**, where sexual selection on males is particularly strong, females can still be sperm-limited and compete aggressively for mating with preferred males (reviewed in [12]). Females can also suffer from sperm limitation due to cryptic male mate choice, where more sperm are allocated to high-quality females [13,14]. In a remarkable case, female triplefin blennies *Tripterygion melanurus* were observed to intrude on a mating pair and displace the spawning female to gain priority in accessing the male, resembling the 'sneaker' male tactic [15]. In addition, female competition and aggression, although often cryptic and indirect, are abundant in animals [12,16]. Substantial female reproductive skew has been found in many cooperatively breeding species where a high proportion of females have no or very low direct fitness [17]. Female mating failure because of a shortage of males has also been found in non-cooperative breeding species with conventional sex roles [18]. If high fitness variance promotes the evolution of ARTs, we should expect to find female ARTs in those species. However, theoretical work has also shown that high variance in male mating success through the conventional tactic does not necessarily lead to the maintenance of ARTs which can be disrupted by female choice and sexual conflict [19].

Given the abundant caveats in these logic chains (Figure 1), further empirical and theoretical studies will be necessary to clarify the evolution of ARTs and examine the causal relationship between differences in investment or fitness variance and the abundance of ARTs in males and females.

### Diverse forms of female ARTs

In the following we provide examples of ARTs in females, including many recent studies supporting our conjecture that female ARTs are abundant in nature but have been overlooked in the literature so far.

#### Intraspecific parasitism

Similar to the 'sneaker' tactic in males, females across diverse taxa are found to parasitize the reproductive investment of other females. For example, conspecific brood parasitism has been found in >250 avian species and is particularly abundant in **precocial** and colonial birds with female philopatry and large clutches (reviewed in [9,20]). It has also been found in the largemouth bass *Micropterus salmoides* [21] and several species of wasps [22,23]. Furthermore, female insects are known to steal resources vital for reproduction from others [24].

#### Polymorphism with distinct reproductive behavior patterns

In several species, females have genetically determined distinct morphs and associated behavioral patterns. In the fire ant *Solenopsis invicta*, the queens have two distinct morphs that are determined by a single genomic element with two variants, commonly referred to as the social B and social b chromosomes (SB and Sb) [25]. SB/SB homozygotes form single-queen colonies, SB/Sb heterozygotes form polygynous colonies, and Sb/Sb homozygotes are not viable. Another example is the white-throated sparrow *Zonotrichia albicollis*, where females have genetically determined white- or tan-colored median crown stripes. The white females are more aggressive, have higher mating rates, and provide less parental care than the tan females [26]. In the side-blotched lizard *Uta stansburiana*, females have genetically determined orange and yellow morphs, corresponding to *r*- and *K*-strategies in reproduction, respectively [27].

#### Independent mate choice versus mate choice copying

When choosing a mate, some individuals make their decisions independently, whereas others copy the preferences of others. For example, in the deer mouse *Peromyscus maniculatus*, some females copy the odor preference of other females, independently of their familiarity and kinship [28]. This type of ART has been found in both sexes but seems to be more common or better-studied in females. A recent meta-analysis containing 22 species of females (149 effect sizes) and nine species of males (14 effect sizes), including arthropods, fishes, birds, and mammals, found that the strength of copying did not differ significantly between the sexes [29].

#### Female morph versus male-mimicry

Analogous to the 'female-mimic' tactic in males, some females resemble the color pattern and morphology of males. This type of ART has been identified in >100 species of damselflies and dragonflies (reviewed in [30]). In addition, female andromorphs have also been found in several butterfly species such as the bog fritillary butterfly *Boloria eunomia*, where the gynomorphs have an advantage in daily survival and precocious emergence, whereas the andromorphs have higher fecundity, lower predation risk, and suffer less from male harassment [31]. Note that not all female color polymorphisms are ARTs. For example, the andromorph female hummingbirds resemble males to reap the benefit of reduced resource competition [32], which does not directly contribute to the production of offspring and is thus not considered to be an ART.

### Glossary

**Alternative reproductive strategies:** genetically determined rather than condition-dependent ARTs; for example the distinct male morphology and mating strategies determined by the *OB* locus alleles in the side-blotched lizard *Uta stansburiana*.

**Alternative reproductive tactics (ARTs):** discontinuous alternative phenotypes directly associated with reproduction that can be observed within the same sex in the same population (e.g., solitary or communal breeding).

**Anisogamy:** the condition in which the male and female gametes are of different sizes. The smaller gamete, a sperm cell, is produced by the male sex, whereas the larger gamete, an egg cell, is produced by the female sex.

**Intralocus tactical conflict:** similar to intralocus sexual conflict, this occurs when ARTs have different optima for traits that are genetically correlated across tactics.

**Lekking species:** in such species males provide females with no resources except gametes, male distribution is clumped in space during the mating season, and females choose males based on criteria other than territorial quality and parental care.

**Negative frequency-dependent selection:** a form of selection that occurs when rare alleles have higher fitness than common alleles. This process can maintain genetic variation within populations.

**Parthenogenesis:** a form of asexual reproduction where offspring are formed without genetic material from a male.

**Precocial:** young animals of a precocial species show a high level of maturity and typically can feed and move independently almost immediately after birth or hatching.

**Sexual antagonism:** conflict arising from traits or genes that are beneficial to one sex but harmful to the other.

### Solitary versus colonial breeding

Females can breed alone or in colonies. The behavioral choice can be genetically determined (such as the aforementioned single- or multiple-queen colonies of fire ants) or condition-dependent. For example, in the tree sparrow *Passer montanus* [33], females can shift between these two ARTs between subsequent broods within the same breeding season. These types of female ARTs have also been found in several mouse species [10,11,34].

### Facultative parthenogenesis

Some females can either reproduce sexually by fertilizing their eggs with sperm or asexually by letting their eggs develop into offspring without being fertilized. This type of ART has been found in various invertebrates [35–37], cartilaginous fishes [38–40], reptiles [41,42] and birds [43,44]. Interestingly, California condor *Gymnogyps californianus* [44] and zebra shark *Stegostoma tigrinum* [40] females have been found to reproduce by **parthenogenesis**, even when they are in regular contact with fertile males. In the remarkable case of the tropical night lizard *Lepidophyma smithii*, offspring produced in the same clutch can be a mixture of individuals produced sexually and parthenogenetically [45]. These new findings indicate that facultative parthenogenesis can be very cryptic and more abundant in nature than was previously thought. More information on the evolutionary dynamics of this female-specific ART is provided in [Box 1](#).

### Discrete sex allocation

The offspring sex ratio is usually continuous, but in some species, particularly Hymenoptera and some families of Diptera, females can specialize in producing either only sons or only daughters (reviewed in [46,47]).

The different types of female ARTs listed above are non-exhaustive, given the diverse ways in which females reproduce in nature. We list polymorphisms with distinct reproductive behavior patterns as a conspicuous type of ART, but it is important to note that, in both sexes, only a fraction of ARTs are associated with distinct morphs. For example, in the green-veined white butterfly *Pieris napi*, female monandry and polyandry are genetically determined, but the two types of females do not seem to differ in morphology [48]. In this case the distinct female mating patterns

#### Box 1. Evolutionary dynamics of facultative parthenogenesis

Facultative parthenogenesis is a special type of ART that occurs only in females. It describes any system where sexual and parthenogenetic reproduction co-occur in the same population. One type of facultative parthenogenesis is cyclical parthenogenesis, which is characterized by periods of asexual reproduction and short bouts of sexual reproduction. Examples include *Daphnia* [92], aphids [93], and rotifers [94]. The period of asexual reproduction allows cyclical parthenogenesis to quickly populate an environment under favorable conditions (e.g., in spring and summer), whereas sexual reproduction is often associated with the production of resting eggs that can survive unfavorable conditions (e.g., winter or drought). The lifespan of such species is often short such that some individuals reproduce only sexually or asexually during their entire life. In cyclical parthenogens it is crucial for females to be able to predict when the environment becomes unfavorable, and several cues are used for this purpose, such as population density [95] and day length [96]. Females differ in their responses to these environmental cues, and therefore sexual and asexual generations typically overlap.

Cyclical parthenogens have attracted much attention from both empiricists and modelers, but cyclical environments are not the only factor that can maintain facultative parthenogenesis. Another mechanism is mate-limitation: a female can fail to find a mate at low population densities. In this case, she benefits from asexual reproduction even if it produces far fewer offspring compared to sexual reproduction. For example, mate-limitation is an essential factor in mayflies [97]. The decision between sexual and asexual reproduction in species of facultative parthenogenesis can also be condition-dependent, where poor condition individuals reproduce sexually to increase genetic variation among offspring such that at least some of them might have a favorable genetic makeup. Condition-dependent parthenogenesis occurs in *Daphnia* [92] and also in species that are not cyclical parthenogens, for example in nematodes [98]. Furthermore, facultative parthenogenesis can be maintained by host–parasite coevolution because it prevents the fixation of obligate parthenogenetic lineages [99,100].

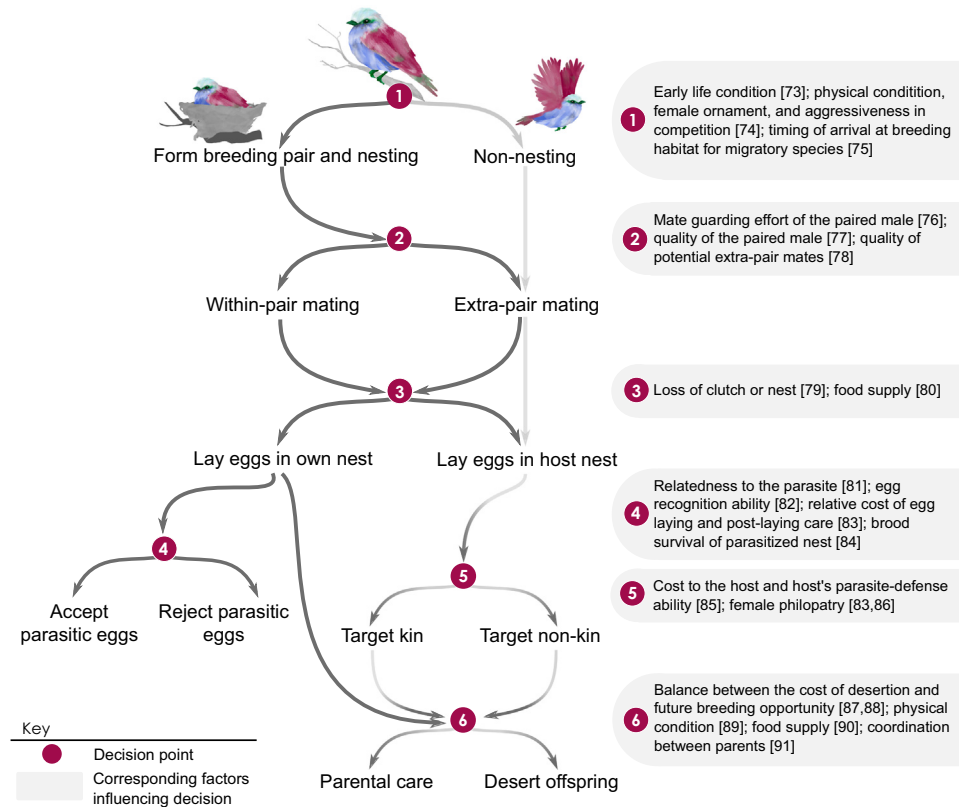
were referred to as 'alternative lifestyles' rather than ARTs. Such terminology differences across subfields could also contribute to many female ARTs remaining hidden in the literature.

### Proximate and ultimate drivers of female ARTs

The proximate and ultimate drivers of female ARTs provide insights into the immediate inducement and the long-term evolutionary causes underlying their evolution and maintenance. Studies on male ARTs have identified hormones, neuroendocrine mechanisms, and genetic and environmental interactions (GEIs) as important proximate drivers (reviewed in part II of [49]). Because males and females share a large part of their genomes, we expect that these factors also play a role in triggering the expression of female ARTs. For example, in the white-throated sparrow, ARTs in both sexes seem to be driven by changes in steroid hormone pathways caused by a chromosomal inversion [26,50]. The steroid hormones not only activate sexual behaviors that directly mediate mate choice, aggressive competition, and mating but also help to steer the development of neural and physical systems that underlie these reproductive traits. At the ultimate level, ARTs can potentially evolve whenever there is fitness to be gained by pursuing divergent reproductive behaviors, and this should also apply to both sexes. For example, large variance in breeding success through the 'conventional tactic', such as aggressive male mate competition or females laying eggs exclusively in their own nest, sets the stage for alternative tactics such as sneaky mating and conspecific brood parasitism in males and females, respectively.

Despite the similarities, the evolution and development of ARTs also have important differences between the sexes. In males, ARTs often only occur pre-mating to achieve fertilization (although other strategies such as providing parental care versus abandoning offspring are viable male ARTs in some species). Therefore, males can often be sorted into categories such as 'fighter versus scrambler', or guarder versus sneaker', etc. It is thus easier to form hypotheses and study the proximate and ultimate drivers of male ARTs, both empirically and theoretically. By contrast, female ARTs can occur in all breeding stages, thus forming a complex network of splitting and merging decision points that can be temporally intermixed. Using breeding female birds as an example (illustrated in Figure 2), although nesting and non-nesting are clear-cut female ARTs, both types of females could subsequently engage in extra-pair mating, lay eggs in conspecific nests, and/or take care of or desert their offspring. Furthermore, the ART of a female in a specific breeding activity can often be influenced by her previous behavior choices, including those that are not ARTs (e.g., whether she has experienced natal dispersal). To understand the drivers of a specific female ART it is often not useful to categorize females solely according to their ARTs at that focal event because the same behavioral choice can have different drivers. For example, conspecific brood parasitism can be caused by floater females doing the 'best of a bad job', by nesting females trying to enhance their reproductive fitness by spreading the predation risk of their offspring, or as a response to nest loss [51,52].

Some correlated female behavior patterns are genetically determined. For example, in the side-blotched lizard, female color morph, territoriality, and the number and size of eggs are determined by linked genetic components [27], and in the white-throated sparrow female aggressiveness, mating rate, and parental care investment are influenced by the same chromosomal inversion [26]. Other female behavior patterns can be correlated because their expression depends on the same aspects of individual condition. For example, in birds, physical condition (i.e., characterized by body mass, parasite load, or stress levels) not only influences the choice between nesting and non-nesting but also influences whether a female deserts her offspring or provides care. Similarly, food supply influences whether a nesting female will lay extra eggs in the nests of other females and whether she will desert her offspring (Figure 2). In many primates, dominant females often suppress the reproduction of subordinates and reduce the survival of



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Figure 2. The diverse female reproductive tactics (using birds as an example) often cannot be clearly characterized into small sets of discrete alternative reproductive tactics (ARTs), such as 'territorials' and 'sneakers' as in males, and instead comprise a complex network of decision points. Each decision point can be influenced by multiple (possibly interacting) factors, and some factors can influence multiple decision points. The list of factors influencing each decision point is not exhaustive. See refs [73–91].

their offspring by causing consistent stress through mild but repeated harassment and aggression [53]. These behaviors are not considered to be ARTs because they usually do not feature discrete alternatives, but they are indispensable for understanding the maintenance and interactions of female behavioral variations in social mammals [12,16,53].

Finally, the interactions between males and females that adopt diverse tactics are crucial in driving the evolution of male and female ARTs [5,19]. A recent study following the establishment of a spotless starling colony and its development over the following 2 years illustrates the feedback between male and female ARTs [54]. As population density and the quality of potential mates and same-sex competitors increased, more males switched from polygyny to monogamy, and the frequency of conspecific brood parasitism also increased in females.

**Evolutionary dynamics of female ARTs**

Status-dependent selection and **negative frequency-dependent selection** are the two most studied types of evolutionary dynamics that underlie the maintenance of ARTs. The former can produce ARTs in populations of genetically identical individuals. In this case the expression of ARTs is triggered by the condition of an individual instead of their genetic background. For

example, female house mice in high condition breed solitarily, whereas those in low condition breed communally and suffer from reduced pup survival [11,34]. In this case, the communally breeding females have likely been doing the 'best of a bad job' given their poor condition. Different female ARTs can also result from polymorphic genotypes and be maintained by negative frequency-dependent selection. For example, color polymorphism associated with ARTs is controlled by a single locus with female-limited expression in several damselfly and butterfly species [55–57]. The coexistence of gynomorphic and andromorphic females is proposed to be maintained by frequency-dependent selection through mechanisms such as learned mate recognition and/or male mimicry [31].

The relative importance of status-dependent and negative frequency-dependent selection has been extensively debated because the two mechanisms are based on different assumptions of the genetic basis of ARTs and have different implications for their evolutionary dynamics (reviewed in [1,58]). In short, if the determination of ARTs is purely status-dependent and not heritable, natural selection cannot act on this response. Therefore, individuals adopting different ARTs can have unequal fitness, and the frequencies of different ARTs should be independent of their relative success. By contrast, if the different ARTs correspond to different genotypes (i.e., **alternative reproductive strategies** [59]), they should be heritable and subject to natural selection. Consequently, negative frequency-dependent selection is expected to lead to a fitness equilibrium between ARTs, and their relative frequencies should be stable or oscillate in cycles. The two idealized mechanisms also respond very differently to changing environments. For example, status-dependent ARTs can be less efficient in purging maladaptive genes than ARTs maintained through frequency-dependent selection in environments that change directionally or in large steps [60].

It is important to note that these two idealized mechanisms can independently or jointly produce the same set of ARTs, such as conspecific brood parasitism [61,62]. Furthermore, the two mechanisms cannot be distinguished solely by comparing the fitness between the ARTs because status-dependent selection may also lead to equal average fitness of different ARTs when there are multiple status-dependent tactic 'switch points' [63]. Similarly, genetically controlled ARTs maintained by negative frequency-dependent selection in the long term can have large frequency fluctuations and very different fitness on the timescales amenable to empirical measurements [64]. In natural populations, the fitness of ARTs can be influenced by diverse environmental factors that change both spatially and temporally, making it even more difficult to pin down the mechanisms maintaining the ARTs over long timescales [65]. It is now widely accepted that status- and frequency-dependent selection are not mutually exclusive. For example, many ARTs seem to be threshold traits where the status-dependent 'switch point' between tactics is influenced by quantitative trait loci. For example, in female striped mice, the choice between solitary and communal breeding can be predicted from their baseline blood corticosterone levels [8], and the expression of stress hormones and stress-related genes has been found to be controlled by quantitative trait loci in various species [66–68]. Such ARTs controlled by evolving reaction norms can be captured theoretically by environmentally cued threshold models. These ARTs are simultaneously status-dependent and heritable, and can be subject to negative frequency-dependent selection (reviewed in [58]).

In addition to status- and frequency-dependent selection, the evolutionary dynamics of ARTs can also be influenced by genetic constraints, leading to **intralocus tactical conflicts** [69,70]. Analogous to the effect of **sexually antagonistic** genes that prevent males and females from reaching their sex-specific fitness optima, constraints of a shared genome can prevent ARTs from reaching their respective phenotypic optima [70]. Empirical evidence consistent with this

prediction has been found in bulb mites and swordtail fish [71,72]. All research to date on intralocus tactical conflict is, to our knowledge, focused on male ARTs. However, there is no reason to think that the phenomenon should be restricted to males, and such conflict is therefore worth considering in the context of female ARTs. Genetic constraints such as **sexual antagonism** and intralocus tactical conflict are expected to impact on eco-evolutionary dynamics and speciation, for example by altering equilibrium frequencies of ARTs among populations or by causing rapid phenotypic evolution after the loss of an ART [69].

### Concluding remarks

ARTs illustrate the variety of solutions that species have evolved to achieve reproductive success among same-sex individuals in a population. In this review we draw attention to the diversity of ARTs in females and question the widespread notion that ARTs are more common in males than females. We show that female ARTs can occur throughout the breeding cycle, often forming a network of splitting and merging points of behavioral choices. The drivers and evolutionary dynamics of ARTs have similarities and important differences between the sexes, and our understanding of how ARTs evolve in each sex is still limited.

To expand our knowledge on this important topic, we need a thorough survey of the diversity and prevalence of different types of ARTs in males and females across taxa, and the use of meta-analysis, modeling, and experiments (e.g., by removing a specific ART, changing the frequency distribution of ARTs, or varying the strength of a selection force) to clarify the driving factors and their interactions. Furthermore, the feedback between female and male ARTs and their impact on evolution needs to be studied at both the genetic and behavioral levels. Addressing the unresolved issues (see [Outstanding questions](#)) provides a starting point to fill in this knowledge gap.

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### Declaration of interests

The authors declare no conflicts of interests.

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### Outstanding questions

Which factors increase or decrease the likelihood of evolving female ARTs?

Are female ARTs more likely to be plastic or genetically determined? Is this relationship different in males?

Are ARTs more likely to evolve as a *de novo* behavior or from a continuous trait under disruptive selection? Is this different between the sexes?

Does the presence of ARTs in one sex influence the likelihood that ARTs will evolve in the other sex?

Can studying correlated reproductive behaviors as a whole help us to understand the causes and consequences of female ART choices in different breeding activities and stages?

Are there cases of intralocus tactical conflict in females? What are the roles of genetic constraints in the evolution of female ARTs?

Does the prevalence of female ARTs differ between major taxonomic groups? Does the type of mating system influence the evolution of female ARTs?

Many plants also have polymorphic reproductive organs, such as color polymorphism of the flowers. Do they serve as ARTs and share the same ultimate drivers as the ARTs in animals? Is there a sex bias regarding the diversity and prevalence of ARTs in plants?

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