Population Viability of Sea Turtles in the Context of Global Warming

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Sea turtles present a model for the potential impacts of climate change on imperiled species, with projected warming generating concern about their persistence. Various sea turtle life-history traits are affected by temperature; most strikingly, warmer egg incubation temperatures cause female-biased sex ratios and higher embryo mortality. Predictions of sea turtle resilience to climate change are often focused on how resulting male limitation or reduced offspring production may affect populations. In the present article, by reviewing research on sea turtles, we provide an overview of how temperature impacts on incubating eggs may cascade through life history to ultimately affect population viability. We explore how sex-specific patterns in survival and breeding periodicity determine the differences among offspring, adult, and operational sex ratios. We then discuss the implications of skewed sex ratios for male-limited reproduction, consider the negative correlation between sex ratio skew and genetic diversity, and examine consequences for adaptive potential. Our synthesis underscores the importance of considering the effects of climate throughout the life history of any species. Lethal effects (e.g., embryo mortality) are relatively direct impacts, but sublethal effects at immature life-history stages may not alter population growth rates until cohorts reach reproductive maturity. This leaves a lag during which some species transition through several stages subject to distinct biological circumstances and climate impacts. These perspectives will help managers conceptualize the drivers of emergent population dynamics and identify existing knowledge gaps under different scenarios of predicted environmental change.

Keywords: climate change, temperature-dependent sex determination, thermal tolerance, operational sex ratio, effective population size

Climate change is driving population extirpations and species extinction at an accelerating rate (Urban 2015). Conservationists increasingly seek to assess what populations and species will persist under future climate scenarios—and why. This trend is at the forefront of sea turtle conservation; the seven extant species are of conservation concern and are susceptible to myriad aspects of environmental change. A principal issue (and focus in the present article) is that sea turtle demography is sensitive to temperature. Warmer incubation temperatures produce female-biased primary sex ratios (Standora and Spotila 1985), and the mortality of developing embryos increases past thermal thresholds (Bustard and Greenham 1968). In a warming world, the threats of extreme sex ratio skew and declining egg viability threaten population persistence. Will there be enough males to maintain populations? Does this even matter if projected temperature increases result in progressively higher embryo mortality? There is a growing concern that sea turtle populations may have limited capacity to persist in the warming world (Hays et al. 2017, Monsinjon et al. 2019).

Despite a dire contemporary outlook for sea turtle persistence, they represent an ancient taxon whose lineage has stood the test of time. Ancestors of the Testudines order survived temperatures that were warmer than today (Fastovsky and Weishampel 2005). A key difference now is that the rise of *Homo sapiens* has contributed to a collapse in turtle populations (Lovich et al. 2018, Stanford et al. 2020). Current abundances have declined from historical levels because of human pressures such as harvest and habitat destruction, leaving today's depleted stocks more vulnerable than their ancestors. Despite this, the fact that sea turtles have endured periodic fluctuations in atmospheric carbon concentrations and temperatures suggests that adaptation may enable their persistence. However, even if sea turtles persist, it is likely that some populations will face extirpation. Biological traits, conservation statuses, and climatic contexts differ greatly among global populations (Fuentes et al. 2013, Mazaris et al. 2015). Therefore, estimating individual population viability against a backdrop of ongoing climate change is an important step to advance conservation.

Inferences of population viability depend on an understanding of demographic composition and the processes driving changes therein (i.e., demographic dynamics), but quantifying these elements in sea turtles is challenging. Lengthy, complex, and cryptic life histories make accurate estimates elusive. With time to sexual maturity ranging from one to three decades, the lifespan of a sea turtle exceeds the duration of most research programs. Rates of offspring survival are low, and if sea turtles reach the juvenile stage, they may inhabit multiple different foraging habitats as

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Table 1. Glossary of key terms related to sea turtle sex ratios.

Biological parameter	Definition
Population (of sea turtles)	A genetically related (i.e., partitioned) group of individuals originating from a nesting area. Natal homing results in highly differentiated maternal lineages and unique genetic markers, and population mixing (gene flow) is most frequently male mediated.
Primary sex ratio (PSR)	Sex ratio of offspring.
Adult sex ratio (ASR)	Sex ratio of reproductively mature adults.
Operational sex ratio (OSR)	Sex ratio of adults seeking to reproduce. In sea turtles, OSRs are typically quantified annually—that is, per breeding season.
Realized sex ratio (RSR)	Used in the present article to refer to the sex ratio of adults contributing (parentage) to offspring in a breeding season. RSRs can vary from OSRs because of behavioral mechanisms such as competition. In many cases referred to as breeding sex ratio.
Breeding periodicity	The frequency with which a sea turtle participates in reproduction—for example, annually, biennially, triennially.

they mature. Adults then generally spend their lives in one home foraging area but undertake sometimes distant migrations to reproduce. Therefore, individuals are difficult to locate and track in open marine habitats throughout their lives. As a result, key demographic parameters (e.g., age structure, sex ratio, and survivorship) remain unresolved for most populations (Rees et al. 2016). Research on the population viability of sea turtles is notably concentrated around demographic effects on offspring, compared with older life-history stages, because of conspicuous effects from temperature (on sex ratios and survival) and the relative ease of conducting research on nesting beaches (versus in marine habitats).

In the present article, we synthesize concepts that frame our current understanding of how warming temperatures may affect the viability of sea turtle populations. Our review highlights that, from a population modeling perspective, the effects of climate change on the population growth rates for any organism will be realized via changes in survival or reproductive output. To comprehend how sublethal climate impacts will affect viability, we must first have a detailed understanding of life history to link these impacts to eventual changes in survival and reproduction. This reality applies across diverse organisms and ecosystems and makes it challenging to predict viability for species whose life history is difficult to study.

Our review is oriented toward impacts on offspring demography and how these outcomes ultimately affect population growth rates (and viability). We first provide an overview of the temperature-sensitive nature of offspring demography. The process of incorporating direct impacts on vital rates (embryo survival) in inferences of viability is relatively immediate and simple when compared with more drawn out and complex predictions for the effects of skewed sex ratios (eventually realized in reproductive output). We examine this reality, exploring how skewed primary sex ratios (PSRs; defined in table 1) may translate to male limitation by reviewing the links among PSR, adult sex ratio (ASR), operational sex ratio (OSR), and mating (figure 1). We transition to considering the implications of skewed sex ratios for genetic diversity—an essential concern for viability but one that is often overlooked for sea turtles. Finally, we examine the importance of possible adaptations to climate change and offer a concluding synthesis.

Effects of temperature on offspring demography

All sea turtle species exhibit temperature-dependent sex determination (TSD), in which the sex ratio among embryos developing in an egg clutch becomes female-biased at warmer temperatures (Yntema and Mrosovsky 1980, Standora and Spotila 1985). The exact mechanism triggering gonad differentiation remains unresolved. However, we know that TSD plays out through temperature-linked gene expression pathways that, in sea turtles, drive increased expression of aromatase and therefore estrogen at high temperatures, compared with testosterone at lower temperatures, consequently leading to the respective development of ovaries or testes (Singh et al. 2020, Weber et al. 2020). Sex determination occurs during the middle third of embryonic development, or the thermosensitive period (Girondot et al. 2018). Two key parameters are typically used to characterize the relationship between incubation temperature and sex ratio, or thermal reaction norm (i.e., a pattern in phenotype across a range of temperatures; figure 2). The first is the *pivotal temperature*, the constant temperature resulting in a balanced sex ratio. It is typically presented as constant because seminal TSD studies took place in laboratories employing constant temperatures (box 1). The second key component is the transitional range of temperatures, between which ratios transition from approximately 95% male to 95% female (Girondot et al. 2018). The temperature values parameterizing thermal reaction norms have been shown to vary among species and populations of the same species (Hulin et al. 2009, Bentley et al. 2020a) and possibly among individuals from the same population (Carter et al. 2017, 2019).

Offspring survival. Determining what factors affect the embryonic survival of sea turtles (i.e., egg hatching success) has been an aim of biologists for decades (box 2; Bustard and Greenham 1968). A diverse suite of factors has been tied to hatching success, both endogenous (e.g., parental genetics;

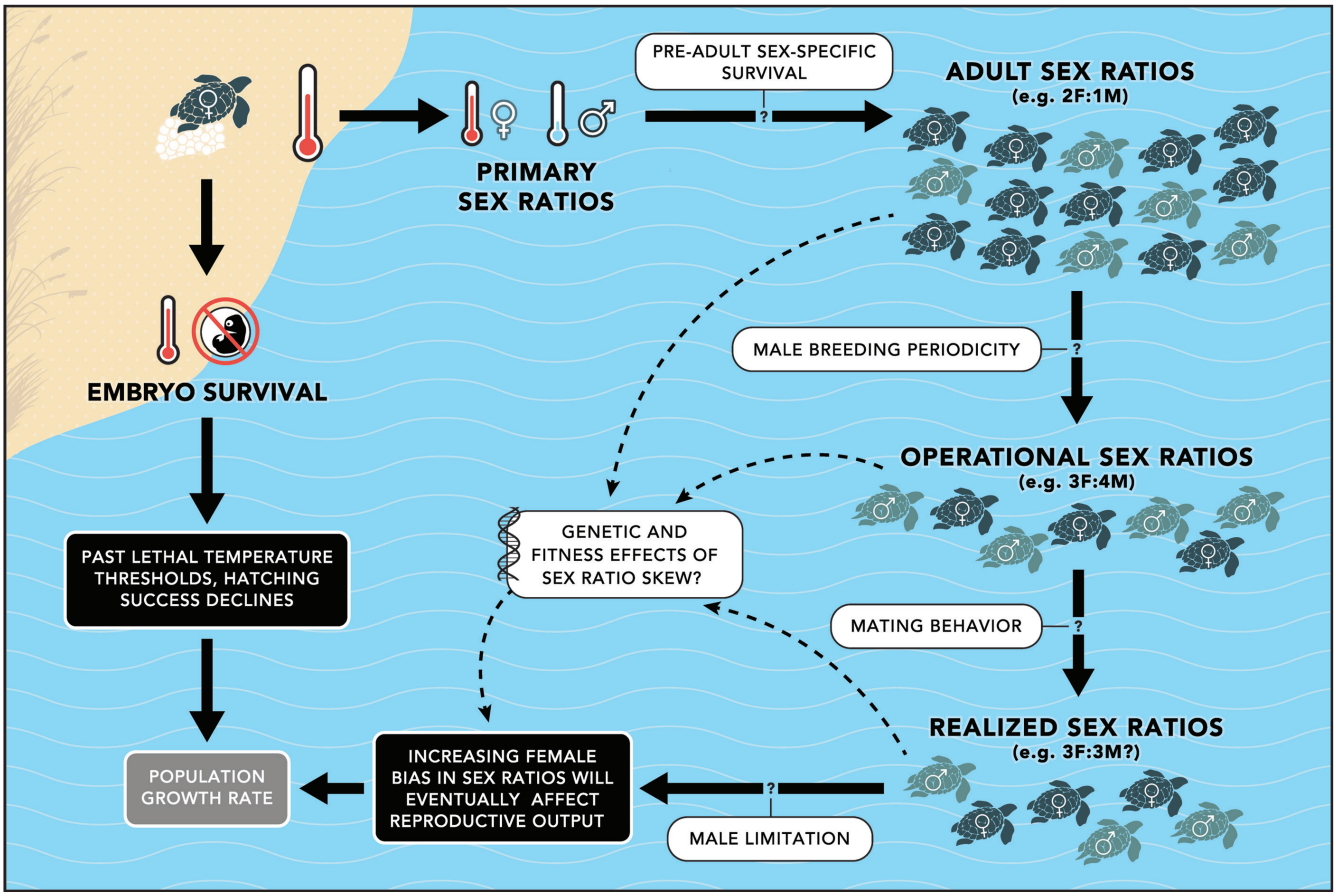

Figure 1. Warming temperatures affect sea turtle embryos via increases in both mortality and female sex ratio bias. In population models, these impacts will affect population growth rates in distinct ways. Changes to embryo survival represent a direct impact on vital rates (or transition probability from stage one in a demographic matrix model). By contrast, impacts on primary sex ratios will eventually affect adult reproductive output; before this impact is realized, offspring cohorts must survive to reproductive maturity and be subject to a suite of factors, including hypothetical changes to sex ratios among life-history stages, reproductive biology, and mating behavior. Longstanding knowledge gaps (denoted with question marks) make it challenging to predict the impacts of temperature-sensitive offspring demography and research continues to address these gaps. Figure created by Kate Maurer.

Phillips et al. 2017) and exogenous (e.g., proximity to beach vegetation; Ditmer and Stapleton 2012). Temperature stands out as a critical exogenous variable; thermal reaction norms described for hatching success (figure 2) consistently show declines at threshold incubation temperatures (Howard et al. 2014). This association between temperature maxima and hatching success poses a clear threat to sea turtle offspring production and is another example of how climate change may affect population persistence (Laloë et al. 2017).

Temperature-sensitive offspring demography and future warming. The associations among temperature, primary sex ratios, and offspring mortality have concerning implications for sea turtle populations in the context of current and projected warming (Santidrián Tomillo et al. 2014). For example, recent evidence from a green turtle (*Chelonia mydas*) in-water aggregation in Australia suggests that nearly female-only populations are possible; juveniles and subadults originating from northern Great Barrier Reef nesting beaches were more than 99% female (Jensen et al. 2018). Such a bias in sex ratio is undoubtedly concerning, but at a broader scale, some postulate that, under the projected warming scenarios, sea turtle population viability may be more sensitive to embryo mortality than to increasing sex ratio skew (Hays et al. 2017).

Predicting the impacts of these two factors is a difficult challenge for population modeling. First, thermal reaction norms appear to be largely context specific (but see Monsinjon et al. 2017), and a suite of environmental parameters may be locally important. Second, whereas hatching success is comparatively easy to accommodate in population models, predicting the effects of skewed PSRs is more complex. This distinction can be illustrated by considering seminal matrix population models (Crouse et al. 1987), although these models center on female fecundity and approaches

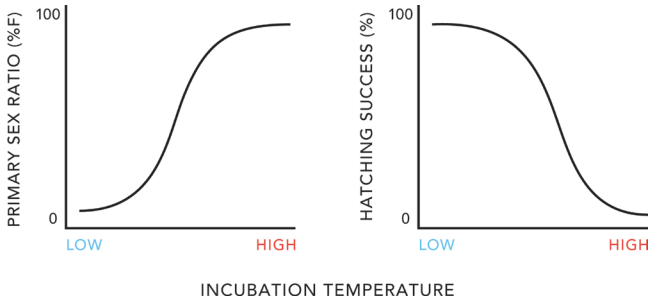

Figure 2. Thermal reaction norms for primary sex ratios (PSRs) and hatching success (i.e., embryonic survival) provide the basis for many predictions regarding the persistence of sea turtles under projected warming scenarios. Two arbitrary examples illustrate the shape of such norms, adapted from Hays and colleagues (2017; not shown, at even lower temperatures, further left on the x-axes, the curve trends would be reversed as PSR bias rises and hatching success declines at cold thresholds). Figure created by Kate Maurer.

accounting for sex ratios would be appropriate. Impacts on offspring survival would be factored directly into the transition probability from the first life stage, but the impacts from PSR skew are difficult to derive and will only be realized in eventual reproductive output. To predict how PSRs will translate to actual measures of adult reproduction, we must account for many factors reflecting changes in sex ratios through life history, adult behavior, and mating system.

How many males are enough? Conceptualizing a male-limited sex ratio

Below, we review research suggesting that female-biased sex ratios are common and adaptive in sea turtles. But how many males are too few? Determining a PSR at which males will become limiting to population growth depends on estimates of several types of sex ratios throughout sea turtle life histories and how these ratios are linked (see table 1). We first need to estimate a future ASR from a PSR, or, more accurately, from the blend of cohort-specific PSRs that contribute to a given ASR. Then, from an ASR, we must derive a seasonal OSR, which differs from the ASR because of sex-specific breeding periodicity. Behavior at mating areas may result in differences between the OSR and the sex ratio of realized parentage; that is, the sex ratio among parents whose genes are passed on to an offspring cohort. This ratio has been referred to as a *breeding sex ratio* in many instances, but in other cases, it is conflated with an OSR. In the present article, we refer to it as the *realized sex ratio* (RSR).

From primary to adult sex ratios: Sex-specific survival. The conversion factor for equating a PSR to an ASR depends on male and female survival between the hatchling stage and sexual maturity. Sometimes, a 1:1 conversion is used (e.g., Hays et al. 2017). However, evolutionary theory provides support for the idea of sex-specific differences in survival and fitness for species with TSD (Schwanz et al. 2016). This theory may play out in sea turtles via hatchling phenotypic plasticity (table 2). Temperature simultaneously affects offspring morphology and sex (Booth 2018), which may result in a generalized trend of reduced fitness at female-producing temperatures below thermal maxima (Kobayashi et al. 2018). This would have a balancing effect on sex ratios as offspring cohorts develop toward maturity. However, the alignment between the thermal reaction norms for TSD and hatchling morphology warrants further investigation.

Hypotheses about sex-specific survival in immature sea turtles remain rooted in theory and lack empirical testing. Information on preadult survival has eluded researchers for decades, especially at the early pelagic stage dubbed the "lost year." Tracking offspring cohorts presents major logistical challenges such that we lack empirical information regarding the distribution of younger individuals in general (but see Mansfield et al. 2014, Putman et al. 2020). Furthermore, *ex-situ* experiments have limited capacity to simulate real sources of mortality—namely, predation. Information about early life survival is increasing via long-term mark–recapture efforts using hatchling genetic fingerprinting (see Dutton and Stewart 2013). After genetically marking hatchlings and waiting until reproductive maturity, females may be recaptured via genetic sampling on nesting beaches, or both parents may be recaptured using parentage analysis of offspring DNA (e.g., Wright et al. 2012a).

Characterizing survival via hatchling genotyping entails immense sampling efforts (for low returns on decadal scales) and is dependent on natal homing back to the study site. Another approach to estimating patterns in sex-specific survival is to compare sex ratios at different life stages. Rees and colleagues (2016) noted a trend in sex ratios for Mediterranean loggerheads (*Caretta caretta*), from strongly female-biased PSRs to balanced or male-biased ASRs. In a similar gradient, Wibbels and colleagues (1991) suggested a juvenile loggerhead sex ratio of 2.1 females per male near Hutchinson Island, Florida, which is notably less biased than the more than 93% female PSRs found at nearby nesting beaches in Cape Canaveral (Mrosovsky and Provancha 1989). Allen and colleagues (2015) likewise documented more female bias in immature green turtles compared with adults in San Diego Bay. Many confounding factors limit inference into causation, such as the mixing of stocks with distinct demographic rates and possible influences from sex-specific behaviors. However, modeling efforts may begin to resolve confounding factors in some systems. For example, Vandeperre and colleagues (2019) used nest numbers at Florida source rookeries with a 3-year lag to predict juvenile loggerhead abundance in Azorean waters, and sex ratio estimates could foreseeably be integrated into such approaches.

Box 1. TSD science: Progress and considerations.

Research advances have pushed TSD science beyond a paradigm developed through controlled laboratory studies that typically used constant temperatures and did not account for a suite of other environmental factors that vary *in situ* (Bowden and Paitz 2018). For example, whereas the thermosensitive period was originally defined as the middle third of incubation duration under constant temperature, it has since been reconceptualized to take into account fluctuations in temperature and associated physiological development (Girondot and Kaska 2014). Reanalyses using this new concept revealed that previous studies may have inflated estimates of the production of male offspring *in situ* (Girondot et al. 2018). Some work has also suggested that when incubation temperatures are inferred from proxies (e.g., air or sand temperatures) instead of directly sampling in egg clutches, resultant estimates of sex ratios can be flawed (Fuentes et al. 2017) and may miss important mediating factors such as sand moisture (Lolavar and Wyneken 2020). We note that most studies have focused on characterizing pivotal temperature, at times at the expense of defining the transitional range of temperatures, which may be equally or more important for understanding links among incubation temperatures, PSRs, and viability (Hulin et al. 2009).

Historically, empirical PSR characterization required researchers to euthanize hatchlings to assess gonadal histology. The permitting obstacles and ethical considerations associated with sacrificing hatchlings have motivated the development of novel, nonlethal approaches. For instance, Tezak and colleagues (2020) developed an immunoassay that, from a small sample of hatchling blood, can identify a marker for antimüllerian hormone that appears to be male specific. There is also promise in other methods that may be extended to hatchlings in the future, such as measuring eggshell steroids (Kobayashi et al. 2015), blood hormone assay techniques for juveniles (Allen et al. 2015), and near-infrared spectroscopy (used to classify sex of amphibians; Vance et al. 2014). All these techniques will facilitate more empirical PSR validation to accompany increasingly sophisticated modeling approaches for *in situ* temperature data (Abreu-Grobois et al. 2020), bolstering our understanding of TSD in sea turtles.

Maternal effects on offspring phenotype (Mousseau and Fox 1998) may be an important area of research for understanding TSD, because some effects may be attributed to and therefore conflated with the underlying thermal reaction norm (figure 2). A substantial body of literature documents how maternal *behaviors* affect offspring phenotype, such as nest site selection (e.g., Reneker and Kamel 2016), in which the ultimate mechanism is the modification of the incubation environment. By contrast, maternal effects can act through different pathways, such as varying sex steroid hormones within eggs (Bowden and Paitz 2018). Carter and colleagues (2017) documented changes in maternally sourced egg estrogen concentrations throughout a nesting season in red-eared sliders (*Trachemys scripta*) and, after controlling for temperature, associated higher concentrations with an increased likelihood of female sex ratio bias. Hormone-mediated maternal effects may act independently from temperature and, when left unaccounted for, are conflated with the underlying sex ratio thermal reaction norm. Therefore, growth in this research area will strengthen the understanding of PSR determination in general (Bowden and Paitz 2018).

We are now more prepared to advance our understanding of sex- and stage-specific survival in sea turtles. The knowledge gap surrounding survival hinders estimation of how PSRs translate to ASRs—a key consideration when projecting the effects of warming on populations. Although the first (difficult) step is to simply derive robust baseline estimates of survival, it is important to note that this parameter, among others, is dynamic and may vary with environmental conditions. For instance, Kobayashi and colleagues (2018) experimentally demonstrated that water temperature affects hatchling swimming performance such that early survival rates may change with spatiotemporal variation in water temperature. Given an accurate PSR estimate, improved estimates of survival (and transition probabilities) will help to refine ASR estimation. However, this step still falls short of estimating reproductive output, a parameter ultimately mediated by OSR and mating biology.

From adult to operational sex ratios: Breeding periodicity. The next consideration for unraveling how warming may affect reproductive output via skewed sex ratios is the relationship between ASR and OSR; the conversion factor between the two is determined by breeding periodicity (table 1, figure 1). Whereas female periodicity has been comparatively well documented by nesting beach-tagging programs (e.g., Kendall et al. 2019), there is a knowledge gap regarding male breeding periodicity because of the difficulty of observing males in marine habitats. We know that male sea turtles can mate with multiple females in a single breeding season (Gaos et al. 2018), and there is compelling evidence that males may participate in breeding seasons more frequently than females (Hays et al. 2014). This greater breeding frequency makes sense energetically, because reproductive energy costs should be lower for males and require shorter foraging periods to replenish (Hays et al. 2014). On the basis of these two criteria alone (polygyny and breeding periodicity), an ASR that maximizes reproductive output would theoretically be female biased. But how many males are too few? Projecting how changes to ASRs will affect OSRs, and therefore mating, depends on detailed knowledge of male breeding periodicity to complement existing data sets documenting female periodicity. We highlight three methodologies advancing the field in this regard: satellite tracking (e.g., Hays et al. 2014), in-water surveys at breeding areas (e.g., Hays et al. 2010), and genetic paternal reconstruction using hatchling DNA (e.g., Wright et al. 2012a).

Box 2. Sea turtle offspring survival.

Contemporary understanding of reaction norms for embryo thermal tolerance (hatching success) has advanced through the description of taxonomic and geographic variation, as well as through more rigorous evaluations of impacts from other environmental variables. Although temperature poses a clear threat, its relative importance (when below lethal extremes) compared with other factors is unclear across species and populations. This is in part because of inter- and intraspecific differences in the temperature at which hatching success declines (Howard et al. 2014). These differences are accompanied by variation in apparent susceptibility to other regional environmental parameters such as aridity and rainfall (Santidrián Tomillo et al. 2015a, Rafferty et al. 2017, Rivas et al. 2018). Varying findings suggest context-specific associations between regional climate variables and hatching success and key trade-offs between temperature and moisture.

In contrast to TSD, there has been less investigation into when temperatures ultimately factor into embryonic survival and how thermal tolerance (i.e., how a given temperature affects embryonic development) may vary through incubation, especially under natural conditions. Whereas lethal upper thresholds exist, certain durations of exposure to lower temperatures may also affect hatching success (Howard et al. 2014, Bladow and Milton 2019).

Warming incubation temperatures also may affect the survival of sea turtle offspring after hatchlings exit nests, although there are fewer empirical data for this stage compared with eggs. Temperature-linked phenotypic variability in reptile offspring affects more than just sex (Singh et al. 2020), and sea turtle hatchling morphology appears to follow a thermal reaction norm with middle temperatures resulting in the best morphological outcomes (Fisher et al. 2014, Mueller et al. 2019). Morphological effects are likely driven by physiological factors, such as the increased conversion of egg yolk to tissue at lower temperatures, as well as effects on muscle fiber development (Booth 2018). The overall result is that warmer temperatures are associated with the development of smaller and slower hatchlings (although perhaps with higher energy reserves; Booth 2018). High variance in incubation temperature may also negatively affect phenotype (Horne et al. 2014). If the average hatchling becomes smaller and slower as temperatures warm, and if these morphological effects are conserved as the hatchling develops (as has been suggested by Noble et al. [2018]), then survival during early life history stages may decline.

Satellite tracking can facilitate inferences of male breeding from the periodicity of movements to breeding areas. We found six published subsets of data for males that were tracked long enough to infer periodicity over multiple seasons (typically more than 365 days). These data included four species and 35 individuals (supplemental table S1; James et al. 2005, van Dam et al. 2008, Casale et al. 2013, Varo-Cruz et al. 2013, Hays et al. 2014, Naro-Maciel et al. 2018). A yearly remigration pattern was exhibited by 19 of these turtles. Unfortunately, this approach is constrained by the duration of transmitter retention and will typically only show whether a male exhibits consecutive annual breeding migrations. Either an annual or biennial pattern is often assumed, although in many cases a triennial (or longer) pattern cannot be ruled out. Moreover, intraindividual variability has not been estimated for males but is likely considering the complexities that dictate reproductive energetics and periodicity. Another caveat for inferring male breeding periodicity on the basis of migrations is that it is unclear what to infer from males that reside in breeding areas (e.g., Varo-Cruz et al. 2013). Although migration is assumed to culminate in reproductive activity, a lack of migration may not be indicative of reproductive status because males may simply remain resident in breeding areas (furthermore, reproductively active males may not successfully mate). For example, Blanvillain and colleagues (2008) found that as high as 15% of males present at a loggerhead breeding area in Florida were not reproductively active. Although satellite tracking males to infer periodicity has clear limitations, these can be alleviated to some degree by complementary in-water work at breeding areas, such as surveys using photo ID or unmanned aerial vehicles (UAVs; Schofield et al. 2017). Hays and colleagues (2010) complemented satellite tracking with photo-ID surveys and female nesting data to suggest that loggerhead males visited a Zakynthos Island breeding area 2.6 times more frequently than females; such a disparity would lead to a greater male component in the OSR relative to ASR.

A newer approach to estimating periodicity is the use of hatchling genetics to reconstruct paternal genotypes (e.g., Wright et al. 2012a). Hatchling DNA contains a definitive record of paternity, and therefore sampling over multiple seasons can reveal periodicity. As molecular techniques advance and continue to decline in cost, this approach holds great promise for answering questions surrounding periodicity and OSRs. We note two key considerations for using this method to estimate male periodicity. First, the strategy is only as good as the detection probability for fathers. This probability is dependent on *a priori* knowledge of the population of interest and associated sampling design. For example, if sired clutches are distributed among several beaches (e.g., Wright et al. 2012b), then sampling hatchlings at one beach will likely not be enough to detect all fathers. In addition, clutch sampling should take into account the potential for multiple paternity. Second, a full record of offspring parentage represents an RSR, not an OSR, unless all males attempting to mate successfully sire offspring. This distinction neutralizes concerns about males that reside at

Table 2. Glossary of key terms related to sea turtle genetics and microevolution.

Genetic term	Definition
Effective population size N_e	A theoretical number of individuals for a genetically idealized population that would have the same loss of heterozygosity because of drift as the true population in question (i.e., census population). N_e can be reduced by nonrandom mating, overlapping generations, high interfamily variance in contribution to offspring, historical population bottlenecks, and sex ratio skew.
Genetic drift	Chance variation in the frequency of different genotypes (i.e., not due to natural selection). Drift is stronger in small populations and can lead to loss or fixation of alleles.
Inbreeding or outbreeding	According to genetic theory, breeding by closely related parents will result in deleterious fitness outcomes for offspring (inbreeding depression), but breeding by distantly related parents can also lead to negative fitness outcomes (outbreeding depression) by—for example, introducing maladapted genes.
Phenotypic plasticity	The ability for a single genotype to encode multiple phenotypes as a function of environmental variation.
Directional selection	Natural selection for genotypes in a directional manner in response to some selection pressure—for example, unidirectional change to the genotype encoding flipper length when swim speed is consistently advantageous.
Selective sweep	Rapid directional selection of a region of the genome due to strong natural selection. Alleles not influenced by selection can be swept up to high frequency or fixation because of physical proximity to an allele under selection.

breeding areas and may be important when conceptualizing male limitation, because it is the OSR that should ultimately dictate mate availability. That is, the male component of an OSR represents all males available to mate and as male numbers decline, competition should decline, and therefore, OSRs may ultimately converge on RSRs. Future research is warranted to evaluate how similar a seasonal RSR is to an associated OSR by quantifying competitive exclusion.

Parentage analyses for a single season can produce an RSR snapshot. For example, Gaos and colleagues (2018) sampled eastern Pacific hawksbill (*Eretmochelys imbricata*) hatchlings and found a single season RSR of 1.41 females per male. Sampling over several nesting seasons can identify trends in RSRs (that may reflect trends in OSRs) and patterns in male breeding periodicity. Wright and colleagues (2012a) used paternal reconstruction to suggest 3 of 99 genotyped male green turtles participated in more than one breeding season over 3 years in Cyprus, despite an estimated RSR of 1.3 males per female. Phillips and colleagues (2014) found that 4 out of 91 Seychelles hawksbill fathers sired clutches in multiple seasons over four nesting seasons. Lasala and colleagues (2013) and (2018) sampled loggerhead hatchlings in Georgia and western Florida over three nesting seasons and did not find any repeat fathers despite male-biased RSRs. Together, these genetic studies may suggest a more infrequent male periodicity pattern when compared with satellite tracking work. However, the more pertinent and broader takeaway may be that the knowledge gap surrounding male periodicity and OSRs is far from being resolved, limiting understanding of how increasingly skewed sex ratios affect mating outcomes.

From operational to male-limited sex ratios: Mating biology and behavior. A primary conclusion thus far is that, although we know strikingly little about the conversion factors between the different sex ratios, our ability to arrive at an OSR or RSR is improving. Genetic parentage analyses may have the most promising future as a single methodology, but in the end, the confluence of different methodological approaches may be necessary to fill knowledge gaps surrounding male biology. For instance, we could learn much from a study that integrates hatchling genetics with UAV surveys, in-water photo ID, and satellite tracking to estimate OSRs or RSRs, residence time at breeding areas, and the levels of male fidelity to a single breeding area. A second conclusion is that given more frequent male mating and polygyny, highly female-biased PSRs may *promote* viability (Hays et al. 2017, Santidrián Tomillo and Spotila 2020), although this idea contrasts with Fisherian sex ratio theory (see Girondot et al. 1998). But what proportion or number of males represents a tipping point? This question represents an impasse in this discussion because even if breeding periodicity is known and an OSR can be estimated, the point at which that OSR will feature insufficient numbers of males to maintain population stability depends on mating behavior. The reality is that we know little about behavioral determinants in sea turtle mating systems in general. For instance, a key question is how many females a single male can mate with. Documenting declines in egg fertility rates represents one approach to inferring when male limitation occurs and is a promising first step if combined with estimates of sex ratios as detailed above (Phillott and Godfrey 2020). However, in a theoretical scenario of warming-driven male limitation, in which a decreasing proportion of males accounts for available paternal DNA, the consequences of skewed sex ratios for population genetics become problematic.

The genetics of skewed sex ratios

Genetic diversity is a central component of population viability, but it is often omitted in considerations of the resilience of sea turtles to climate change (but see Fuentes et al. 2013). Because extremely skewed sex ratios should theoretically lead to negative effects on diversity and fitness (Allendorf et al. 2013), omitting genetic diversity may lead to overly optimistic conclusions. Advances in conservation genetic research and molecular techniques will be critical

for evaluating how global warming will affect the viability of sea turtle populations via skewed sex ratios (see Komoroske et al. 2017 for relevant technical detail on genetic markers and methodological advances).

Genetic diversity, effective population size, and fitness. Monitoring genetic diversity through time can illuminate the effects of TSD on effective population size (N_e; defined in table 2 along with other terms). Although other measures of genetic diversity are important to monitor, such as expected heterozygosity and allelic richness (Allendorf et al. 2013), we focus on N_e in the present article because it integrates genetic effects with life history and is therefore highly relevant to viability inferences (Hare et al. 2011). Notably, for a TSD context, N_e for a mating population is maximized at a balanced sex ratio and declines precipitously at highly skewed sex ratios. For instance, at increasingly female-skewed sex ratios a closed mating population's offspring are fathered by a decreasing proportion of males. As such, all offspring must receive paternal genes from a dwindling genetic pool. As this process iterates through generations amid ongoing warming, genetic diversity becomes a major concern. Changes in N_e over time are therefore important to monitor as they may reveal when skewed sex ratios start to limit genetic diversity. This information is fundamental because genetic variation dictates adaptive potential (Lande and Barrowclough 1987, Hare et al. 2011), a concern in the context of ongoing climate change.

Estimating N_e is challenging for sea turtle populations that exhibit complex genetic structure with highly differentiated maternal lineages at rookeries, male-mediated gene flow, and overlapping generations (Bowen and Karl 2007, Hare et al. 2011). Most studies characterize a static N_e value or back-cast changes to assess bottlenecks (e.g., LeRoux et al. 2012), and few investigate contemporary change—a reality that may be related to the difficulty of observing change given long generation times. Phillips and colleagues (2014) estimated N_e for a hawksbill population in Seychelles and concluded that mating behavior and population connectivity maintained elevated N_e, which may confer adaptive resilience. González-Garza and colleagues (2015) did not derive estimates of N_e, but provided evidence that hawksbill neophytes (first-time reproducers) nesting in the Yucatán Peninsula exhibited decreased individual genetic diversity compared with older remigrants. This result may support the idea that genetic diversity is declining through generations, although mechanisms may exist in other contexts for the maintenance of diversity even amid population decline. Frandsen and colleagues (2020) reported stable population-level genetic diversity in Kemp's ridley turtles (*Lepidochelys kempii*) despite a marked population decline (and perhaps the most severe historical bottleneck experienced by extant sea turtle populations). As more studies track genetic diversity through time, we will be better able to assess how population genetics vary with demographic composition (e.g., abundance, generation time, and sex ratio).

The concept that reduced genetic diversity can have negative effects on fitness is well established (Allendorf et al. 2013); however, this idea lacks empirical testing in sea turtles. Fitness is difficult to measure for sea turtles, and proxies are typically used such as hatching success, emergence success, or clutch size. Two innovative studies involving hawksbill sea turtles attempted to relate measures of genetic diversity to such proxies. In the study of Yucatán hawksbills, there was no association between genetic diversity and selected fitness proxies such as clutch size (González-Garza et al. 2015). Phillips and colleagues (2017) provided more nuanced results, using inbreeding and outbreeding hypotheses (table 2) to explain that when parental relatedness was high, hawksbill reproductive success was reduced, but when parents were unrelated, lower paternal diversity increased success. However, although Phillips and colleagues (2017) did control for maternal body size and incubation duration in analyses of clutch size and hatching success, respectively, there are many important variables they did not account for, such as incubation conditions (though a relatively large data set of 142 clutches may help to overcome this). Studies such as these pave the way for more research investigating the consequences that genetic diversity has on sea turtle population dynamics, a crucial research area for sea turtle conservation.

The genetic future. A better understanding of the ties among sex ratio skew, genetic diversity, and fitness will be key to forecasting sea turtle resilience under projected climate change scenarios. As climate change unfolds in the near term, many sea turtle populations may increase because of greater female production and population-level fecundity (Santidrián Tomillo et al. 2015b, Laloë et al. 2017), although a suite of climate change impacts across sea turtle habitats may negate this scenario. If populations do increase, it will be important to monitor the genetic diversity patterns underlying this trend. Mechanisms such as male-mediated gene flow may help to maintain N_e but, in general, as sex ratios change, proportional decreases would be expected in N_e relative to the census population size. If N_e reaches a critical threshold, populations will decline. Indeed, if genetic theory holds, many populations could already be at risk. This is especially true for small populations because of heightened loss of genetic diversity owing to genetic drift and associated increases in inbreeding depression, leading to the loss of adaptive capacity (Hare et al. 2011). This reflection on genetic diversity logically leads to a discussion of adaptive responses.

Adaptive responses

Adaptive responses represent a source of uncertainty (and perhaps optimism) for inferences into population viability. Above, we highlighted that genetic diversity is key to long-term population viability, but a more mechanistic understanding of potential adaptive responses and their likelihood (i.e., by determining if certain traits are under directional

selection) would be useful for management and conservation. There is concern that adaptation via microevolution in sea turtles may be too slow to cope with the current pace of climate change; we discuss this idea later in the section. Adaptive potential is inherently linked to sex ratios, a relationship mediated via N_e and genetic diversity (although we note that other factors affecting phenotypic expression, beyond the scope of our discussion, are also important to adaptive potential; Allendorf et al. 2013). The implications of skewed sex ratios for population genetics mean that when projecting impacts on viability from skewed PSRs, accounting for effects on possible adaptive responses represents yet another layer of complexity.

To persist in the context of warming climates, populations will have to respond via genetic adaptation (microevolution) or phenotypic plasticity. As temperatures increase, there should be a corresponding increase in selection pressure for those traits that confer fitness benefits. For sea turtles, responses to warming could include changes in geographic distributions (explored in depth in supplemental box S1), thermal reaction norms, reproductive phenology, and maternal effects on offspring phenotype. Trait variation has been demonstrated for philopatry (i.e., fidelity to a geographic region; e.g., Levasseur et al. 2019), thermal reaction norms (e.g., Carter et al. 2019), and nesting behaviors that may confer maternal effects (e.g., Reneker and Kamel 2016). Physiological maternal effects, such as maternally sourced egg hormone concentrations, may also be relevant (Bowden and Paitz 2018). Given this variation, these traits should be subject to natural selection to the extent that genotypic variation underlies phenotypic variation. Shifts to reproductive phenology are unique in that they may not represent a change in traits but, rather, the maintenance of a trait (cueing phenology to sea surface temperatures) while climates change (e.g., Patel et al. 2016). In the end, when evaluating all the possible ways in which sea turtles may respond to climate change, combinations of multiple responses should be considered. For instance, Monsinjon and colleagues (2019) suggested that phenological shifts alone may be insufficient for many loggerhead populations to persist under projected warming scenarios.

Quantitatively evaluating the suite of responses that sea turtles may exhibit to cope with climate change is a complex undertaking. Shifts in distributions may be the most proximate to consider, because unless the thermal traits that dictate sea turtle geographic ranges change through selection or plasticity, warming temperatures will drive ranges poleward. Mechanistic species distribution models that take into account biophysical attributes (e.g., thermal niches) can be especially useful to predict and understand shifts (Dudley et al. 2016). Furthermore, the mechanistic nature of such approaches leaves them open to incorporate various environmental forces, aspects of species biology, and responses beyond distributional shifts (Mitchell et al. 2008, Wang et al. 2018, Bentley et al. 2020b, Stubbs et al. 2020). Considering range shifts, in particular, exposes a possible interplay of trade-offs: Sea turtles have high philopatry for both foraging and nesting areas that presumably evolved to ensure access to suitable habitats (Levasseur et al. 2019, Shimada et al. 2020), but philopatry may impede range shifts (box S1).

For any phenotypic response, it will be important to distinguish between (directional) selection and plasticity, because these have distinct implications for population-level responses to climate change (Fox et al. 2019). Plasticity may be more advantageous for coping with short-term environmental fluctuations (e.g., annual temperature extremes), whereas directional selection may be more advantageous in the long run for dealing with environmental trends such as long-term warming. Genomic approaches will be instrumental in distinguishing between the two—for example, through identifying genomic regions under selective sweeps due to directional selection (table 2).

Can evolution keep pace with climate change? Although long generation times slow the negative effects of genetic drift, they can also decelerate the process of evolution. Moreover, microevolutionary rates are estimated to be slower for the Testudines lineage relative to other reptilian and vertebrate lineages (Avise et al. 1992). High throughput genetic sequencing and genomic approaches, such as genome-wide association studies (Korte and Farlow 2013), have great potential to elucidate the relationship between genotype and phenotype. Isolating critical genomic regions and genes under selection will help to monitor responses, determine rates of change, and assess adaptive capacity (Pardo-Diaz et al. 2015). Chow and colleagues (2019) offered some of the first findings in this area of research, presenting loggerhead genomic regions that may be under selection. The next step is understanding the function of these genes. Genomic techniques may also aid in evaluating the long-term efficacy of controversial management strategies, in particular those that attempt to improve survival by removing sea turtles from their natural environments at key developmental stages. Functional genomics could help to reveal to what extent such methods interfere with beneficial natural selection (see supplemental box S2).

Forecasting viability: Synthesis and conclusions

As regional climates change, the persistence of populations will ultimately depend on how local environmental changes affect population-specific demographic parameters. For sea turtles, research on climate impacts is frequently focused on the embryo stage because of notable associations among temperature, survival, and PSRs, and because so much research occurs at nesting beaches. We reviewed concepts and literature that frame the implications of temperature-sensitive offspring demography for viability, and we focused this narrative on discussing sex ratios because of the complex nature of linking PSRs to (adult) population dynamics. Impacts on populations from decreases in hatching success are relatively straightforward to estimate given accurate temperature projections and well-described thermal reaction

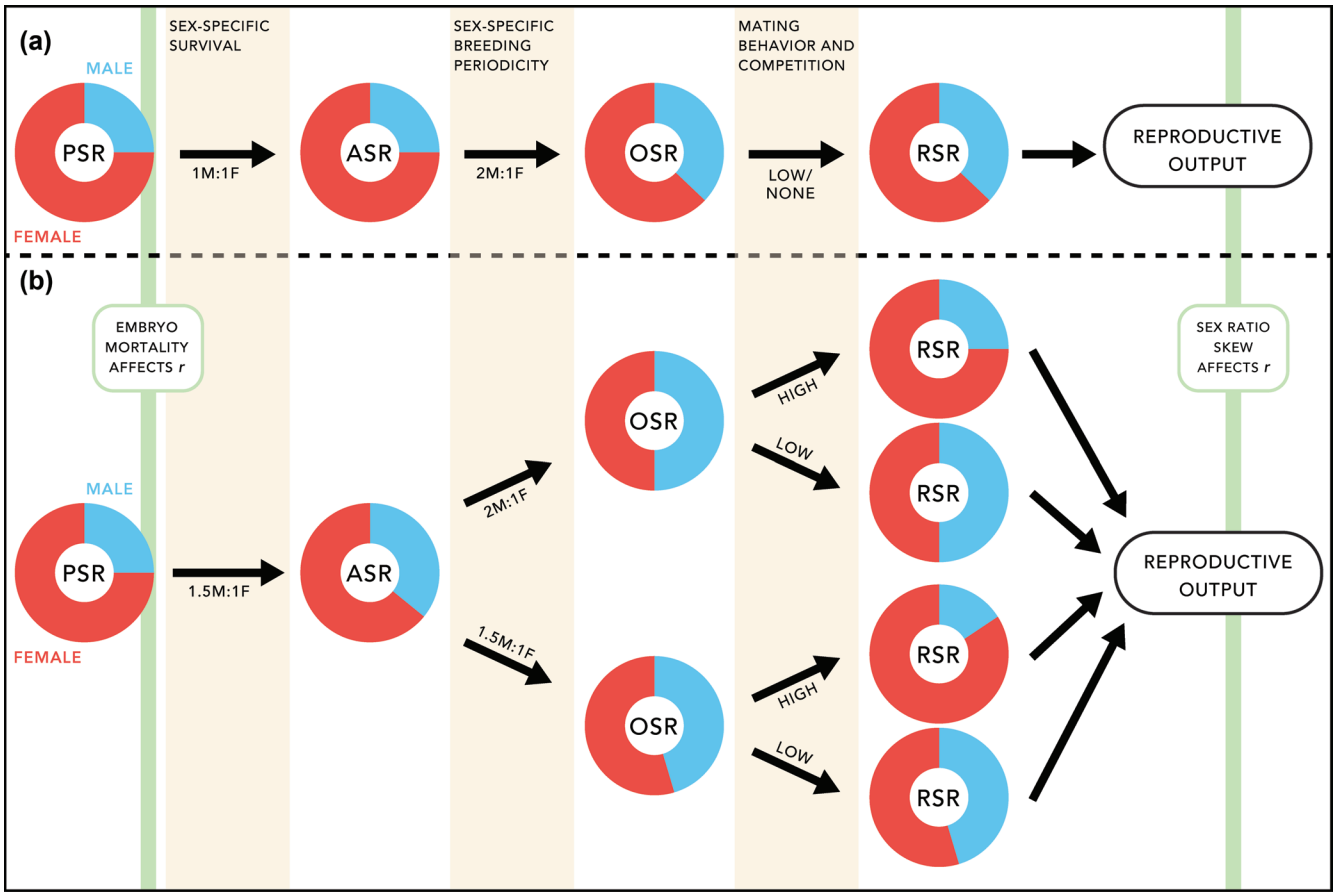

Figure 3. Sex ratios are core parameters dictating mating opportunities, reproductive output, and, therefore, population growth rates. In scenarios (a) and (b), a starting 75% female primary sex ratio (PSR) is used to explore how different possible rates of sex-specific survival to adulthood, sex-specific adult breeding periodicity, and levels of male competition for mating opportunities may cascade to affect the sex ratio of sea turtles contributing parentage (realized sex ratio; RSR) to an offspring cohort. We encourage readers to consider alternative starting PSRs. At some level of female bias, we expect male limitation will affect reproductive output. In scenario a, we show how this process is sometimes represented, with primary sex ratios directly equated to adult sex ratios (ASRs) and assuming single rates (for the shaded transitions) when converting to the next sex ratio. Although this approach may work well for single, well-studied populations, for broader inferences with less certain demographic rates and transitions, we suggest embracing uncertainty and considering a range of values. In scenario b, we explore various arbitrarily chosen rates that reflect some of the myriad possibilities that might be considered. We further note that warming impacts on embryo mortality factor into population growth rate r at the beginning of a sea turtle life cycle (i.e., the far-left narrow bar in this figure), whereas impacts on sex ratios affect r through reproductive output after the cascade of factors affecting sex ratios (i.e., the far-right bar). Figure created by Kate Maurer.

norms. By contrast, PSR skew cascades through life history to eventually affect population growth rate through changes in reproductive output (figure 3). Scrutinizing this cascade exposes a suite of research areas to prioritize as the field continues to better understand the implications of warming for viability. We summarize these areas with six points below.

Variation in thermal reaction norms. The understanding of how temperature affects embryonic survival and sex ratios has a longstanding basis, but more empirical description of such norms continues to capture variation among species, populations, and even in individuals (Howard et al. 2014, Carter et al. 2019). Notably, sex ratio thermal reaction norms are more difficult to quantify, and empirical data are lacking; many studies have used egg incubation temperature proxies or base predictions about one population on the norm described for another. Cutting-edge techniques in endocrinology are making it easier to characterize and describe variation in sex ratio reaction norms (e.g., Tezak et al. 2020).

Preadult survival. It remains difficult to quantify survival to maturity in sea turtles. Theory regarding the evolution and adaptive significance of TSD suggests the possibility of sex-specific patterns in survival (Schwanz et al. 2016), but with

any such patterns mostly unknown, it is unclear how PSRs may translate to an eventual ASR. We highlighted productive approaches to understanding preadult survival, including hatchling genetic fingerprinting (Dutton and Stewart 2013) and monitoring sex ratios among life-history stages (Jensen et al. 2018).

Male breeding periodicity. Our ability to convert between an ASR and OSR is improving as we develop more of an understanding of male breeding intervals. Methods such as satellite tracking (Hays et al. 2014) and genetic parentage analysis (Lasala et al. 2018) continue to make important progress in this realm.

Mating system and behavior. The behavioral ecology for sea turtle mating systems represents a key frontier for future research to understand population viability. Importantly, levels and consequences of competition are difficult to describe, such that we do not know how different an OSR may be from a corresponding RSR. Parentage analysis as a means of tracking breeding intervals does provide essential RSR information (Wright et al. 2012a) but does not shed light on what a given OSR:RSR ratio may be. Characterizing mating systems will require innovative strategies that integrate research methods—for example, combining in-water monitoring and hatchling genetic sampling.

Reproductive biology and male limitation. Knowledge gaps surrounding reproductive biology make it difficult to conceptualize what proportion or number of males in a mating population may be limiting. Given an understanding of OSRs and RSRs for a population, monitoring egg fertility rates shows promise toward addressing this gap (Phillott and Godfrey 2020).

Sex ratio skew, genetics, and adaptive potential. We are building toward a future in which sea turtle genetics and genomics will be integrated into population assessments more routinely. Genetic diversity should be included when considering male limitation. Even if a population is not male limited in terms of females being able to find mates, it may be male limited genetically. That is, at extreme sex ratio skew the decreasing proportion of males in the population represents a shrinking pool of genetic diversity, and as this pattern iterates through generations of warming the risk of inbreeding and deleterious fitness effects increases. Moreover, as genetic diversity declines, adaptive potential declines with it and may limit resilience to ongoing climate change. Broader, more intensive sampling of genetic diversity and monitoring of N_e will be crucial moving forward, as will genomic techniques to evaluate avenues for adaptive response.

These research topics present data deficient areas of need as sea turtle conservation moves into a future with accelerating climate change. In the absence of empirical data for key demographic parameters, predicting viability across a range of biologically realistic values may be prudent (e.g., exploring varying male breeding intervals or rates of sex-specific survival). Such exercises can help to quantify uncertainty and may aid in identifying what demographic variables should be prioritized for future research. Embracing variation will also be important for elucidating the effects of warming on viability, because characterizing traits such as thermal reaction norms at the population level can gloss over key intrapopulation and intraindividual variation (e.g., Carter et al. 2019). From refining the understanding of thermal reaction norms to documenting breeding periodicity and identifying genomic regions of accelerated change, research continues to address data deficiencies and push the field toward answers.

As the understanding of demographic dynamics (especially male demography) expands, so too will the ability to project the future impacts of warming. As such, this review has focused primarily on sex ratios and male biology. We note, however, that impacts on egg survival may be more threatening to populations than changes to sex ratios (Saba et al. 2012, Hays et al. 2017), and they are easier to understand and project. Nonetheless, in a scenario in which sea turtles can adapt and persist, we suggest that working toward a comprehensive understanding of warming's impacts is warranted. We acknowledge that climate-associated changes to demography across all life-history stages, rather than just offspring, will be important to accommodate in modeling and projections (Hamann et al. 2013). Furthermore, it will be beneficial to advance the capacity to incorporate diverse facets of global change into viability inferences (see box 3). In the present article, we focused on warming temperatures but recognize that other factors may be equally important to evaluate. Hamann and colleagues (2013) reviewed many environmental changes relevant to sea turtles, including changes in sea level, sea surface temperatures, and precipitation. Much work has advanced our understanding of how these factors may affect populations, and a promising trend is the integration of multiple facets within a single analysis (e.g., Montero et al. 2018, Patrício et al. 2019). Mechanistic models represent a cohesive approach to such integration. For instance, Stubbs and colleagues (2020) used mechanistic modeling to evaluate different pressures on an Australian green turtle population and suggested that climate change impacts on food availability could have more severe effects than direct impacts on demographic parameters.

Projecting population persistence is an important exercise to evaluate and inform conservation action. However, tracking the fate of sea turtle cohorts is logistically challenging and resource intensive, leaving information gaps for fundamental aspects of demography. Currently, predictions must rely on assumptions lacking empirical support about important aspects of viability (e.g., genetic diversity, male reproductive ecology). However, we highlighted advances across diverse disciplines that provide evidence for an accelerating wave of research on how global climate change will affect sea turtle population viability. As research builds and continues to address data deficiencies, the field of sea turtle conservation has a solid base to inform adaptive management and future

Box 3. Global change and sea turtles: Emergent threats.

Beyond many relatively well-documented aspects of climate change, new threats continue to emerge and may interact with each other or with longstanding threats to populations. We highlight five threats garnering research attention. First, broadscale ecological regime shifts may unfold with changing climates. Bjorndal and colleagues (2017) implicated such a regime shift in association with somatic growth rate declines in immature turtles across three species throughout the Western Atlantic. Second, plastics in the marine environment are increasingly linked to sea turtle mortality (Wilcox et al. 2018). Third, apparent increases in episodic proliferation of algae may inundate nesting habitats (e.g., *Sargassum* spp.; Maurer et al. 2015) or cause the release of toxins in coastal environments (e.g., red tides; Foley et al. 2019). Fourth, the rising incidence of disease associated with anthropogenic impacts on the marine environment threatens many populations (e.g., fibropapillomatosis; Jones et al. 2016). Fifth, and related to the fourth, environmental contaminants from products such as pharmaceuticals and pesticides have been shown to affect immune, neurological, and endocrine function in aquatic wildlife (e.g., Arnold et al. 2014, Desforges et al. 2016). The feminizing effects of certain plasticizers—even at low doses—are particularly relevant to sea turtle biology given projected changes to sex ratios (Vandenberg et al. 2012). Epigenetic effects from certain contaminants may be heritable and therefore influence microevolutionary pathways for adaptation (Anway et al. 2005).

studies under changing climates. The lessons we glean from sea turtles also apply broadly to any population viability context: To understand how sublethal impacts of climate at one life-history stage will affect reproductive output or survival at another life-history stage, we must consider the full natural history of organisms.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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