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SYMPOSIUM

Sex-Differences in Phenology: A Tinbergian Perspective

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Synopsis Shifts in the timing of cyclic seasonal life-history events are among the most commonly reported responses to climate change, with differences in response rates among interacting species leading to phenological mismatches. Within a species, however, males and females can also exhibit differential sensitivity to environmental cues and may, therefore, differ in their responsiveness to climate change, potentially leading to phenological mismatches between the sexes. This occurs because males differ from females in when and how energy is allocated to reproduction, resulting in marked sex-differences in life-history timing across the annual cycle. In this review, we take a Tinbergian perspective and examine sex-differences in timing of vertebrates from adaptive, ontogenetic, mechanistic, and phylogenetic viewpoints with the goal of informing and motivating more integrative research on sexually dimorphic phenologies. We argue that sexual and natural selection lead to sex-differences in life-history timing and that understanding the ecological and evolutionary drivers of these differences is critical for connecting climate-driven phenological shifts to population resilience. Ontogeny may influence how and when sex-differences in life-history timing arise because the early-life environment can profoundly affect developmental trajectory, rates of reproductive maturation, and seasonal timing. The molecular mechanisms underlying these organismal traits are relevant to identifying the diversity and genetic basis of population- and species-level responses to climate change, and promisingly, the molecular basis of phenology is becoming increasingly well-understood. However, because most studies focus on a single sex, the causes of sex-differences in phenology critical to population resilience often remain unclear. New sequencing tools and analyses informed by phylogeny may help generate hypotheses about mechanism as well as insight into the general "evolvability" of sex-differences across phylogenetic scales, especially as trait and genome resources grow. We recommend that greater attention be placed on determining sex-differences in timing mechanisms and monitoring climate change responses in both sexes, and we discuss how new tools may provide key insights into sex-differences in phenology from all four Tinbergian domains.

Introduction

Vertebrates have evolved a variety of life-history strategies in response to seasonality that involve partitioning energetically demanding processes across the annual cycle, with reproduction often occurring when resources are plentiful (Bronson 1985; Daan et al. 1988). Additionally, many species employ strategies to mitigate predictable intervals of low resource availability and/or high thermoregulatory costs (Åkesson et al. 2017; Wilsterman et al. 2021). The seasonal timing or "phenology" of these annually recurring life-cycle events, such as migration, hibernation, reproduction, and molt, is changing in many species in response to climate change (Parmesan 2006; Renner and Zohner 2018). However, the magnitude of change varies considerably within and among species with widespread indication that phenological plasticity is a key component of resilience (i.e., the capacity of populations to absorb, resist, or recover from disturbances; Møller et al. (2008); Canale and Henry (2010); Morecroft et al. (2012)).

Populations are comprised of both males and females, yet relatively little attention has been given to the

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potential for sex-differences in phenological responses to climate change (but see Ball and Ketterson (2008); Tolla and Stevenson (2020)). This is important as sex-differences in seasonal timing may lead to differential survival or disrupted intraspecific interactions, and consequently negative fitness and population outcomes (Møller 2004). Further, many long-term studies use a single metric for assessing phenology (e.g., egg-laying), despite evidence that different control mechanisms are often used for different life-history stages (Pérez et al. 2018; Dardente et al. 2019). As such, current predictions about how climate change will alter seasonal timing may be biased by the choice of life-history stage as well as the sex for which the timing effects is being measured, and thus they may not accurately predict species- and population-level outcomes.

The effects of climate change on sex-ratios in species with temperature dependent sex determination (Janzen 1994; Honeycutt et al. 2019) or when resource needs are sex-dependent (Bowers et al. 2015; Petry et al. 2016) have been extensively studied, and these changes have been shown to have important demographic consequences (Hays et al. 2017; Valenzuela et al. 2019). Given recent reviews on these topics (e.g., Santidrián Tomillo et al. (2015); Mainwaring et al. (2017)), we will not focus on these issues here. Instead, we ask why males and females differ in their phenology and outline some of the potential consequences of sex-differences in seasonal timing. In asking this question, we apply a Tinbergian perspective to address adaptive, ontogenetic, mechanistic, and phylogenetic viewpoints (Tinbergen 1963; Fig. 1). A Tinbergian perspective offers multi-dimensional and integrative insight by articulating discrete areas from which broad questions can be approached, and thus answered. Ultimately, all four perspectives (adaptive, ontogenetic, mechanistic, and phylogenetic) are important for explaining and predicting evolution of a trait, and thus each of these pieces can inform how we assess the contribution of sexually dimorphic phenologies to population and species resilience to climate change. We also briefly describe how new methodological approaches may facilitate more targeted research and better integration across Tinbergen's four questions, providing a more holistic view of sex-dependent phenology, specifically within the context of climate change responses.

Sex vs. gender

Throughout this review, we discuss differences between the sexes. It is important to note that the term "sex" implies biological mechanism and is distinct from "gender," which is typically applied only to humans, involves sociocultural norms (Unger 1979), and encompasses how an individual self-identifies (Wood and Eagly 2015). In terms of biological sex, males are defined as the sex with smaller gametes (i.e., sperm vs. egg cells). The terminology used for sex-differences often overlaps with what is used for gender-differences, which can create misunderstanding—for example, we avoid use of the term masculinization to refer to phenotypic changes that are characteristic of the male sex, even though this use is common, because this term is also frequently used to characterize behaviors that are culturally identified as belonging to males in humans (Hayssen and Orr 2020). Further, we acknowledge sex is not binary (nor is gender) and intersex conditions are common in the natural world (Bahamonde et al. 2013; Adolfi et al. 2019). For example, hermaphrodism, in which an individual simultaneously has functional female and male reproductive organs is particularly common in fishes (Avise and Mank 2009; Erisman et al. 2013), as is sex-reversal, in which an animal changes sex during its lifetime (Baroiller and d'Cotta 2016). For the purposes of this review, however, we restrict our discussion to differences between biological males and females and do not focus on intersex or hermaphroditic individuals. It has also been argued that the term "gender" can be applied beyond humans in reference to the morphology, behavior, and life-history of a sexed body, with sex classified with respect to the size of gamete it produces (Roughgarden 2004). Although we agree that not all members of a sex behave in the same way and that traits such as morphology and behavior can frequently overlap between the sexes (i.e., the distribution of traits should not be ignored even when the means differ), we do not use the term "gender" to describe differences in traits within a sex because the term is linked to human stereotypes and culturally determined role expectations. Nevertheless, frequency- and status-dependent selection can lead to alternative phenotypes within the sexes (Gross 1996), and this is important as selection pressures on phenology can vary between different life-history strategies within the same sex (Koch and Narum 2021).

Sex-differences in seasonal timing—*adaptive significance*

Sex-differences in timing of seasonal life-history events likely co-evolved with mating and parental care systems, whose basis can be traced to the interacting forces of sexual and natural selection. For example, many vertebrate taxa feature male-male competition, female mate choice, and female-biased parental care. Anisogamy creates a permissive environment for sexual selection to lead to mating and parental care systems with these attributes because males produce more gametes per capita

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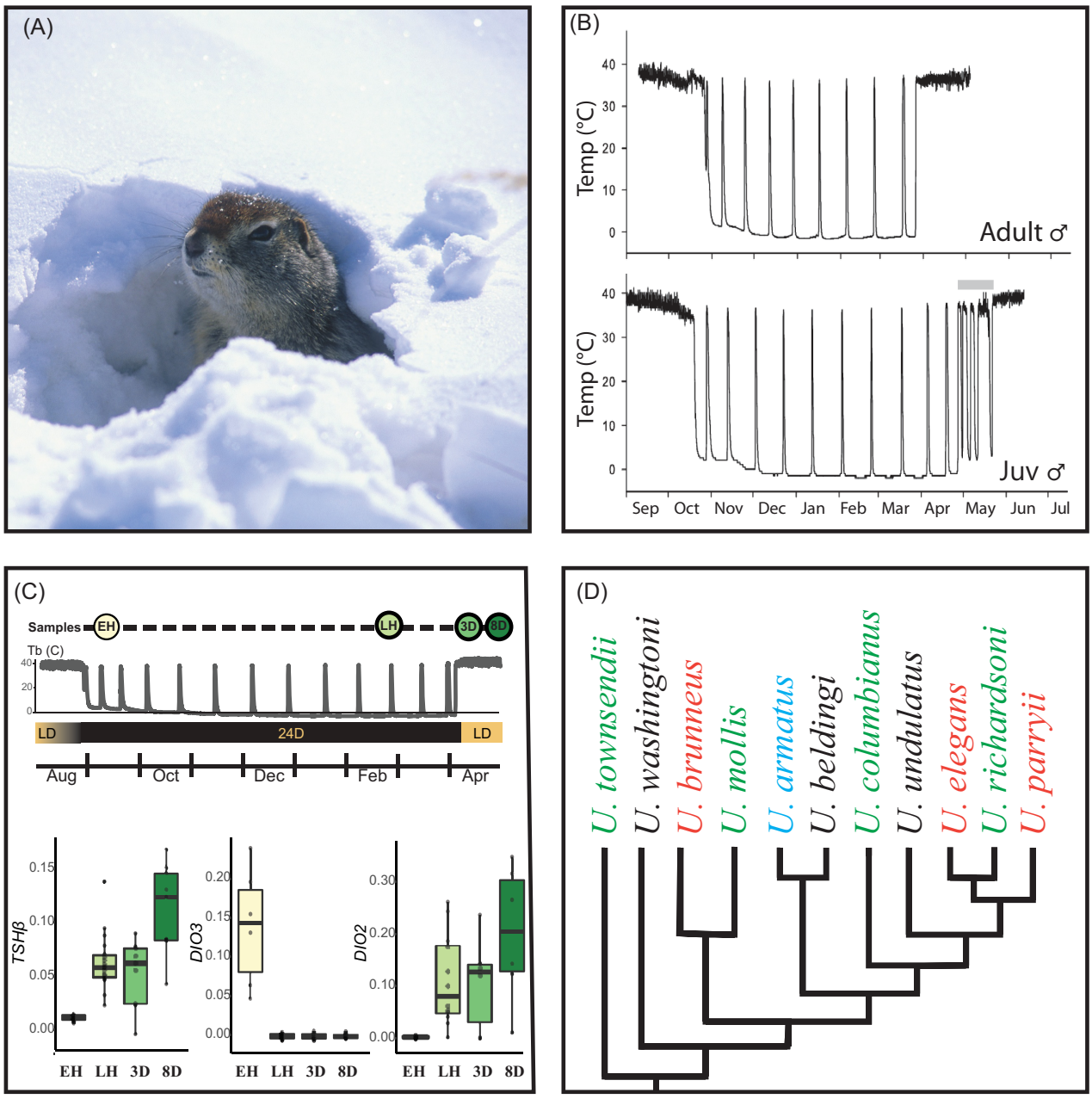

Fig. 1 Sex-differences in phenology from the standpoint of Tinbergen's four questions in one species, the arctic ground squirrel. (**A**) Adaptive value—male ground squirrels end hibernation early so that they can undergo gonadal development and spermatogenesis in preparation for the mating season, which begins shortly after females end hibernation (Sheriff et al. 2010). (**B**) Ontogeny—adult males initiate hibernation later and terminate hibernation earlier than juvenile males that do not become reproductively competent. Juvenile males also exhibit plasticity in the termination of hibernation (region below gray bar) in response to inclement weather (Williams et al. 2017). In contrast, juvenile females enter hibernation later than adult females but terminate hibernation at approximately the same time. (**C**) Mechanism—although the exact trigger for the termination of hibernation remains unclear, it has now been shown that expression of TSH-β in the pars tuberalis increases across hibernation, along with changes in deiodinase expression in tanycytes, leading to increased availability of T3 in the hypothalamus and activation of the reproductive axis. Although the reproductive axis is activated in both sexes, neuroendocrine changes are more pronounced in females compared to males (Chmura et al. 2022). (**D**) Phylogeny—sex-differences in timing may reflect evolutionary history. However, within the genus *Urocitellus*, a phylogenetic signal for sex-differences in hibernation onset is unclear—in some species males initiate hibernation earlier (green), whereas in other species the onset in males is simultaneous (blue) or later (orange) than females [black = no data]. Data for panel (D) from Alcorn (1940); Knopf and Balph (1977); Rickart (1982); Fagerstone (1988); Young (1990); Michener (1992); Sheriff et al. (2010); Goldberg and Conway (2021). Photo in panel A by Øivind Tøien, used with permission

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than females and these abundant male gametes compete for access to female gametes (Kokko and Jennions 2003). Sexual selection and competition cause higher paternity uncertainty (increasing costs of paternal care) and this, in combination with nonrandom variance in mating success for males, increases the benefits of seeking additional mating opportunities for males (reducing benefits of investing in the current brood; Kokko and Jennions 2003). While anisogamy is an important player in the evolution of mating and parental systems, it is not the only factor that matters, and this is important for understanding the diversity of mating and parental care systems. Survival costs to the competing or the caring parent can augment or minimize sex-role divergence promoting either uniparental or biparental care (Kokko and Jennions 2008). Abundant food availability for provisioning young may be a pre-requisite for uniparental (especially male) care (reviewed in Safari and Goymann (2021). Additionally, when females prefer males that exhibit care (e.g., Forsgren et al. (1996)), when paternal care presents minimal limits on mating opportunities (Gross and Sargent 1985), and/or when paternal care creates opportunities to ensure paternity (e.g., egg guarding in systems with external fertilization; Kvarnemo 2006; Kahn et al. 2013), male-biased care may be favored. Ultimately, the type of mating and parental care activities that males and females engage in shape the reproductive opportunities and survival costs they experience across their lifetime. When males and females face different reproductive opportunities and survival costs, sex differentiation in seasonal timing of key life-history events may co-occur.

There is enormous selective pressure on seasonal timing to ensure offspring production and survival. A large body of theory and empirical work has evaluated the optimal timing of hatch and lay under different resource regimes and developmental trajectories (Perrins 1970; Drent 2006; Verhulst and Nilsson 2008). However, in many systems, there are asymmetries in exactly when males and females invest resources into reproduction. In species where one sex competes for access to mating opportunities, energetic investment from the competing sex may be particularly high during mate competition in the pre-breeding and breeding period. In contrast, in systems with highly sex-biased parental care, the sex that must gestate, brood, or provision young may experience high energetic costs later in the reproductive season. For example, the highest energetic costs to male red deer (*Cervus elaphus*) occur during the fall rut (Yoccoz et al. 2002), while females incur the greatest costs during lactation in spring and summer (Clutton-Brock et al. 1989). These differences can also affect other life-history transitions—in species without paternal care, males sometimes migrate to wintering grounds, molt, and/or hibernate earlier than females (Fig. 2). Males may also devote considerable time during the non-breeding season to acquire food/energy stores in preparation for episodes of intense male–male competition (Kenagy et al. 1989) or simply to fuel gonad development and spermatogenesis (Williams et al. 2014a). The opposite relationship is expected in animals like the black coucal (*Centropus grilli*), in which females aggressively defend territories and only males incubate and provision young (Goymann et al. 2017). When sex biases in competition and parental care co-occur, we might predict that this would lead to a system in which there is sexual conflict, with one sex favoring optimization of early breeding activities and the other optimizing timing of later parental care activities. Some echidna (*Tachyglossus aculeatus setosus*) populations have evolved a unique solution to this conflict: females can re-enter hibernation after being impregnated by early emerging males and this delay allows females to push back parental care and invest in offspring at a more energetically favorable time of year (Nicol et al. 2019). More generally, the evolution of sperm storage and delayed implantation in vertebrates with internal fertilization allows them to temporally separate mating from conception (Orr and Brennan 2015). Sex-differences in the seasonal patterns of energy storage and expenditure for reproduction, along with sex-differences in time devoted to reproductive and parental behaviors, shape the timing and sequence of other life-history events (Fig. 2).

These energetic drivers of sex-differences in seasonal timing are intimately connected with sexual selection. Indeed, a recent review notes that sexual selection is an understudied and underappreciated force that may drive seasonal timing decisions (Hau et al. 2017). In many migratory bird species, males arriving on the breeding grounds must compete with each other to secure high-quality territories because territorial quality is associated with access to high quality mates (see Kokko et al. (2006) for a discussion of the roles of territory acquisition and mate opportunity). As a result, many (but not all) of these species exhibit protandry, in which males arrive on breeding grounds prior to females (Morbey and Ydenberg 2001). Similarly, male ground squirrels terminate hibernation before females, likely due to their polygynous mating system and scramble competition for access to territories and defense of associated females (Lacey et al. 1997; Lacey and Wieczorek 2001; Williams et al. 2014a). It is interesting to note that sex-differences in seasonal timing, once extant, may strengthen sexual selection by increasing the potential for mate monopolization—if females become available for mating opportunities asynchronously and males can readily mate with multiple females in sequence, this will reinforce the bene-

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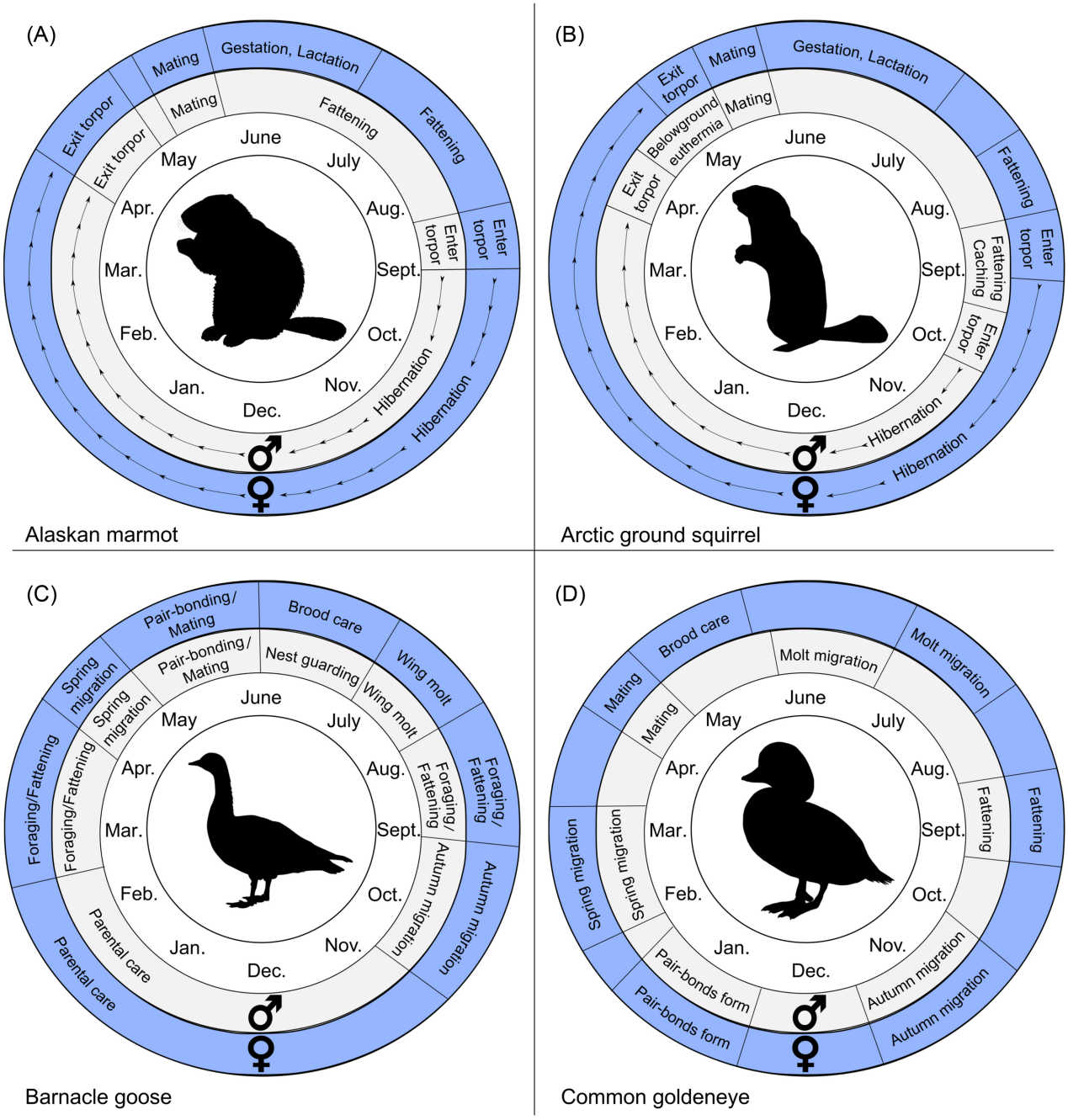

Fig. 2 Sex-differences in annual phenology between closely related rodents and closely related birds: Alaskan marmot (*Marmota broweri*) (**A**) vs. arctic ground squirrel (*Urocitellus parryii* (**B**); Barnacle goose (*Branta leucopsis*) (**C**) vs. common goldeneye (*Bucephala clangula*) (**D**). Unlike arctic ground squirrels, which are solitary hibernators and exhibit sex-differences in the timing and duration of hibernation, Alaskan marmots live in family groups throughout the year, including their near 8-month hibernation season. This promotes synchrony between the sexes in torpor entrance and exit for Alaska marmots (Lee et al. 2009, 2016). Female arctic ground squirrels fatten immediately after weaning during a relatively short window immediately prior to entering hibernation, whereas males delay fattening and entry as they store a food cache that will be used during below-ground euthermy in the subsequent spring (Williams et al. 2011, 2012; Sheriff et al. 2013). Barnacle goose and common goldeneye are both long distance migratory waterfowl that time reproduction so that chick growth and development coincides with the annual peak in resource availability. Barnacle geese are monogamous, exhibit biparental offspring care, whereas common goldeneye only display maternal care (Pöysä et al. 1997; Jonker et al. 2011). These differences in parental care strategies lead to sex-differences in molt migration timing of common goldeneye that precedes fattening and the autumn migration (Jehl 1990; Eadie et al. 1995); barnacle geese exhibit biparental care and greater synchrony in life-history timing as they travel to wintering grounds as a family group (Owen and Black 1989; Black 2001)

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fit of males competing for the earliest arriving females (Emlen and Oring 1977; Kokko et al. 2012).

The studies above indicate that the sexes can diverge in timing to accommodate their own energy requirements, while still managing to maintain sufficient synchrony for successful fertilization to occur. However, rapid climate change presents a challenge to this—for example, in Richardson's ground squirrels (*Urocitellus richardsonii*), it was recently shown that a heatwave in spring led to earlier breeding by receptive females while the majority of males still had nonmotile sperm and were not yet physiologically capable of fertilizing eggs (Kucheravy et al. 2021). This climate-driven mismatch between the sexes likely occurred because the process of sexual maturation requires several weeks of post-hibernation euthermia in male ground squirrels (Barnes 1996), and thus males were likely physiologically incapable of accelerating this process sufficiently to align their timing with females that can breed within days of terminating hibernation. Thus, we anticipate that the persistent advancement of spring under climate change may result in selection on earlier phenology in male ground squirrels, and in other species that experience similar phenological shifts.

Sexual selection can also interact with natural selection to shape sex-differences in seasonal timing. A classic example of interacting selection forces and sexual dimorphism in seasonal timing comes from the rock ptarmigan (*Lagopus mutus*): females undergo an early spring molt from white-plumage to mottled brown to minimize predation risk as snow melts, however, males delay plumage molt, perhaps because the brilliant white feathers serve as a signal to potential mates (Montgomerie et al. 2001). Similarly, the degree of migratory protandry is predicted to vary inversely with environmental severity: when the environment becomes more severe, the survival costs to the earliest arriving males increase, which favors a shift to less extreme sexual differentiation in arrival (Kokko et al. 2006).

Sex-biases in investment in mating and parental care can also be associated with differential timing of post-breeding life-history stages. In many (but not all) ground squirrel species, males begin pre-hibernation fattening while females are still lactating, which allows them to enter hibernation sooner (Michener 1998). Sex-differences in breeding trade-offs between parental care and self-maintenance are also seen in the hooded warbler (*Setophaga citrina*). Male warblers typically begin molt about 16 days earlier than females and early molt in males is associated with nest desertion (Mumme 2018). Males that desert do not appear to lose the reproductive benefit of survival of the current brood to fledge; females whose partners desert compensate by doubling provisioning rates and nest survival rates are similar regardless of uniparental desertion (Harrod and Mumme 2021). While the exact benefits of desertion by males are unclear, it may be driven by the energetic costs of molt, the difficulty of male foraging during heavy molt, and/or the potential for increased selective pressure on males to migrate early and acquire a high quality wintering ground territory (Mumme 2018; Harrod and Mumme 2021). It is difficult to assess whether sex-differences in migratory timing are widespread in autumn, as autumn migration is less studied than spring migration. Although it has been suggested that protogyny (females first) may be common in fall migration (Mills 2005), other studies indicate substantial variation among species in whether protandry, protogyny, or no sex-differences are observed (e.g., Mueller et al. (2000); Jarjour et al. (2017)). Sex-differences in the phenology of fall migration may be influenced by geographic differences in where males and females overwinter (Nolan and Ketterson 1990)—this is important as climate change has been shown to have differential effects on long-distance vs. short-distance migrants (Jenni and Kéry 2003). These cases show that seasonal timing, while strongly influenced by reproductive demands, is also shaped by energetic demands imposed by other life-history events that promote self-maintenance and survival (McNamara and Houston 2008).

Sex-differences in seasonal timing—*ontogeny*

The consideration of ontogenetic effects is often overlooked in phenological studies. However, given the potential for climate change to disrupt trophic interactions and alter the environment experienced by offspring, it deserves further attention. This is particularly true when considering that species interactions change over the lifetime of an organism and are strongly affected by ontogenetic stages of the interacting species (reviewed in Yang and Rudolf (2010)). Young predatory fishes, for example, may compete with species that subsequently become prey following ontogenetic niche shifts (Sánchez-Hernández et al. 2017). The environment experienced by offspring can also profoundly affect development, influencing reproductive maturation and altering seasonal timing. For example, food (Vincenzi et al. 2013) and parental care (Charpentier et al. 2008) have been shown to alter age at maturity, and these effects can differ depending on sex. Higher paternal care (grooming and carrying), for example, is associated with delayed sexual maturation in female marmosets (*Callithrix Geoffroy*), but advanced maturation in males (Huffman et al. 2017).

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In many species, natural and sexual selection on body size differs between the sexes, which leads to sexual size dimorphism. Because the larger sex often takes longer to develop (Kell and Bromley 2004; Zhang and Lu 2013; Auttila et al. 2016) and seasonal timing often differs between reproductively mature and immature individuals, sex-differences in seasonal timing vary with age or developmental stage. Sex-differences in the timing of molt in pinnipeds, for example, depends on age because, in many species, females mature at a younger age than males (Ling 1969). Additionally, the magnitude of the ontogenetic shift in molt timing can also differ between the sexes (Daniel et al. 2003). Similarly, differential migration and sexual segregation in sexually dimorphic northern elephant seals (*Mirounga angustirostris*) develops during puberty, when growth rates of males are substantially greater than those of females (Stewart 1997).

While this review is focused on sex-differences in phenology, it is important to acknowledge that all males and females are not the same. For example, differential seasonal timing may be common for members of the same sex that are employing alternative mating tactics or exhibiting extreme phenotypic variation. In Chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*), and coho salmon (*O. kisutch*), high juvenile growth rates in males promote the transition to an alternative reproductive phenotype (i.e., a "jack") that matures earlier and at a substantially smaller size than non-jack males from the same population (Berejikian et al. 2011). Importantly, responses to climate change can also vary depending on these mating tactics. In sockeye salmon, jacks are migrating earlier in response to climate change whereas non-jack sockeye are migrating later in the year (Kovach et al. 2013).

While sex-differences in seasonal timing can emerge during the transition from juvenile to adult stages, there are also well-described shifts in phenology after individuals reach sexual maturity, although data on sex-differences in age-effects appears to be relatively limited. In birds and mammals, "prime" age animals that have the highest reproductive success often breed earlier than younger animals and older individuals (McCleery et al. 2008; Williams et al. 2014b; Saraux and Chiaradia 2021). In one of the few studies to investigate the effects of aging on phenology and reproductive traits in both sexes, Nussey et al. (2009) found that while male red deer (*C. elaphus*) exhibited much more rapid age-related declines in annual breeding success than females, the pattern was reversed for phenological traits: older females gave birth later than younger females, but antler phenology in sexually mature males exhibited little to no change with age.

Sex-differences in seasonal timing—*mechanisms*

The brains of males and females differ in their structure and function (McCarthy et al. 2012), and this sexual dimorphism likely underlies some aspects of sex-differences in seasonal timing. Sex-differences in the brain are due, in large part, to organizational actions of hormones during development and from activating effects of hormones at subsequent life-stages (Phoenix et al. 1959; Wade 2011; Maekawa et al. 2014). Organizational effects are driven principally by hormones released from the gonads during critical perinatal windows that alter the developmental trajectory of peripheral and central tissues, leading to irreversible sex-differences in morphology, physiology, and behavior. In contrast, activational effects, which are also often driven by steroid secretion from the gonads, lead to sex-specific phenotypes that are transient and reversible (Adkins-Regan 1983; Remage-Healey and Bass 2007). Although gonadal hormones are critically important drivers of sex-differences in physiology and behavior, genes on sex chromosomes acting within cells in the brain also contribute to sex-differences in cellular function and behavior (Agate et al. 2003; McCarthy et al. 2012). Here, we provide a brief overview of how organizational and activational effects result in sexual differences in neurobiology and behavior. Although significant effort has gone into delineating the mechanistic basis of sex-differences in mating behavior and social behavior, far less attention has been placed on describing the mechanisms that underlie sex-differences in seasonal timing—we, therefore, describe what is known regarding the mechanisms that underlie seasonal timing and sex-differences in regions of the brain that are critical to timing. Finally, we discuss how the sexes may differ in their sensitivity to the proximate cues that influence seasonal timing.

Sex-differences in the endocrine environment early in life lead to sexual differentiation in cellular and structural attributes of the brain and, consequently, distinct sex-specific behaviors during later life-history stages. For example, the timed release of testosterone from the gonads is critically important for developing male prenatal neural circuitry and abolishing female circuitry in rodents; lack of a testosterone surge leads to a female phenotype in the central nervous system (Phoenix et al. 1959; Wallen and Baum 2002). Aromatases in the brain convert testosterone to estrogen, which triggers development of a central male phenotype (McCarthy 2010). In rodents, the ovaries are quiescent during these early life-stages and the female brain appears to be prevented from acquiring male circuitry by α-fetoprotein, which binds estrogens with high affinity (Bakker and Baum 2008). Far less research has been conducted on organi-

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zational effects of ovarian steroids in female mammals (McCarthy et al. 2012). However, estradiol appears to trigger the development of some female circuitry in the brains of rodents weeks after birth (Bakker and Braum 2008), and we now know that organizational effects also occur in pubertal and adolescent life stages (Schulz et al. 2009). In contrast to mammals, avian brains (specifically Galliformes) appear to switch from a male phenotype to a female phenotype with perinatal exposure to ovarian estrogens (Maekawa et al. 2014). Organizational events are more difficult to identify in fish due to their high levels of plasticity in neural circuitry; this may be linked to widespread sexual plasticity, the ability of individuals to change phenotypic sex, in the teleost lineage (Rosenfeld et al. 2017).

While organizational effects during development can lead to sex-differences in the anatomy, circuitry, and cellular make-up of the brain (McCarthy 2010), sex-differences may also stem from activational effects during adulthood. One clear example of how gonadal steroids can alter seasonal timing comes from studies of ground squirrels, which have demonstrated that testosterone secretion late in hibernation causes males to end hibernation weeks earlier than females (Barnes et al. 1988; Williams et al. 2014a). Testosterone also likely plays a role in protandry, with exogenous testosterone leading to earlier migratory preparation in songbirds (Tonra et al. 2011). Surprisingly little is known regarding the importance of sex-steroids on timing in females.

While substantial progress has been made in identifying the mechanistic basis of sex-differences in behavior, much of this ongoing work is focused on mating behaviors and social behaviors, rather than on sex-differences in life-history timing. Although sex-differences in seasonal timing systems are understudied, the systems themselves are relatively well-described and we briefly review major components before highlighting preliminary findings about sex-differences. In mammals, light enters the eye and entrains circadian clocks within the suprachiasmatic nucleus (SCN) of the hypothalamus. The SCN, in turn, controls the rhythmic production of melatonin, which is secreted in the dark period (Stehle et al. 2003). This melatonin signal is subsequently decoded by circadian clocks in the pars tuberalis (PT) of the pituitary gland (Prendergast et al. 2013). Specialized TSH-secreting thyrotroph cells in the PT are a critical target for melatonin action, and, under long days, are stimulated by the short duration melatonin signal (Dupré et al. 2010; Wood et al. 2015). In non-mammalian vertebrates, light acts on extra-retinal photoreceptors, the melatonin signal appears unnecessary for seasonal photoperiodic responses, and the functional connections between extra-retinal photoreceptors and circadian clocks are unclear (Perez et al. 2019). However, these divergent photosensory mechanisms reconverge in the PT (or saccus vasculosus in fish) where TSH triggers changes in hypothalamic deiodinase expression, leading to increased availability of triiodothyronine (T3), the most biologically active form of thyroid hormone (Hazlerigg and Loudon 2008; Nakane et al. 2013). This retrograde TSH/Deiodinase/T3 signaling pathway regulates annual cycles of energy intake, storage, and expenditure in seasonal species (reviewed by Helfer et al. (2019)). Further, the increase in hypothalamic T3 activates the hypothalamus–pituitary–gonadal (HPG) axis in long-day breeders, likely via changes in the neuropeptides kisspeptin (KISS) and gonadotropin inhibiting hormone (GnIH or the mammalian ortholog RFRP3), leading to reproductive maturation (Yoshimura et al. 2003; Henson et al. 2013; Simonneaux 2020). Melatonin from the pineal also acts via an anterograde route that controls prolactin release from lactotrophic cells in the pars distalis; prolactin regulates seasonal molt and coat color change (Dardente et al. 2019).

Most studies on seasonal mechanisms utilize a single sex (typically males) and this has hampered progress in understanding the mechanistic basis for sex-differences in seasonal timing. Nevertheless, circadian systems exhibit pronounced sexual dimorphism (Bailey and Silver 2014; Yan and Silver 2016) and given their role in transducing photoperiodic signals (see above), this may underlie sex-differences in seasonal timing. In support of this, correlations have been found between polymorphisms in clock-associated genes and phenological metrics and these correlations often differ between the sexes. In barn swallows (*Hirundo rustica*), females bearing a rare allele of the *Clock* gene with the largest number of C-terminal polyglutamine repeats reproduce and molt later; the number of polyglutamine repeats has no effect in males (Caprioli et al. 2012; Bazzi et al. 2015). Similarly, in female blue tits (*Cyanistes caeruleus*), individuals with a *Clock* gene allele with fewer polyglutamine repeats breed earlier (Liedvogel et al. 2009). Conversely, in willow warbler (*Phylloscopus trochilus*) the *Clock* paralog *Npas2* predicts spring migration date in males but not females, with more polyglutamine repeats leading to earlier migration (Bazzi et al. 2017). Similar polymorphisms exist in salmonidae clock-associated genes, and they explain differences in run timing (O'Malley et al. 2013; Madsen et al. 2020) and offspring spawning date (Leder et al. 2006). Although much of the evidence for genetic effects on timing comes from targeted gene approaches, the rapid expansion of whole genome sequencing now allows for the association of specific genetic variations with seasonal chronotypes using genome wide association scans (e.g., Grabek et al. (2019)).

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Sex steroids also have well-described effects on circadian function (reviewed in Bailey and Silver (2014); Yan and Silver (2016)), and this may be a mechanism that drives sex-differences in seasonal timing. A key feature of circadian clock systems is the presence of sex steroid receptors, namely estrogen receptors (ER) and androgen receptors (AR), on neurons of all regulatory components (i.e., the neural inputs, SCN, and neural outputs; Bailey and Silver 2014). Clear sex-specific differences exist in the density of ARs and ERs in the SCN (Fernández-Guasti et al. 2000; Vida et al. 2008). Sex-differences in the expression of other critical clock-associated genes—such as arginine vasopressin (AVP), have also been shown (Zhou et al. 1995; Hofman et al. 1996; Mahoney et al. 2009; Krajnak et al. 1998). Finally, differences in timing between the sexes may also be a function of sexual dimorphism in the neural circuits driving GnRH secretion (reviewed in Kriegsfeld and Silver (2006); Semaan and Kauffman (2010)).

Sex-specific differences in phenology can also arise due to differential responses to a variety of non-photic proximate cues that are used to modulate seasonal timing (Simmonds et al. 2019). Biotic and abiotic cues, such as food availability, social interactions, and temperature, provide supplementary information that synchronizes seasonal physiology with environmental conditions (Ball and Ketterson 2008; Chmura et al. 2020; Tolla and Stevenson 2020). In mammals, for example, nutritional deficits reduce the expression of TSHβ expression in the PT and KISS expression in the hypothalamus (Castellano et al. 2005; van Rosmalen and Hut 2021). Birds lack a functional kisspeptin system (Pasquier et al. 2014) and, instead, effects of food restriction on the reproductive axis may occur through modulation of GnIH (Valle et al. 2015; Wilsterman et al. 2020); however, sex-differences have rarely been quantified (Davies and Deviche 2014). In wild-type zebrafish (*Danio rerio*), females exhibit greater sensitivity to food deprivation, both in the neural circuits that regulate appetite and in their interaction with the reproductive axis (London and Volkoff 2019). Social cues are also important, as they can synchronize clocks between mating pairs and across social groups, especially during reproduction (Helm et al. 2013). Reproductive initiation and termination may differ in males and females due to sex-specific responses to social cues (Runfeldt and Wingfield 1985; Silverin and Westin 1995; Watts et al. 2016). In European starlings (*Sturnus vulgaris*), for example, social cues regulate reciprocal switching of hypothalamic DIO2/DIO3 expression and the timing of final follicle maturation (Perfito et al. 2015). Social cues have also been studied extensively in sheep, where exposure to a ram or the odor of a ram stimulates the HPG axis in females and promotes estrus (Hawken and Martin 2012; Fabre-Nys et al. 2015). Similarly, while the arrival timing of male breeding toadlets (*Pseudophryne coriacea*) is determined by rainfall, female arrival appears to be insensitive to abiotic cues and instead cued by the onset of male vocalizations (O'Brien et al. 2021). Sex-differences in temperature sensitivity could be critically important to mediating responses to climate change, although the mechanisms that underlie thermal sensitivity are understudied (Caro et al. 2013; Chmura and Williams 2022). We know that temperature can alter TH signaling in the brain of fish, birds, and mammals (David and Degani 2011; Levy et al. 2011; Shahjahan et al. 2013, 2017; Trivedi et al. 2019; Renthlei et al. 2021; van Rosmalen and Hut 2021), which shapes seasonal reproduction and physiology. However, in most cases we lack direct comparisons between the sexes. Thus, while differences between males and females in sensitivity to environmental cues has the potential to drive sex-differences in phenological responses, and potentially even mismatches between the sexes (Williams et al. 2017; Kucheravy et al. 2021), experiments designed to compare the sexes directly are lacking. Further, recent advances in sequencing technology now permit single-cell RNA sequencing ($scRNA_{seq}$) approaches, which will facilitate investigations linking differences in timing to sex-specific cellular specialization (e.g., Welch et al. (2019)).

Sex-differences in seasonal timing—*phylogeny*

Phylogenetic perspectives are useful for answering two broadly connected questions about the evolution of sex-differences in timing: (1) How "evolvable" are sex-differences in timing, meaning how rapidly or easily do sex-specific phenologies evolve? (2) What is the genomic or genetic basis of evolved sex-differences in timing? Whereas the former question can help us understand the phylogenetic inertia and selection pressures that lead to sex-differences in phenology (or prevent it), the latter speaks to the functional basis of these differences and their convergence among lineages (i.e., does the evolution of sex-differences in phenology across lineages use similar or unique genes and/or alleles?). Together, the answers to these questions can provide insight into lineage-specific evolutionary inertia or constraints on these traits and may allow the field to generalize about or predict how sets of traits may respond to climate change (Davis et al. 2010).

Few studies to date have addressed questions about the evolution of sex-differences in phenology using a phylogenetic framework. For those studies that do exist, phylogenetic models have primarily been used to control multi-species correlations between sex-differences in timing and other traits of interest (e.g., protandry and

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sexual dimorphism) that appear due to common descent rather than some other evolutionary process. In these types of analyses, the intensity of the phylogenetic signal (often Pagel's λ (Pagel 1999) or Blomberg et al.'s *K* (Blomberg et al. 2003)) may also provide clues as to the degree to which common descent constrains evolution of phenological traits. For example, Saino et al. (2010) use phylogenetically controlled models to differentiate among competing hypotheses to explain the degree of protandry in songbirds, and their estimate of Pagel's λ suggests that common descent has little to no effect on sex-differences in timing. Unfortunately, Saino et al. (2010) remains a unique instance in which the strength of phylogenetic signal underlying sexual dimorphism in phenology is reported. Whether sex-differences in timing are likely to be dominated by common descent across lineages and traits thus remains a relatively open question.

Nonetheless, phylogenetic signal can be predicted to some degree based on the type of trait being investigated. Among vertebrates, life-history traits (e.g., migratory timing, sexual dimorphism, and incubation duration) and physiological traits (e.g., critical thermal maxima or metabolic rates) tend to contain high phylogenetic signal (Freckleton et al. 2002; Blomberg et al. 2003; Végvári et al. 2010), whereas behavioral traits (e.g., daily movement distance or display characteristics) tend to have a lower phylogenetic signal (Freckleton et al. 2002; Blomberg et al. 2003). Considering that sex-differences in timing are often intimately connected to a species' life history and annual schedules, we might expect the phylogenetic signal in comparative analyses of sex-differences in timing to be substantial. Consistent with this expectation, large-scale analyses looking at climate-induced shifts in breeding of boreal birds and seabirds find that the capacity to shift timing is substantially constrained by phylogeny (Descamps et al. 2019; Hällfors et al. 2020). However, these results contrast with the relatively low estimate of phylogenetic signal reported by Saino et al. (2010) for protandry in songbirds. This contrast could reflect differences in the "evolvability" of protandry relative to shifts in timing more generally, or they could reflect misestimates of phylogenetic signal. Because *a priori* reasoning and some empirical tests suggest that phylogenetic constraint or inertia is high for phenological traits, common descent should be considered an important variable to estimate when testing hypotheses about the evolution of sex-specific phenologies.

Inferring evolutionary mechanisms by controlling for or excluding phylogenetic explanations is not without methodological caveats as well. First, these approaches and the strength of the inference that can be drawn from them depends to a large degree on the extent of sampling—a small number of lineages (fewer than 20) provides limited power to detect phylogenetic signal (Freckleton et al. 2002; Blomberg et al. 2003). For this reason, (Saino et al.'s 2010) estimate of phylogenetic signal using 22 species of songbirds (see above) provides somewhat weak evidence for phylogenetic independence of sex-differences in timing. Second, these approaches depend on an accurate phylogeny in addition to trait data. Phylogenetic uncertainty, especially polytomies and short branch lengths, often lead to overestimates of phylogenetic signal; Pagel's λ is more robust than other measures (Molina-Venegas and Rodríguez 2017). Though discussions to improve performance of phylogenetic analyses using complex phylogenies are on-going (e.g., Jermiin et al. (2020)), genomic tools continue to increase our understanding of complexity underlying genome evolution (e.g., incomplete lineage sorting and historic hybridization; Alda et al. 2019; Sun et al. 2021). This rapid growth means that best practices for accurately estimating phylogenetic signal are likely to continue to develop beyond the considerations and approaches discussed here.

To understand microevolutionary processes that contribute to sex-differences in phenology within species, concepts similar to those used for cross-species comparisons can be applied at the population-level. However, the genomic patterns used to diagnose evolution on shorter timescales differ, and thus the analyses and metrics used also differ from the aforementioned approaches. Population genomics and genetics approaches should explicitly model demographic processes, which include events like bottlenecks and founder effects that impact genetic diversity, to account for ancestry-driven effects on shorter time-scales. These approaches are uniquely suited to identifying the genomic basis of changes to sex-differences in phenology because they can identify specific genomic regions associated with traits of interest. These genomic regions can then be used to identify genes or alleles of interest. There is ample and interesting work investigating the genomic basis of differences in phenology among populations (e.g., Verhagen et al. (2019); Madsen et al. (2020); Thompson et al. (2020)). Polyglutamate repeats associated with *Clock* gene alleles and timing across species are suggestive of convergent or parallel evolution of some timing mechanisms among species (see discussion in *mechanisms*). Unfortunately, without a broader mechanistic understanding of how sex-based differences in timing arise, making sense of the results from genomic analyses in an adaptive and evolutionary context will continue to be largely speculative.

A lack of trait data and knowledge about mechanisms remain the major limitations to understanding the evolutionary history of sex-differences in tim-

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ing. Identifying suitable systems for studying the evolution of these traits in a comparative context is important to making progress in this area. Systems that are likely to be particularly useful moving forward include those with sexually dimorphic phenological traits that can be readily quantified at scale, and those that contain diversity among these traits within comparable lineages. For example, bats have well-described diversity in migratory and reproductive timing that differ between the sexes (Racey 1982; Racey and Entwistle 2000), and thus are well-suited to broad comparative analyses of species-level divergence in phenological traits between the sexes. Obtaining comprehensive data on the timing of migration, hibernation, and reproduction, along with generating high-quality genomes across a larger number of species is likely needed to further pursue this system. Avian species are likely to be particularly useful for deep evolutionary insight, as well as within-species evolution of sexually dimorphic phenological traits. Protandry and protogyny are already well-studied among songbirds such that the trait data are largely available or methods for collecting such data are well-established. High quality complimentary or matched genetic data are often still needed. Of particular interest are species where migratory phenotypes differ among populations, including northern wheatears (*Oenanthe oenanthe*; Schmaljohann et al. 2016), Eurasian blackcaps (*Sylvia atricapilla*; Izhaki and Maitav 1998; Delmore et al. 2020), white-crowned sparrows (*Zonotrichia leucophrys*; Chilton et al. 1995), and dark-eyed juncos (*Junco hyemalis*; Holberton 1993). More specifically, in the case of white-crowned sparrows and dark-eyed juncos, these species have both migratory and non-migratory populations, for which migratory phenotype generally corresponds to changes in reproductive phenology within each sex (Wingfield et al. 1996, 1997, 2003; Bauer et al. 2018; Kimmitt et al. 2019, 2020). For those populations that migrate, protandry or protogyny is common, meaning the sexes differ in at least some aspects of their phenology. However, work addressing divergence in sex-differences between migrant and non-migrant populations is still missing. A similar lack of data plagues wheatears and blackcaps, where populations differ in the migration distance. Thus, although likely, the evolution of sex-differences in phenology in these species can only be speculated on here. Additional trait data is needed to guide such studies.

Conclusions

A Tinbergian perspective offers a multi-faceted understanding of the origins of sexually dimorphic phenology. However, beyond adaptive explanations, we find that relatively little is known about how sex-based differences in timing emerge and evolve across species. Significant progress has been made in understanding how sexual selection and natural selection leads to different mating systems, and this has significantly informed our understanding of the adaptive value of sex-differences in timing. Because the seasonal timing of all annually recurring life-cycle events is strongly influenced by the need to match energetically expensive reproduction with peaks in resource availability, sexual maturation strongly affects phenology, such that differences in development rates between males and females leads to age-dependent sex-differences in phenology. Meanwhile, there has been a relative dearth of physiology studies using females as subjects (Kim et al. 2010; Zucker and Beery 2010), which has led to significant bias in our understanding of the mechanistic basis of sex-differences in seasonal timing. Although research focused on females has increased over the past decade, many studies still only report results for a single sex. Nevertheless, it is well-established that organizational and activational effects lead to sexual dimorphism in brain circuits that may influence timing. In particular, it is evident that sex-differences in the organization of circadian timing systems, along with responsiveness of these systems to sex steroids, likely underlie some of the observed sex-differences in phenology. Phylogeny, or common descent, also likely explains a substantial amount of the pattern of species-level diversity in sex-biased phenologies; however, empirical estimates are still lacking, and the degree to which species share mechanisms underlying these differences (e.g., convergent or parallel evolution) is virtually unknown.

Filling these gaps in our understanding of the origins of sex-based differences in timing of life-history events is essential for determining the consequences of climate change for populations and species. This is in large part because sex-differences in seasonal timing and differential sensitivity to environmental cues among the sexes will impact intraspecific interactions; just as climate change may disrupt synchrony between predator and prey (Ramakers et al. 2020), or between plant and pollinator (Miller-Struttmann et al. 2015), it may also lead to phenological mismatches between the sexes. It is first critical to monitor timing in both sexes across phenological events. Further, multiple metrics should be used to assess phenological change; using a single metric (e.g., egg-laying) fails to capture sex-differences in timing and/or temporal shifts of other seasonal life-history events with important fitness consequences (e.g., molt, migration, and hibernation). Finally, both plasticity and evolutionary potential for phenological change must be better quantified, and thus molecular and genetic mechanisms require further at-

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tention. The capacity of animals to flexibly adjust their timing (i.e., adaptive phenotypic plasticity) is an important component of population resilience to climate change in the short term (Charmantier et al. 2008). However, the evolution of timing systems and/or the evolution of plasticity of timing systems to the changing environment will likely play an increasingly important role over longer time scales (Boutin and Lane 2014; Charmantier and Gienapp 2014).

Despite the large number of unknowns, new technology and increasing emphasis on open data holds promise for understanding how sexually dimorphic phenology will impact climate change resilience. For example, the development of biologging techniques holds significant promise for generating datasets that capture similar metrics among sexes and across the annual cycle. By measuring phenology across the annual cycle, biologging may also offer the opportunity to connect conditions at one stage to carry-over effects on timing at subsequent stages at the individual level (Saino et al. 2017; Chmura et al. 2018). In combination with on-going bioinformatic advances and lower sequencing costs, genomes and other genetic resources may facilitate mechanistic advance by linking trait variation from large datasets with genomic variation. Thus, although Tinbergen's perspective here highlights substantial blindspots in our understanding of potential phenological mismatch between the sexes, current technology and tools provide a strong position from which we can make advances in the coming decades.

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