



## ECOLOGICAL CONSEQUENCES OF SEXUALLY SELECTED TRAITS: AN ECO-EVOLUTIONARY PERSPECTIVE

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### ABSTRACT

*Evolution is rapidly gaining attention as an important driver of ecological process. Yet, evolution via sexual selection has generally been omitted from this emerging synthesis. Our goal in this paper is to illustrate causative links by which sexually selected traits affect fundamental ecological interactions and processes. We summarize evidence, primarily from vertebrate studies under field conditions, which shows: sexually selected traits have ecological effects; and that their evolution has diverse influences on ecological systems. We conclude with a brief discussion of future research directions to encourage study of sexual selection from a more integrative and eco-evolutionary perspective.*

### INTRODUCTION

**S**EXUAL selection, variance in reproductive success arising from competition for mating opportunities and fertilization success, is a potent evolutionary force. Sexually selected traits (SSTs) evolve by sexual selection and include a wide range of behavioral, morphological, and physiological characters that increase performance in competition for mate and fertilization suc-

cess (Andersson 1994). The extraordinary form, structural complexity, and apparent maladaptiveness of SSTs have drawn the attention of theorists and empiricists for over a century (Darwin 1871; Fisher 1930; Trivers 1972). Although nonecological (i.e., Fisherian) models of sexual trait evolution have existed since initial efforts to understand how SSTs evolve (see Prum 2012), a particularly productive approach to understanding

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how these adaptations evolve has been to study sexual selection in an ecological context (Emlen and Oring 1977; Grafen 1990; Maynard Smith 1991; Endler 1993). Indeed, it is widely appreciated that ecological factors generating fitness costs of mate competition, variability in resource availability, and environmental heterogeneity are crucial underpinnings of SST evolution and diversification (Trivers 1972; Emlen and Oring 1977; Maynard Smith 1991; Kokko et al. 2002; Arnqvist and Rowe 2005; Emlen 2008; Maan and Seehausen 2011; Ryan and Cummings 2013; Servedio and Boughman 2017; Rico-Guevara and Hurme 2019). The resulting integration of sexual selection and ecology constitutes the model framing our contemporary understanding of how SSTs evolve and diversify.

But an emerging synthesis—eco-evolutionary dynamics—has identified some overlooked aspects of this ecological model of sexual selection. A major objective of eco-evolutionary perspectives is to account for interactions between ecological and microevolutionary processes (Hairston et al. 2005; Lankau 2011; Schoener 2011; Hendry 2016). This broad and integrative model has successfully illustrated the diverse ways in which microevolution can influence ecological processes and patterns, from population growth to ecosystem function. It has also revealed numerous gaps in evolutionary ecology research programs, both theoretical and empirical (McPeck 2017). An obvious bare spot involves sexual selection—specifically, a lack of research illustrating how sexual selection might influence ecological process and pattern (Svensson 2018). Why this apparent oversight exists is at first puzzling; surely sexual selection would have widespread and potent ecological consequences? After all, sexual selection can drive the evolution of intraspecific phenotypic diversity (Gross 1996; Sih et al. 2004; Svensson et al. 2009; McKinnon and Pierotti 2010; Servedio and Boughman 2017; Rico-Guevara and Hurme 2019), generate fitness costs for one or both sexes via sexual conflict (Clutton-Brock et al. 1982; Arnqvist and Rowe 2005), promote adaptation (Agrawal 2001; Whitlock and Agrawal 2009; Agrawal and Whitlock 2012; Servedio

and Boughman 2017), and influence the evolution of traits (e.g., body size, aggression) already linked to fundamental ecological processes (King 1973; Peters 1983; Elser et al. 1996; Woodward et al. 2005; Réale et al. 2007).

Thus, it appears that ecological consequences of sexual selection are likely. But despite a reasonable expectation that sexual selection will have pervasive effects on ecological systems, attribution of ecological dynamics to sexual selection is largely restricted to a few model systems: red deer (*Cervus elaphus*; Clutton-Brock et al. 1982), Soay sheep (*Ovis aries*; Clutton-Brock and Pemberton 2004), and red grouse (*Lagopus lagopus*; Mougeot et al. 2003). Consequently, a broad analysis of the effects of sexual selection on ecological process and pattern does not exist—a reality that seems to preclude a synthetic eco-evolutionary model integrating sexual selection dynamics.

Our objective here is to advance an eco-evolutionary perspective on sexual selection. A full synthesis will require integrating multiple aspects of ecology and evolution; from trait-based approaches emphasizing the direct and indirect effects of the evolved phenotype to those emphasizing the effect of sexual selection on genetic load (Agrawal 2001; Whitlock and Agrawal 2009; Agrawal and Whitlock 2012). However, we focus this review on the former and conducted a broad literature survey for evidence that SSTs influence ecological processes and patterns. We relied heavily on vertebrate studies conducted under natural or semi-natural conditions (see Supplemental Table 1, available at <https://www.journals.uchicago.edu/loi/qrb>). This focus on vertebrates is not meant to imply that other taxonomic groups do not express SSTs with ecological consequences—indeed they do (Valiela et al. 1974; Caravello and Cameron 1987; Svensson et al. 2005; Gosden and Svensson 2009; Smallegange and Deere 2014; Godwin et al. 2018; Yun et al. 2018). Rather, such circumscription reflects the scope our own expertise and our goal of illustrating ecological processes in natural systems. Although our taxonomic scope is somewhat narrow, our definition of ecological conse-

quence is rather broad—and, in some cases, the supporting links are admittedly speculative. Because the focus of this review is on illustrating diverse and important ecological consequences of SSTs, not the processes underlying their evolution, we have structured our review to emphasize three commonly employed levels of ecological analysis: interspecific interactions and community dynamics, population ecology: distribution, population ecology: demography, and ecosystems before moving on to discuss future opportunities for research and some overall generalities.

#### INTERSPECIFIC INTERACTIONS AND COMMUNITY DYNAMICS TROPHIC ECOLOGY

Foraging traits are commonly subject to evolutionary tension between viability and sexual selection that can shape resource capture efficacy (Emlen 2008; Rico-Guevara and Hurme 2019). To date, most empirical studies of foraging ecology do not consider this complexity. Nevertheless, evidence for sexual selection effects on trophic relationships and foraging behaviors exist for a wide range of systems and organisms (Supplemental Table 1). Below we review the effect of SSTs on feeding relationships and discuss ways in which SSTs affect more fundamental aspects of foraging ecology: foraging rate and optimal diet. We consider two routes by which sexual selection can influence trophic ecology: direct and indirect. Direct links arise when traits used in feeding evolve by sexual selection. For example, the evolution of enlarged canines or increased bite force evolved by intrasexual competition for mating opportunities. Alternatively, indirect effects are those in which sexual selection influences foraging traits through pleiotropic effects—for example, the indirect effect of sexual selection on foraging behavior mediated by large male body size.

Many traits used in intraspecific interactions such as fighting or coercive mating are also involved with prey capture or handling (Valiela et al. 1974; Emlen 2008; Morris and Carrier 2016; Rico-Guevara and Hurme 2019). Therefore, evolution of SSTs

such as enlarged teeth (e.g., tusks) or increased bite force should affect what organisms eat. This dual role of foraging traits is obvious in taxa where bite force contributes to mating success and foraging. In lizards, for example, sexual selection on bite force produces males with the ability to consume prey requiring additional force (Vitt and Cooper 1985; Gvozdík and Van Damme 2003; Lappin and Husak 2005; Huyghe et al. 2009; Vanhooydonck et al. 2010). Indeed, many studies show that sexual selection on foraging traits expands population trophic niche width when males consume larger or well-defended prey taxa, an example of a direct effect of sexual selection on foraging traits (Fritts and Sealander 1978; Birks and Dunstone 1985; Vitt and Cooper 1985; Verwajen et al. 2002; Vincent and Herrel 2007; Scali et al. 2016; Figure 1a).

Although combat-mediated competition between males seems to be a major driver of trophic trait evolution, selection by female choice can also shape trophic morphology. For example, in fishes, paternal care is well developed and taxonomically widespread, ranging from nest construction and brood defense to mouthbrooding (Oppenheimer 1970; Ridley 1978; Baylis 1981; Gross and Sargent 1985). Although parental care can evolve by selection on male fecundity, female discrimination among males based on traits indicating the quality of parental care introduces a sexual selection component to the evolution of parental traits such as mouthbrooding (Hoelzer 1989; Alonzo 2011). It therefore seems likely that sexual selection underlies evolutionary modification of trophic morphology in paternal-brooding fishes: reduced gill raker number in cichlids (Lowe McConnell 1959), as well as increased in male head size, jaw length, and buccal volume in other fishes (Hess 1993; Barnett and Bellwood 2005; Hoey et al. 2012)—all of which are linked to feeding performance (Wainwright and Richard 1995). Ultimately, sexual selection on trophic traits in paternal-brooding fishes remains unaddressed, as does the effect of mouthbrooding morphology on feeding performance and foraging ecology (but see Lowe McConnell 1959; Hoey et al. 2012).

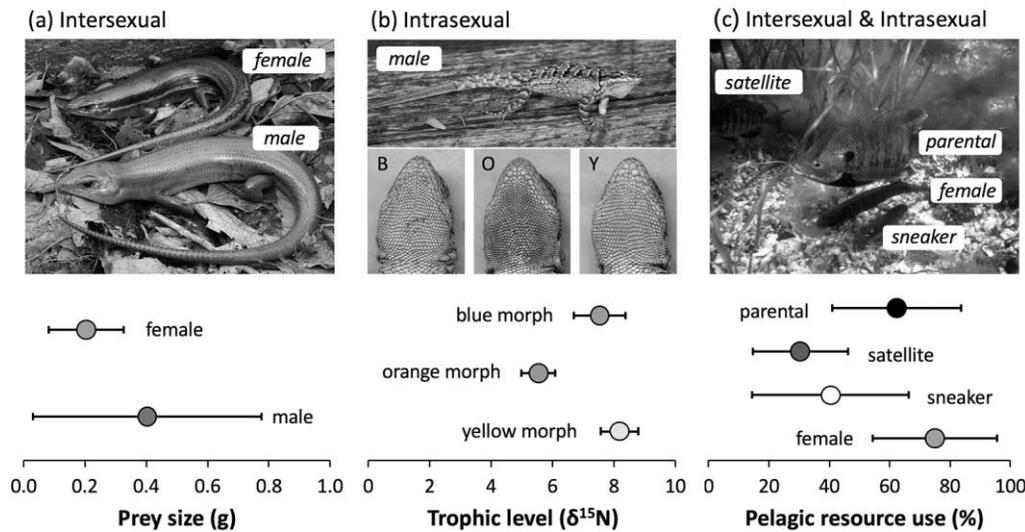


FIGURE 1. THREE EXAMPLES OF INTRAPOPULATION NICHE DIVERGENCE AMONG AND WITHIN SEXES DRIVEN, IN PART, BY SEXUAL SELECTION

Intersexual dietary niche variation in mature broadhead skink (*Plestiodon laticeps*); mean prey size differs between mature males and females with males consuming larger prey. Also note the greater variation of prey size consumed by males, suggesting that males consume small and large prey (a). Intrasexual dietary niche variation among male color morphs, blue (B), orange (O), and yellow (y), in the ornate tree lizard (*Urosaurus ornatus*). Stable isotope data show blue and yellow morph males occupy higher trophic levels than orange morph males (b). Intra- and intersexual niche divergence in bluegill sunfish (*Lepomis macrochirus*). Polymorphic male types differ in pelagic resource use, with satellite and sneaker males using littoral habitats and prey, while paternal males and females tend to use pelagic habitats (c). Plots are redrawn from data in: Vitt and Cooper (1985; a), Lattanzio and Miles (2016; b), and Colborne et al. (2013; c). Photo credits: Edward Prinzier (a), Alice Abela (top b), Matthew Lattanzio (inset b), and Bryan D. Neff (c). See the online edition for a color version of this figure.

In addition to direct selection on foraging traits, sexual selection can influence diet indirectly. Because organisms are genetically and developmentally integrated, evolutionary pressures such as sexual selection will impact a range of traits via correlated selection. Indeed, evolution of male body size, a frequent target of sexual selection, affects nearly all aspects of organismal biology, including trophic ecology (Owen-Smith 1988; Cohen et al. 1993; Layman et al. 2005; Brose et al. 2006; Owen-Smith and Mills 2008). These indirect mechanisms arise because of the effect of body size on digestive physiology, stress tolerance, locomotor performance, and handling costs. Below, we briefly review a few examples.

The effect of body size on digestive physiology is a well-known driver of intersexual trophic divergence arising through an indirect effect of sexual selection. The Jarman-Bell

principle describes the positive allometric relationship between body size and digestion efficiency observed among ruminant species (Geist 1974; Demment and Van Soest 1985). The Jarman-Bell principle also helps explain why large males in size-dimorphic ruminants often consume lower quality foods and/or spend less time foraging than females (Clutton-Brock et al. 1987; Mooring et al. 2005; Pérez-Barberia et al. 2008).

In aquatic air-breathing animals, sexual selection for large male body size affects physiological capacity to tolerate extreme physical environments. In size-dimorphic diving animals such as pinnipeds and marine iguanas, larger males store more oxygen (Le Boeuf et al. 1993; Kooyman and Ponganis 1998) and heat (Bartholomew 1966) than females. These intersexual physiological differences indirectly contribute to divergent diets when males forage in more extreme en-

vironments (usually colder and deeper) and consume different prey taxa than females (Trillmich and Trillmich 1986; Le Boeuf et al. 2000; McIntyre et al. 2010a,b).

Intersexual variation in body size can also translate to divergent foraging niches when locomotor performance is size-dependent. In seabirds, sexual selection on male body size is widespread (Serrano-Menses and Székely 2006), as is intersexual diet variation (Lewis et al. 2002; Phillips et al. 2011; Mancini et al. 2013). Although behavioral differences between males and females are often important, intersexual diet variation in sexually dimorphic seabirds is often explained by the effect of body size on flight and diving performance (e.g., Weimerskirch et al. 2006, 2009). Ultimately, body size influences performance—when and where individual seabirds forage as well as what taxa are consumed (Phillips et al. 2004; Lewis et al. 2005; Weimerskirch et al. 2009; Quintana et al. 2011; Camphuysen et al. 2015).

Sexual selection for large body size is also likely to cause correlated shifts in foraging trait sizes. Often, the larger sex will have larger trophic traits (e.g., canine teeth, head size). Given that the size (relative to prey) of traits such as gape width and bite force determine handling costs and prey suitability, intersexual dietary variation driven by indirect sexual selection on trophic traits should be widespread (Gittleman and Van Valkenburgh 1997). However, identifying the indirect effect of sexually selected body size on trophic ecology is complicated by the fact that sex-specific allometries often arise from direct sexual selection on trophic morphology (e.g., as discussed above, large males often have relatively strong bite force due to sexual selection). These sex-specific allometries make it difficult to determine whether intersexual diet variation in size-dimorphic species can be attributable to body size variation or a relative shift in trophic traits (e.g., a shift in relative bite force). For this reason, an effect of sexually selected body size on trophic ecology is perhaps clearest in weasels (*Mustela* spp.), a group exhibiting sexually selected, male-biased size dimorphism and relatively minor allometric variation between sexes in skull

length (Moors 1980; King and Moody 1982; Dayan et al. 1989). Given that head size scales with body size similarly in both sexes, the fact that male weasels generally consume larger prey taxa more frequently than females helps isolate the indirect contribution of sexually selected body size to intersexual variation in trophic ecology.

Female preference for ornaments and indicators of parental care can also influence trophic ecology indirectly. Elongated tails, common targets of sexual selection in fishes and birds, can reduce locomotor performance (Balmford et al. 1993; Basolo and Alcaraz 2003). And if prey capture depends on the ability to capture fast-moving or maneuverable prey, one might expect ornament elaboration to shape the trophic niche. Few data are available to test this prediction; however, in the barn swallow (*Hirundo rustica*), streamer length and the size of insect prey are negatively correlated, suggesting a performance-based link between ornament evolution and foraging ecology (Møller 1989; Møller et al. 1995a). Sexual selection on nest size or quality can also shape trophic morphology. For example, male stickleback (*Gasterosteus aculeatus*) build and defend nests in which females spawn. Nest construction is aided by morphological modifications, including enlarged heads and protruding jaws in males (Van Iersel 1953; Kitano et al. 2007), a biomechanical link that McGee and Wainwright (2013) argue can drive intersexual diet variation in stickleback. However, the links between female choice, foraging trait evolution, and trophic ecology remain to be understood in this system.

At a more fundamental level, individuals trade off foraging with other activities, routinely alternating between periods of feeding and other behaviors. Much has been written about the ecological effects of such foraging tradeoffs, from individual fitness to whole ecosystems (Lima and Dill 1990; Werner and Peacor 2003; Schmitz et al. 2004; Ford et al. 2014). Indeed, the magnitude of predation risk effects on ecosystems are now known to be on par with the direct effects of predators (Preisser et al. 2005). But competition for mates also shapes forag-

ing behavior, generating tradeoffs between foraging and reproduction. For example, when competition for mates is strong, males reduce foraging rate and duration to pursue reproductive opportunities (Durtsche 1992; Cowles and Gibson 2015). Outside of periods of intensive sexual activity, this energetic deficit may be compensated by increased foraging rate, either during or prior to intensive mating activity (Ferretti et al. 2014)—a strategy for enduring periods of high reproductive investment (Lindstedt and Boyce 1985; Millar and Hickling 1990). High investment in mate competition also negatively impacts female foraging behavior, as illustrated by poeciliid fishes in which persistent copulation attempts and coercive mating by males reduces female feeding rates (Magurran and Seghers 1994; Pilastro et al. 2003; Köhler et al. 2011; Tobler et al. 2011). In effect, mate defence, direct combat, and mate searching reduce and interfere with foraging and energy acquisition in males and females. Indeed, experimental manipulation of sex ratios in western mosquitofish (*Gambusia affinis*) reveal the effects of sex-specific foraging ecology on prey community composition and food web structure—specifically, a dampening of top-down control in male-biased populations—effects consistent with sex-specific foraging behavior and/or a negative effect of male harassment on female foraging (Fryxell et al. 2015). Ultimately, these foraging-reproduction tradeoffs drive temporal variation in the strength of consumer-resource interactions—inducing or relaxing trophic cascades depending on the intensity of mate competition.

The production and maintenance of SSTs also entails substantial nutritional demands (Morehouse et al. 2010; Morehouse 2014; Snell-Rood et al. 2015). These costs of SSTs can be energetic (Vehrencamp et al. 1989; Deutsch et al. 1990; Plaistow et al. 2003; Galimberti et al. 2007; Cummings and Gelineau-Kattner 2009; Stoddard and Salazar 2011), stoichiometric (Goos et al. 2016), and macromolecular (Hill 1992; Hill et al. 2002; Svensson and Wong 2011; Sentinella et al. 2013). Emerging research on nutritional ecology routinely shows that nutritionally optimal diets for males and females often

differ (Raubenheimer et al. 2009). These optimal diets reflect adaptive, sex-specific life-history investments—increasing fecundity in females and maximizing fertilization in males. Substantial departure from these optima can severely impact individual mating success. But although the field of nutritional ecology is steadily evolving—and offers a much-needed framework for understanding the evolution of foraging ecology—evidence from natural systems is surprisingly limited (Kohl et al. 2015). Indeed, a study of diets in wild hihi (*Notiomystis cincta*) demonstrating male preference for carotenoid-rich fruits (carotenoids are incorporated into male plumage displays) provides a rare example of intersexual diet variation that seems to have evolved by sexual selection on dietary preferences (Walker et al. 2014).

Hence, it remains unclear how common sexually selected dietary biases are. If judged by data from natural systems it seems that although sexual selection should favor sex-specific diets (such as when carotenoid intake limits reproductive success in guppies, *Poecilia reticulata*, and house finches, *Haemorrhous mexicanus*), sex-specific optimal diets do not evolve or realize under field conditions (Kohl et al. 2015). This supposition is, however, provisional. Indeed, a substantial body of experimental work with invertebrates routinely shows that sex-specific diets do evolve as a consequence of sexual selection (Lee et al. 2008; Maklakov et al. 2008; Lee 2010; South et al. 2011; Harrison et al. 2014; Gray et al. 2018). Obviously, more work on the role of sexual selection on sex-specific diets is needed and we encourage additional research on the evolutionary ecology of SSTs to incorporate nutritional frameworks such as nutritional geometry and ecological stoichiometry (Raubenheimer et al. 2009; Morehouse et al. 2010; Jeyasingh et al. 2014; Snell-Rood et al. 2015).

#### POSITIVE INTERSPECIFIC INTERACTIONS: SEED DISPERSAL AND FACILITATION

Interspecific interactions such as predation and parasitism underpin much of the theory and empirical evidence for the evolution of sexual traits (Hamilton and Zuk

1982; Endler 1983; Milinski and Bakker 1990; Folstad and Karter 1992; Zuk and Kolluru 1998; Giery and Layman 2015). Yet, recent research is expanding the types of ecological interactions that SSTs influence, generally indicating that the evolutionary ecology of SSTs are relevant for a broad range of interspecific interactions and community dynamics. The examples presented below show SSTs can also mediate positive interspecific interactions—seed dispersal and facilitation.

Seed dispersal mediated by SSTs follows two modes. The first is the typical endozoochorous pathway where seeds are dispersed postconsumption. The second mode is similar, except fruits and seeds are moved and aggregated without being consumed. The former case is exemplified by several species of bird (and at least one mammal) that forage widely yet spend disproportionate time at focal sites dedicated to sexual display and mate choice, i.e., leks or singing perches. This spatial bias—in defecation—toward specific locations within the landscape generates clumped patterns of seeds and seedlings at lekking sites (Théry and Larpin 1993; Krijger et al. 1997; Cestari and Pizo 2013a,b; Jadeja et al. 2013) and treefall gaps where displays are focused (Wenny and Levey 1998; Karubian et al. 2012; Karubian and Durães 2014). In another case, male spotted bowerbirds (*Ptilonorhynchus maculatus*) also disperse and aggregate seeds in an interaction not mediated by endozoochory. Like other bowerbirds, they gather forest materials to construct bowers, complex structures subject to female choice (Borgia 1985). Fruits and seeds aggregated at (and disposed near) bowers can subsequently germinate, thereby altering nearby plant communities (Madden et al. 2012).

Understanding the effects of seed dispersal on forest dynamics involves many factors. Simply put, dispersal does not increase parental fitness if seeds are aggregated at suboptimal locations, i.e., those with high seed(ling) densities or suboptimal abiotic conditions. Nevertheless, birds that aggregate seeds at display sites may be especially valuable as dispersers if these negative effects are absent or are countered by positive

effects of being aggregated there. Indeed, as shown in Karubian and Durães (2014) and Karubian et al. (2016), dispersal to long-wattled umbrellabird (*Cephalopterus penduliger*) lek sites is a prime example of directed dispersal—deposition at sites favorable for establishment (Howe and Smallwood 1982). In this system, males deposit large numbers of seeds at lek sites (more than 50% of ingested seeds) and transport seeds farther than females (18% farther for large-seeded and 33% for small-seeded fruits). Although such dense seed aggregations can limit seedling fitness via negative density dependence, experimental and observational data show that lek-deposited seeds do not suffer from negative density dependence as expected. That is, seeds deposited at lek sites have similar germination rates, seedling survival, and growth as seeds deposited elsewhere because long-distance dispersal increases local genetic diversity of seeds at lek sites, an effect that ameliorates—to some degree—the negative effects of conspecific density (Karubian et al. 2016).

These seed dispersal examples are generally derived from a few species of highly frugivorous tropical birds. Yet, they clearly show that habitual attendance at sexual display sites (up to 95% of time in umbrellabirds) can affect plant community structure in a variety of ways. Much remains to be learned about the effectiveness of dispersal to display sites and its effect on forest structure, but data from umbrellabirds and bowerbirds appear to show that directed dispersal mediated by site-specific and long-term male breeding display sites can increase recruitment for focal species and alter plant community structure. Given the abundance and diversity of frugivorous birds in tropical forests, we suspect that these examples reflect a link between sexually selected behavior and seed dispersal more common than the low number of case studies might suggest.

Another example of positive interactions comes from rivers and streams of North America. Male cyprinid fishes in the genera *Semotilus*, *Camptostoma*, *Nocomis*, and *Notropis* build large, mounded, silt-free structures of stone and gravel at the tail end of pools (Ross 1977; Ross and Reed 1978; Vives 1990;

Sabaj et al. 2000). Part nest, part display structure, males actively tend, solicit spawnings at, and protect eggs laid in their mounds. These structures are also hubs of spawning activity for a variety of fishes. For example, in the Virginia stretch of New River, U.S., 11 species of nest-associated fishes were recorded spawning in *Nocomis* spp. mounds (Pendleton et al. 2012). Moderately sized and abundant, nest mounds are a conspicuous feature of shallow lotic waters; however, the foundational ecological role of mound-building cyprinids has only recently garnered much excitement from ecologists. Nevertheless, recent research suggests that these mounds provide limited (protected and silt-free) spawning habitats for other cyprinid species, some of which rarely spawn away from heterospecific mounds (Pendleton et al. 2012; Peoples and Frimpong 2013). The resulting pattern is one in which the presence of nest-associate fishes is contingent on the existence of silt-free nesting habitats created by mound-building cyprinids; a keystone interaction detectible at basinwide scales (Peoples et al. 2015; Peoples and Frimpong 2016).

A greater appreciation for the role of positive interactions in community and ecosystem dynamics is still emerging (Stachowicz 2001; Bruno et al. 2003). Although we think the examples presented above are compelling, in general, we found relatively few studies illustrating a positive effect of SSTs on heterospecifics. We also note that the range of interactions uncovered is quite narrow—seed dispersal in tropical birds and habitat creation in lotic minnows. Nevertheless, additional research on facilitation is likely to yield more insights for two reasons. First, seed dispersal and habitat modification are taxonomically and geographically widespread, suggesting that positive interactions mediated by SSTs are likely to be quite common. Second, other positive interactions are likely to emerge with additional study. For example, in laboratory trials, several species of newts (*Lissotriton vulgaris*, *L. helveticus*, *Triturus cristatus*, and *T. marmoratus*) exhibit positive phonotactic responses to the mating calls of sympatric anurans (Diego-Rasilla and Luengo 2004, 2007; Pupin et al. 2007; Madden and Jehle 2017). Whether orientation toward the

mating calls of heterospecifics facilitates location of high-quality breeding habitats has yet to be evaluated. Indeed, further attention to positive heterospecific interactions is likely to uncover a variety of community-level consequences of SSTs.

#### PARASITES AND DISEASE DYNAMICS

Few patterns in animal ecology are as pervasive as the highly aggregated distribution of parasite infestations in host populations (Shaw and Dobson 1995). There is remarkable heterogeneity among individuals in the prevalence, intensity, and diversity of parasite burdens. However, infestation variation is also regularly seen among demographic classes, particularly age and sex (Wilson et al. 2003). Although not universal (Kiffner et al. 2013), the prevalence (frequency of hosts infected) and intensity (number of parasites per host) of parasite infestation is often higher in adult male birds (Isomursu et al. 2006; Robinson et al. 2008), mammals (Schalk and Forbes 1997; Ezenwa 2004; Morand et al. 2004), amphibians (Dare and Forbes 2008), reptiles (Cox and John-Alder 2007; Godfrey et al. 2010), and fish (Reimchen and Nosil 2001). In addition, male-biased infections span a range of micro- and macroparasites, including viral, bacterial, protozoan, and arthropod organisms (Poulin 1996; Zuk and McKean 1996; Moore and Wilson 2002; Robinson and Klein 2012).

A popular and long-standing explanation for male-biased infection is that physiological costs underlying SST production suppress male resistance to infection by parasites and other disease-causing organisms (Hamilton and Zuk 1982; Folstad and Karter 1992; Klein 2004; Klein and Flanagan 2016). The mechanisms underlying these immunological costs are diverse, complex, and nonexclusive (reviewed in Jacobs and Zuk 2012). But, in general, they include one or more of the following: sex hormones such as testosterone are immunosuppressive, immunoprotective macromolecules such as carotenoids used in sexual trait production are limited, and allocation of energy to mate competition reduces immune function. Consequently, males

must trade off investment in sexual fitness against the viability costs of lowered immune function and corresponding infection vulnerability (Sheldon and Verhulst 1996; Olson and Owens 1998; Stoehr and Kokko 2006). However, years of ambiguous and often conflicting empirical results obscure the mechanistic links between sexual selection and infection vulnerability.

Despite this prolonged uncertainty, evidence that physiological costs of sexual trait expression underpin immunological vulnerability and pervasive male-biased infections is growing stronger (Roberts et al. 2004; Jacobs and Zuk 2012; Foo et al. 2017). Yet the importance of sex-specific physiology for parasite population dynamics remains unclear. Although male vulnerability can increase infection prevalence and intensity, without mechanisms that describe transmission heterogeneity, a purely physiological model is incomplete (Zuk and McKean 1996; Wilson et al. 2003; Hawley and Altizer 2011; Hawley et al. 2011; Ezenwa et al. 2016). A more ecological model is needed to account for heterogeneity in exposure and transmission rates (Zuk and McKean 1996).

Exposure and transmission rates commonly influenced by traits evolved by sexual selection: high movement rates, large home range, persistence at mating sites, intra-sexual aggression, high mating rates, and large body size (Tinsley 1989; Olsson et al. 2000; Gear et al. 2009; Godfrey et al. 2010; Devevey and Brisson 2012). For example, using experimental manipulations of sex-specific infection Ferrari et al. (2004) and Gear et al. (2012) showed that removal of female parasite infections in yellow-necked mice (*Apodemus flavicollis*) had a negligible effect on male infections, while removal of male infections led to a drastic reduction in female infection prevalence and intensity. Because sex-biased infections were not apparent in the untreated control plots, these studies clearly suggest that physiological vulnerability mechanisms are not driving the observed effect of males on parasite persistence in these systems. Rather, the infection amplifying effect of males was driven by ecological mechanisms that increased exposure for both sexes—via high conspecific

contact rates (Randolph 1977; Ferrari et al. 2007; Perkins et al. 2008) or high contact frequencies with intermediate hosts (Luong et al. 2009; Gear et al. 2012). Here, the evolutionary effect of sexual selection on male behaviors mediates the ecological mechanism of parasite transmission, providing a clear demonstration that sex-dependent physiological vulnerability is not necessary for the perpetuation of pathogen populations by males.

More often than not, physiological mechanisms and ecological mechanisms coincide (Hawley et al. 2011). Population dynamics of *Ixodes* ticks (Salvador et al. 1996; Olsson et al. 2000; Hughes and Randolph 2001), nematodes (Seiwright et al. 2005; Mougeot et al. 2006), and hantaviruses (Glass et al. 1988; Bernshtein et al. 1999; Mills et al. 1999; Olsson et al. 2002; Hinson et al. 2004; Easterbrook et al. 2007; Adler et al. 2008; Hannah et al. 2008; Amman et al. 2013; Khalil et al. 2014) clearly involve male vulnerability and behavior. Indeed, without the combination of mechanisms many of these host-parasite systems are projected to simply fade out. Tick-borne encephalitis (TBE), for example, is a well-known tick-borne disease in which host vulnerability and high exposure are required for TBE persistence. Specifically, because *Ixodes* tick hosts, wood mice (*A. sylvaticus*), and bank voles (*Myodes glareolus*), do not sustain systemic TBE infections, vector-vector transmission between synchronously feeding (co-feeding) *Ixodes* ticks is necessary for TBE persistence (Randolph et al. 1996, 1999; Randolph 2011). It is the large aggregations of ticks on male rodents, products of immunosuppression and high tick exposure, which facilitate vector co-feeding crucial for TBE transmission (Talleklint and Jaenson 1997; Randolph et al. 1999; Hughes and Randolph 2001; Harrison et al. 2010; Cagnacci et al. 2012). Without the contribution of immunosuppression and high tick exposure driven by sexually selected male physiology and behavior, Perkins et al. (2003) estimate TBE transmission potential declines 74%, probably causing TBE to fade out.

Similarly, males are key hosts in the perpetuation of hantaviruses (Mills et al. 1999; Robinson and Klein 2012; Khalil et al. 2014).

Males tend to exhibit higher infection vulnerability and maintain infectiousness for longer periods than females. Although not universal (e.g., Clay et al. 2009), most new hantavirus infections occur during violent interactions between adult males and reproductive contact between adult males and females (Glass et al. 1988; Bernshtein et al. 1999; Olsson et al. 2002; Hinson et al. 2004; Klein et al. 2004; Easterbrook et al. 2007; Adler et al. 2008; Amman et al. 2013; Khalil et al. 2014). Interestingly, transmission is amplified by virus-mediated manipulation of male behaviors—driving hyperaggressive male-male interactions when hosts are most infectious (Klein 2003; Klein et al. 2004), and increasing movement rates, although this latter mechanism is less clear (Escutenaire et al. 2002; Amman et al. 2013). The data clearly indicate that hantavirus infection amplifies male physiology and ecology in ways that dampen density-dependent transmission, therefore promoting hantavirus persistence during periods of low susceptible host densities (Adler et al. 2008; Luis et al. 2012; Kallio et al. 2013).

Understanding the role of host heterogeneity in parasite infections is critical for determining fundamental components of wildlife disease and parasite dynamics (Zuk and McKean 1996; Woolhouse et al. 1997; Wilson et al. 2003). The fact that relatively few key individuals host and/or transmit a majority of parasite infections has been crucial for determining how parasites persist (Woolhouse et al. 1997; Lloyd-Smith et al. 2005; Tompkins et al. 2011; Godfrey 2013; White et al. 2017). Our scan of this large literature features cases in which SSTs contribute to a disproportionate impact of host sex in a variety of host-parasite systems—not a particularly new finding, but an important one to illustrate here (Zuk and McKean 1996; Jacobs and Zuk 2012). These studies suggest that males are key hosts because their sexually selected physiology makes them highly susceptible to infection (physiological mechanism) and their sexually selected ecology increases parasite encounter and transmission rates (ecological mechanism). Indeed, our brief review of the topic also shows that sex-biased infection preva-

lence and intensity are not the only ways that males impact parasite populations. Rather, the cases we focus on here suggest many parasite populations are maintained by SSTs that simply amplify transmission rates between infected and susceptible individuals (Tinsley 1989; Ferrari et al. 2004; Perkins et al. 2008; Gear et al. 2009, 2012, 2013; Luong et al. 2009; Godfrey et al. 2010; Godfrey 2013; Ezenwa et al. 2016). Nevertheless, ecological and physiological mechanisms often co-occur, reinforcing the effect of males in disease dynamics such as TBE and hantaviruses. So, although the individual characteristics that make a fraction of the population more vulnerable to infection and/or more likely to transmit infections varies among systems, key hosts are usually characterized by one or more of the following: immunological vulnerability, high contact rates with infectious stages, and high contact rates with vulnerable individuals (Lloyd-Smith et al. 2005; Paull et al. 2012). The correspondence between these traits and those targeted by sexual selection is in part what makes males a key demographic in the perpetuation of many zoonoses.

#### REPRODUCTIVE INTERFERENCE

Heterospecific sexual activity has long interested evolutionary biologists investigating speciation (Servedio and Noor 2003; Coyne and Orr 2004). The ecological implications of heterospecific sexual interaction, called reproductive interference (RI), have only recently garnered serious attention from ecologists (Gröning and Hochkirch 2008; Burdfield-Steel and Shuker 2011; Kyogoku 2015; Grether et al. 2017). RI constitutes a diverse set of heterospecific interactions but can be divided into indirect and direct reproductive interference. In a classic example of indirect reproductive interference, heterospecific male frogs interfere with each other's call transmission when they overlap—in time, space, and acoustic properties—sufficiently to mask or “jam” the sexual display of one or both species (Gerhardt 1994). Thus, signaling males indirectly interfere with various hetero-

specific reproductive behaviors such as mate attraction, territorial defense, and perhaps female preference. Most other examples of RI include more direct interactions between heterospecifics: same-sex aggression, courtship, attempted mating, mating and, at the far end of the spectrum, hybridization (reviewed in Gröning and Hochkirch 2008). Direct interferences often resemble instances of mistaken identification of heterospecifics as potential mates. They can arise from: female preferences for heterospecific SSTs or evolution of high mating rates in males (Burdfield-Steel and Shuker 2011). Both of these direct interference mechanisms can have negative fitness consequences for one, or both, species involved (but see Schlupp et al. 1994; Castillo et al. 2010). Here, we focus on RI occurring as a consequence of heterospecific reproductive interactions arising from sexually selected male behaviors rather than female preference.

Given the fitness consequences of heterospecific reproductive efforts, the evolutionary import of RI seems quite clear. For example, where RI is strong, such as regions of sympatry between closely related and/or phenotypically similar species, reproductive character displacement—an adaptive evolutionary response abating costs of deleterious heterospecific reproductive interactions—is favored and may foster coexistence (e.g., Lemmon 2009). Evidence for reproductive character displacement is building, as is understanding of the heterospecific reproductive interactions (i.e., RI) that drive its evolution (Pfennig and Pfennig 2012). Now emerging is a greater appreciation of the ecological consequences of RI in species for which reproductive character displacement and species recognition mechanisms are insufficient for complete behavioral and/or reproductive isolation (Grether et al. 2017). Specifically, RI can reduce individual fitness by costly energetic expenditure, increased physical injury, lost opportunity (reproduction or otherwise), and outbreeding depression (Rhymer and Simberloff 1996; Randler 2002; Tynkynen et al. 2005; Largiadèr 2007; Kishi 2015). If sufficiently intense or prolonged, the consequence of these “mistakes” can

have negative impacts on population mean fitness and persistence (Best et al. 1981; Ribeiro and Spielman 1986; Dame and Petren 2006).

At present, a majority of empirical evidence for RI comes from experiments with model organisms such as seed beetles (e.g., Kishi et al. 2009). Nevertheless, well-documented declines in several species illustrate the strong deleterious effects of RI in natural systems. The clearest demonstrations of ecological consequences of RI includes cases in which species are displaced, due in part to asymmetrical reproductive interference following range extensions by closely related species (Bolger and Case 1992; Rhymer and Simberloff 1996; Dame and Petren 2006). Below, we review two cases in which direct forms of RI driven by male-biased heterospecific interaction have strong effects on wild populations. In all of these cases, traits mediating RI are SSTs: male-male aggression, large male body size, male courtship intensity, and forced copulation. Although an updated review of the ecological effects of hybridization and outbreeding depression is needed, we do not cover it here.

The pervasiveness of resource competition makes it a prime explanation for spatial and temporal patterns in species distributions and abundances (Hardin 1960; Diamond 1978; Schoener 1983). Yet, RI can produce ecological patterns that mimic resource competition, i.e., displacement, exclusion, and extinction. This is particularly clear in the rapidly shifting pantropical distributions of house geckos, a group of phenotypically similar, reproductively isolated lizards (*Hemidactylus turcicus*, *H. mabouia*, *H. frenatus*, and *H. garnotii*). The distribution and abundances of these ecologically similar species continues to shift—most notably through local displacement of *H. garnotii*—a parthenogenic species often among the first to invade anthropogenic ecosystems. Initial studies (Bolger and Case 1992; Petren et al. 1993; Case et al. 1994) concluded that displacement was mediated by frequent agonistic interactions between male *H. frenatus* and the all-female *H. garnotii*—that is, interference competition over foraging sites. Later, a similar experiment performed

by Dame and Petren (2006) found little support for resource competition between these species. Rather, they conclude that *H. garnotii* exclusion is driven by RI; specifically, persistent heterospecific courtship and copulations by male *H. frenatus*. Whether the wave of *H. garnotii* replacement is driven entirely by RI is not clear. However, these data do suggest that coexistence models excluding RI are likely incomplete for phenotypically and ecologically conserved taxa such as *Hemidactylus* geckos.

In the example above, RI was mediated by male-female sexual harassment and copulation costs—a combination of behaviors and physical interactions negatively affecting female viability and perhaps fecundity. Because one of the species was parthenogenetic there was no risk of fertilization, and therefore no risk of indirect fitness costs (i.e., outbreeding depression). However, many well-known cases of RI include multiple interference mechanisms underlying direct and indirect fitness costs (Gröning and Hochkirch 2008). For example, rangewide decline of European mink (*Mustela lutreola*) has been linked to pervasive existential threats such as habitat loss and intraguild predation by introduced American mink (*M. vison*; Fournier et al. 2007; Põdra et al. 2013). However, RI may also contribute to the decline of the European mink. RI is important here because males of two other mustelids, American mink and polecats (*M. putorius*), outcompete the smaller European mink males for access to females (Maran and Henttonen 1995; Cabria et al. 2011). In turn, these heterospecific pairings have unique deleterious effects on European mink populations. Mink pairings (European  $\times$  American) reduce European mink birth rates because resulting embryos are resorbed (Maran and Henttonen 1995). So, although hybrid offspring are not produced, reproductive opportunities are “used up.” Alternatively, polecat matings (European mink  $\times$  polecat) do result in hybrid offspring, a hybrid sink that exacerbates low reproductive success in an already sparse European mink population. In all likelihood, multiple fitness costs of RI involving American mink and polecats contribute to the declining European mink population (Lodé et al. 2005; Cabria et al. 2011).

Much remains to be learned about the ecological consequences of RI under natural conditions (Burdfield-Steel and Shuker 2011; Cothran 2015). Nevertheless, evidence clearly indicates that heterospecific mating is an important mechanism underlying coexistence patterns and community assembly processes (Bull 1991; Thum 2007). Modeling efforts (Ribeiro and Spielman 1986; Kuno 1992), and the prevalence of reproductive character displacement, suggest that RI shapes many aspects of species ecology (Brown and Wilson 1956; Grether et al. 2009, 2013; Pfennig and Pfennig 2009). But because RI can mimic resource competition the importance of RI is likely underestimated, especially in communities that include species with strong sexual selection and imperfect species recognition. Whether RI will substantially impact our understanding of interspecific interactions and species coexistence remains to be seen.

#### POPULATION ECOLOGY: DISTRIBUTION

How individuals are distributed in space reflects a range of ecological factors. Individuals are both repelled by and attracted to conspecifics, heterospecifics, resources, and abiotic conditions (Allee 1931; Brown and Orians 1970). Resulting patterns of space use within populations often reflect shared ecological forces within, and divergent ecological forces between, demographic classes such as sex. Sex-specific distribution patterns within populations often emerge as a consequence. Indeed, several types of sex-specific distribution: sexual segregation, sex-specific distribution, sex-biased arrival, and differential migration are well known and have been the focus of research for decades (Brown 1969; Fretwell and Lucas 1969; Brown and Orians 1970; Morbey and Ydenberg 2001; Ruckstuhl and Neuhaus 2002; Wearmouth and Sims 2008). Despite decades of attention, a systematic treatment of the various patterns and processes underlying sex-specific distributions has yet to emerge (Ruckstuhl 2007). Such an effort is beyond the scope of this review. However, below we briefly examine how SSTs influence the spatial distribution of populations. We structure our treatment around an important prediction

of sexual selection dynamics—sex-specific distribution by resources.

#### DISTRIBUTION BY RESOURCES

The spatial distribution of individuals is a fundamental component of sexual selection theory. In polyandrous or polygynous species, mating opportunities determine, to a large extent, the quality of occupied space for the limited sex (males, in polygynous species). However, for the limiting sex (females, in polygynous species), food, predation, and suitable abiotic features are thought to be the primary factors determining space use (Emlen and Oring 1977). Therefore, selection on mating opportunities should decouple space use from resource distribution in a predictable sex-specific manner: the distribution of females depends on resource dispersion (e.g., spatial variation in food abundance) while males distribute themselves according to mating opportunities as predicted by Emlen and Oring (1977). Here, we briefly scan the literature for support of this prediction (hereafter, the EO assumption).

Evidence for population distribution by sex-specific resources is best illustrated in rodents where long-term studies and experimental manipulations have been used to assess the controls of sex-specific distributions (Ostfeld 1986, 1990). Generally, the EO prediction is supported in polygynous rodents: females tend to match the distribution of resources while males distribute themselves according to reproductive opportunities (e.g., Myllymäki 1977; Ostfeld 1985; Ims 1988; Montgomery et al. 1991). Interestingly, male distributions do not necessarily match female space use because aggressive male-male competition can disrupt the ability of males to track female location directly, ultimately resulting in overdispersed distributions of males (Ostfeld 1990). For example, an experimental manipulation of resources (e.g., food) demonstrated that home range size and overlap for female California voles (*Microtus californicus*) were mediated by food resources, but male home ranges were not (Ostfeld 1986). Coupled with field data, these data suggest that the unresponsiveness of male spatial distribution to additional food and the shifting

distribution of females indicate that male space use is mediated by male-male aggressive competition over access to females (Ostfeld et al. 1985). Sex-specific space use in the San Pedro side-blotched lizard (*Uta palmeri*) follows a similar pattern: males maximize average male-male distance while female spacing responds to the distribution of food resources (Hews 1993). Interestingly, the optimal distribution of males appears to arise from a compromise between maximizing overlap with female distributions and maximizing distance from competitors.

In many taxa, sex-specific space use varies over time if mating opportunities are temporary (e.g., rookeries, leks, or synchronous estrous). In these cases, seasonal fluctuation in mating opportunity coupled with divergent physiology and life history of males and females can produce cycles of sex-specific spacing: males follow female distributions when reproductive opportunities are present, and then redistribute over the remainder of the year. In ruminants such as red deer, this temporal signature is quite clear. Males and females routinely segregate outside of the breeding season—with females often constrained to overgrazed patches of high-quality food (Clutton-Brock et al. 1982, 1987; Main 2008). Similarly, great bustards (*Otis tarda*) also exhibit sex-specific distributions outside of the breeding season. Once courtship and mating are complete, male bustards, which are many times larger than females, often migrate several hundred miles to higher elevations, presumably to escape the physiological stress of lowland breeding grounds (Alonso et al. 2009, 2016; Palacín et al. 2009; Bravo et al. 2016). In both cases, sex-specific variation in physiology, digestion efficiency in red deer, and heat stress in great bustards underlies population distributions outside of the breeding season. Hence, redistribution of males to costly or suboptimal habitats once breeding opportunities return supports the sex-specific resource prediction.

Evidence for population distribution by sex-specific resources also emerges from intersexual variation in phenology. In migratory taxa (best studied in birds), males often depart nonbreeding grounds earlier, migrate more rapidly (Myers 1981; Møller 1994; Ru-

bolini et al. 2004), or use nonbreeding habitats closer to breeding habitats (Ketterson and Nolan 1976, 1983; Belthoff and Gauthreaux 1991; Cristol et al. 1999; Jenkins and Cristol 2002). A common evolutionary explanation for male-biased arrival timing, protandry, is sexual selection: early males better secure and defend high-quality habitats against conspecific males; early arriving males also increase the potential for multiple matings (Kokko 1999; Morbey and Ydenberg 2001). However, early arrival can be a risky strategy. Protandry can entail substantial energetic costs, an increased risk of inclement weather (Møller 1994), as well as increased predation risk (Quinn et al. 2001). Nevertheless, the ubiquity of protandry in migratory birds and fish suggest that males are deviating from resource suitability to a greater extent than females because of sexually selected territory acquisition on breeding grounds (Møller 1994; Hasselquist 1998; Morbey and Ydenberg 2001; Coppack et al. 2006; Spottiswoode et al. 2006). Indeed, the fitness benefits of temporal priority can be strong enough to produce partial migration—an extreme form of differential migration in which some males occupy breeding grounds year-round (Cristol et al. 1999; Jenkins and Cristol 2002; Cagnacci et al. 2011; Chapman et al. 2011).

Nonmigratory species can also differ in temporal aspects of space use that match the EO prediction. In species with periods of inactivity such as hibernation, early onset of activity (i.e., emergence protandry) can maximize mating opportunities (Clutton-Brock and Vincent 1991). The fitness benefits of early male emergence includes earlier spermatogenesis (Prestt 1971; Díaz et al. 1994; Olsson and Madsen 1996; Veiga and Salvador 2001), increased potential for encountering females of higher reproductive value (Bauwens and Verheyen 1985), and increased number of female encounters (Gregory 1974; Douglas 1979; Michener 1983, 1992; Graves and Duvall 1990; Young 1990; Sheriff et al. 2011, 2013). Sexual selection can also drive the evolution of protogyny (female arrive first) in nonmigratory species. Many species breed prior to entering torpor—a scenario that should favor the evolution of protogyny (Gregory 1984; Senior et al. 2005). Although data supporting sex-

biased arrival in fall-breeding animals are sparse, Norquay and Willis (2014) show that female little brown bats (*Myotis lucifugus*) enter torpor (immersion) before males, a pattern we believe suggests sexually selected phenological differences in late-season breeders. Whether late immersion in males reflects a strategy for maximizing reproductive interactions is unclear, but given abundant evidence for protandry in other vertebrates, such an effect seems likely for little brown bats and other species that breed prior to prolonged periods of inactivity.

In all of these examples, sexual selection shapes population distribution in ways matching the EO prediction. However, the observed patterns of sex-specific spatial distributions among taxa are also highly variable. In territorial species, male-male competition has a large effect on the distribution of males. Indeed, even a spatial redistribution of females has little effect on male distributions in some cases. For example, the overdispersed distributions of males in polygynous small mammals might not appear to reflect the distribution of females or food, but the influence of other males can be readily apparent (Ostfeld et al. 1985; Ostfeld 1986). Similarly, sexual selection on temporal activity in migratory birds, fish, and mammals generates sex-specific patterns of space use (protandry and partial migration) that appear to depart from the EO prediction. Furthermore, and perhaps most obviously, detecting sex-specific distributions depends on the potential to mate: sex-specific distributions should not match the EO prediction when mating opportunities are absent. Indeed, temporal variation in the opportunity to mate is often accompanied by a departure from the EO prediction in ruminants (Clutton-Brock et al. 1982, 1987; Deutsch et al. 1990; Crocker et al. 2012).

#### DISTRIBUTION DESPITE RESOURCES

An important development in the evolutionary ecology of sexual selection is an increasing integration of sexual conflict theory, specifically that sexual antagonisms commonly arise from divergent evolutionary interests of the sexes (Trivers 1972). These

conflicting interests drive the sexually selected evolution of aggressive male mating tactics (sexual harassment and coercion) and infanticide (Hrdy 1979; Palombit 2015). They also drive the evolution of female defensive strategies that dilute these costs (Agrell et al. 1998; Ebensperger 1998; Opie et al. 2013; Lukas and Huchard 2014; Palombit 2015). Females show a tendency to dilute the risk of aggressive mating tactics and sexually selected infanticide by altering their use of space: isolating themselves or forming aggregations. These risk-diluting strategies lead to important deviations from optimal resource use in females and departures from the EO prediction.

Females often reduce risk by isolation—increasing the distance between themselves and males. For example, in brown bears (*Ursus arctos*), African lions (*Panthera leo*), and puma (*Felis concolor*), infanticide is a common threat to young. Emerging evidence shows that females with cubs minimize these costs by occupying smaller home ranges and using unproductive foraging areas where male density is low (Packer and Pusey 1983; Wielgus and Bunnell 1994, 2000; Dahle and Swenson 2003; Ben-David et al. 2004; Bellemain et al. 2006; Libal et al. 2011; Steyaert et al. 2013; Keehner et al. 2015). Similarly, aggressive male mating tactics can also drive female fish and dolphins into unproductive, predator-rich, and physiologically stressful habitats (Martin and da Silva 2004; Darden and Croft 2008; Wearmouth et al. 2012; Wallen et al. 2016). The general effect of female isolation seems to be population overdispersion, with females occupying enemy-free space in low-quality habitats.

Alternatively, females can reduce risk by aggregating—decreasing the distance between themselves and conspecifics. For example, coalitions of females, such as a pride of lionesses, can reduce infanticide by repelling invading males (Packer and Pusey 1983; Packer et al. 1990). And in horses and zebras (*Equus* spp.), mares that join harems are protected from harassment and infanticide by a dominant stallion (Rubenstein 1994; Linklater et al. 1999; Sundaresan et al. 2007). Similarly, cooperative defense of shared young against infanticide can favor the formation

of male-female pairs in house mice (*Mus musculus*; Palanza et al. 1996). Finally, just as herding can dilute predation risk (Hamilton 1971; Sterck et al. 1997), dense aggregations of females, such as that seen at pinniped rookeries or same-sex fish shoals, dilutes the per capita risk of infanticide and/or sexual harassment (Le Boeuf and Mesnick 1991; Boness et al. 1995; Galimberti et al. 2000; Pilastro et al. 2003).

How individuals in populations use space is controlled by resources as well as the distribution of aggressive males, specifically those increasing the risk of sexual harassment, coercive mating, and infanticide. These results suggest that a foundational assumption of sexual selection systems—the EO prediction—is generally supported except when and where aggressive mating strategies are common and infanticide risk is high. Under those conditions, female space use appears to depart from the distribution of resources, favoring instead dispersion patterns that dilute risk through isolation or aggregation.

#### POPULATION ECOLOGY: DEMOGRAPHY

Of the ecological dynamics for which sexual selection might be important, demography and population dynamics have received the most attention. The traditional focus of this research program has been to document how sexual selection contributes to male-biased mortality and female-skewed sex ratios in natural populations (Clutton-Brock et al. 1985; Clutton-Brock 1986; Promislow 1992; Promislow et al. 1992, 1994; Tidière et al. 2015). Indeed, the expression of SSTs can decrease male survival (Owen-Smith 1993; Brooks 2000; Quinn et al. 2001; Costantini et al. 2007), increase parasite burdens (Zuk and McKean 1996), cause nutritional stress and physical exhaustion (Mysterud et al. 2005), and lead to combat-related injury (Christian 1971; Clutton-Brock et al. 1979; Clutton-Brock 1982). However, recent analyses and new insights have begun to modify this consensus view on the role of sexual selection in population dynamics.

First, meta-analyses of the fitness consequences of SSTs suggest there is substantial

variation in the viability costs of SSTs because condition-dependent mechanisms underpin sexual trait expression (Jennions et al. 2001; Kotiaho 2001). This may arise because viability costs paid by individuals for the development and expression of SST are proportional to their physical condition. Therefore, condition-dependent investment in sexual selection should help mitigate the ecological cost of SSTs. Indeed, one overall finding of Jennions et al. (2001) is a positive correlation between SSTs and survivorship (Jennions et al. 2001). Second, an increasing body of literature shows the viability costs of SSTs can be ameliorated through the coevolution of compensatory traits that neutralize viability costs of SSTs (Oufiero and Garland 2007; Husak and Swallow 2011; Husak and Lailvaux 2014). For example, unmitigated, the aerodynamics of elongated tail feathers used in sexual displays should hinder flight performance (Balmford et al. 1993; Thomas 1993). Yet these fitness costs do not necessarily accrue if selection on performance leads to the evolution of compensatory traits such as longer wings in male birds with long tails (Balmford et al. 1994; Møller et al. 1995b). Third, in many cases, predators are thought to mediate the cost of SSTs (Endler 1983; Quinn et al. 2001). However, SSTs do not always increase predation vulnerability. Rather, SSTs can decrease mortality risk in some cases by increasing handling costs and the likelihood of predator injury (Mukherjee and Heithaus 2013). Certainly, there are many cases in which large body size, increased locomotor performance, and intrasexually selected weapons render some prey too formidable or otherwise unsuitable as prey (Sinclair et al. 2003; Emlen 2008; Owen-Smith and Mills 2008; Metz et al. 2018). For example, large male body size in African elephants (*Loxodonta africana*; Joubert 2006) and bluegill sunfish (*Lepomis macrochirus*)—largely a result of sexual selection—reduces male vulnerability to predators (Mittelbach 1981; Hambright 1991), while sexually selected locomotor performance in male collared lizards (*Crotaphytus collaris*) mitigates predation risk associated with territory defense and conspicuous coloration (Husak et al. 2006; Husak and Lailvaux 2014). It is also

worth considering that behaviors favored by intrasexual combat, aggression, and boldness, can deter predators, especially when coupled with large size and weaponry (Huntingford 1976; Sih et al. 2004; Kirkwood and Dickie 2005; Metz et al. 2018). Together, the evolution of condition-dependent expression, compensation traits, and offensive traits may help explain positive correlations between SST expression and survivorship in wild populations (Jennions et al. 2001).

Despite these changing ideas about the role of extrinsic costs of SSTs in population dynamics, the historical focus on extrinsic control is understandable. Because vital rates such as female fertility are not limited by the density of males in species with strong male reproductive skew, males can be exempted from population models in some cases (Myserud et al. 2002). This apparent insensitivity of female vital rates and population growth rate to male density tempts simplification of population dynamics via the exclusion of male vital rates. However, this assumption can preclude important effects of males on population dynamics, especially in species with strong sexual selection (Myserud et al. 2002; Milner-Gulland et al. 2003; Rankin and Kokko 2007). This realization has helped to revive interest in the effects of male behavior on population dynamics. For the rest of this section, we focus on evidence for intrinsic population regulation via SSTs. Specifically, we explore the ways in which male-male aggression, sexual harassment and coercion, and sexually selected infanticide influence vital rates in females and juveniles.

Aggression among males for control of breeding territories and females can generate strong density-dependent population regulation (Christian 1961; Watson 1967; Watson and Jenkins 1968; Brown 1969; Krebs and Myers 1974). Such aggressive interactions are particularly common in small mammals (Christian 1971) and birds (Moss et al. 1994; Searcy and Yasukawa 1995) and usually peak during intense breeding activity (Sadleir 1965; Turner and Iverson 1973). These male-driven aggressive interactions limit recruitment by increasing juvenile mortality and emigration, and reducing male immigration (Sadleir 1965; Healey 1967; Mougeot et al.

2003), especially at high population density (Rose and Gaines 1976).

Reproductive females can also suffer survival and fecundity decreases due to sexually selected male behaviors. Coercive mating and harassment from aggressive males can have devastating effects on female survivorship and fecundity (Le Boeuf and Mesnick 1991; Hiruki et al. 1993; Réale et al. 1996; Le Galliard et al. 2005, 2008). To date, several model systems have demonstrated that the effects of sexual harassment on population dynamics can be quite strong. For example, Le Galliard et al. (2005, 2008) show that sexual harassment and coercion by male common lizards (*Zootoca vivipara*) can generate negative population growth rates in populations with male-biased sex ratios. Sexual harassment and coercion can also reduce female fitness indirectly. In fishes, persistent copulation attempts drive females into sub-optimal habitats, substantially reducing female survivorship and fecundity (Magurran and Seghers 1994; Croft et al. 2006; Darden and Croft 2008; Wearmouth et al. 2012). In general, sexual harassment and sexual coercion seem to have substantial negative effects on female viability and population growth rate. Detailed studies in several systems repeatedly show strong negative effects on demographic classes important for population growth, female fecundity, and survival.

Sexually selected infanticide is a common adaptation in polygynous mammals and can have substantial effects on juvenile recruitment (Hrdy 1979; Agrell et al. 1998; Packer 2000; Palombit 2015). Original work on the demographic consequences of infanticide was centered on small mammals such as voles and mice, specifically whether male aggression toward unrelated young could regulate populations (Mallory and Brooks 1978; Webster et al. 1981). In general, results show that adult males reduced recruitment by killing unrelated young, and driving emigration (Gipps and Jewell 1979). These effects are not limited to rodents (Lukas and Huchard 2014). Male brown bears (*Ursus arctos*), puma (*Felis concolor*), and leopards (*Panthera pardus*) kill unrelated juveniles within their territories, a behavioral adaptation with direct negative effects on population growth rate

(Swenson et al. 1997; Wielgus and Bunnell 2000; Whitman et al. 2004; Cooley et al. 2009; Balme et al. 2012; Gosselin et al. 2015).

Similar to trait-mediated interactions (Preisser et al. 2005) the risk of infanticide alone can also reduce population growth rate. Although the physiological mechanisms are cryptic, some mammals adaptively reduce maternal investment by suppressing fertility (Packer and Pusey 1983) or terminating pregnancies when the risk of infanticide is high (Labov 1981; Zippel et al. 2017). This latter effect, called the “Bruce effect,” is activated when pregnant females are exposed to unfamiliar males—presumably those most likely to engage in infanticidal behavior (Bruce 1959). So far, polygynous mammals, including primates (Roberts et al. 2012), rodents (Hackländer and Arnold 1999), and ungulates (Berger 1983), have shown evidence of this cryptic effect on female fecundity. Although female suppression of fertility and termination of pregnancies appears to be a relatively widespread adaptation for mitigating the cost of infanticide (Palombit 2015), the impact of the Bruce effect on population dynamics is unclear. However, in combination with effects of infanticide on juvenile survival, suppression of female fertility would exacerbate the negative effects of infanticide on population growth.

Male-male aggression, sexual harassment, and infanticide routinely have negative effects on population growth rates by increasing male mortality, increasing juvenile mortality and emigration, and reducing female fecundity. Based on these general findings, a reasonable expectation is that male density is inversely related to population size and growth rate in taxa where aggressive mating tactics and infanticidal behaviors have evolved. Although such a relationship may be true under some circumstances, detailed study of brown bear populations in North America and Europe have revealed that a simple prediction such as this will fail because it does not incorporate some behavioral intricacies of infanticidal behavior. Specifically, a series of studies have revealed that increased male mortality does not lead to a decline in infanticide. Instead, increased adult male mortality increases infanticide rates substantially, presumably because the

rapid turnover of subdominant males creates conditions that favor infanticide (Swenson et al. 1997; Wielgus and Bunnell 2000; Bellemain et al. 2006; Gosselin et al. 2015). Insights such as these suggest that population-level consequences of SSTs such as infanticide are indeed substantial, and likely to vary across contexts and taxa.

## ECOSYSTEMS

### MATERIAL AND ENERGY FLUX

Linking individual organism traits to fundamental ecological processes, such as energy flux and nutrient cycling, can be challenging (Elser 2006; Jeyasingh et al. 2014). Despite conceptual integration of SSTs with ecosystem frameworks (Morehouse et al. 2010; Snell-Rood et al. 2015), empirical evidence is generally lacking (Matthews et al. 2011). An increasing interest in the ecological stoichiometry of sexually dimorphic data is addressing this gap, however, progress has been slow. Indeed, several SSTs are likely to influence energy and nutrient cycling. First, body size affects nutrient cycling: larger animals have higher storage and lower (per unit body mass) excretion rates. Second, metabolic rate scales with body size (Hemmingsson 1960) and should differ between sexes in species with pronounced sexual size dimorphism. Third, morphological variation between sexes results in compositional differences in stoichiometrically distinct tissues such as bone (Hendry and Berg 1999; Hall et al. 2007). Fourth, stoichiometric needs related to SST development may drive feedbacks on trophic ecology (Cothran et al. 2014; Goos et al. 2014, 2016). Intersexual variation in body size and tissue composition could have strong effects on the flow of energy and material through ecosystems; but, at this point, the data are simply too sparse to tell.

Sexually selected behaviors are also likely to interact with morphological variation to drive spatial and temporal heterogeneity in the distribution of energy and material. Consumer-mediated patchiness in the distribution of biogeochemical cycles are increasingly appreciated sources of ecological heterogeneity (McClain et al. 2003; Bernhardt et al. 2017). Given that the distribution, behavior,

and physiology of animals are shaped by sexual selection, SSTs should alter biogeochemical cycles accordingly. For example, aggregations of courting birds (e.g., leks) can occupy the same site for decades, likely altering local biogeochemical cycles through physical disturbance (Uy and Endler 2004) and nutrient translocation (Scott 1942). Indeed, dense aggregations of consumers have been shown to affect fundamental ecological processes such as primary productivity at local scales (Flecker et al. 2010; Layman et al. 2013); yet courtship aggregations have not been investigated from this ecosystem-based perspective (but see Archer et al. 2015).

### ECOSYSTEM ENGINEERS

Structural changes to habitats are also likely to influence ecosystem processes. Many organisms modify physical features of their environment through extended phenotypes subject to female choice (Schaedelin and Taborsky 2009). Below we present three case studies that exemplify how SSTs might mediate ecosystem-level consequences. The focal organisms are well-known ecosystem engineers that alter ecosystem processes through environmental modification and targeted interspecific interactions (Jones et al. 1994). In each case, the magnitude of the ecological impact is generated or exacerbated by SSTs. Nevertheless, the mechanistic linkages between sexual selection and ecosystem process are somewhat speculative. We include them here to promote additional study of SSTs in the context of ecosystem processes, striving toward a more complete understanding of the mechanisms that give rise to ecological patterns.

### BIOTURBATION AND ESTUARY PRODUCTIVITY

Estuaries provide ecologically and economically important services and products often driven by myriad chemical processes in sediments (Barbier et al. 2011). Burrowing invertebrates turn over sediments, consequently influencing a range of biogeochemical processes (Katz 1980; Gribsholt et al. 2003; Wang et al. 2010) that can influence a range of eco-

system functions such as primary production (Montague 1982; Bertness 1985; Smith et al. 2009). Indeed, an experimental halving of the number of fiddler crab (*Uca pugnax*) burrows in a coastal marsh halved aboveground production of the dominant herbaceous vegetation, smooth cordgrass (*Spartina alterniflora*; Bertness 1985). Burrow size also matters for ecosystem function, with effects being proportional to the volume of soil turnover (Wang et al. 2010). Hence, we speculate that the evolution of SST in a widespread and abundant burrower, the fiddler crab (*Uca* spp.), may amplify the ecological effects of these fundamental processes because sexual selection has altered the number and size of burrows.

Indeed, several studies show that sexual selection appears to influence burrow number and morphology in fiddler crabs. In *U. capricornis*, burrow numbers increase when males evict competitors from their burrows—a monopolizing adaptation that attracts females and generates a net increase in the number of burrows (Mautz et al. 2011). Females also express preferences for burrow characteristics. In *U. tangeri*, female preference for large burrows could shape the morphology of male burrows—especially their size (Latruffe et al. 1999). Furthermore, a familiar target of sexual selection, enlarged chela, increases burrow size and alters their shape in *U. annulipes* (Lim and Diong 2003; Lim et al. 2015; Tina et al. 2015). Ultimately, given that ecological effects of crab burrows are proportional to their size (Wang et al. 2010) and number (Bertness 1985), sexual selection on fiddler crab behavior and morphology is likely to contribute to their per capita effect on bioturbation and primary productivity.

#### ALGAE FARMING AND REEF PRODUCTIVITY

Effects of herbivores on reef ecosystems are exceedingly complex (Ceccarelli et al. 2011; Burkepille et al. 2013; Shantz et al. 2015). Fishes such as damselfishes (Pomacentridae) are engaged in intimate and complex interactions with benthic algae communities and coral (Ceccarelli 2007; Irving and Witman 2009; Hoey and Bellwood 2010). These small, highly territorial, and

brightly colored fish are abundant in shallow reefs systems throughout the tropics and occasionally in temperate zones. Many of the nearly 350+ species maintain exclusive territories and are highly aggressive toward conspecifics and heterospecifics that approach them (Ceccarelli 2007). Ecological and life-history traits within this speciose group are highly variable (Hata and Nishihira 2002; Hata et al. 2010); however, many are well known for their habit of cultivating algal “farms”—mats of filamentous algae on which they feed (Ceccarelli et al. 2001).

Sexual selection is strong in damselfish and successful males will often have multiple egg clutches within their territories (Peterson 1995). In fact, the best predictor of whether a female will spawn with a given male is the existence of fresh eggs, which raises the question: what traits engender that first clutch? Although details of courtship are variable among species, male territory quality is often an important target of sexual selection by female choice. Using a series of experiments and observational studies on garibaldi (*Hypsypops rubicundus*), Cortez damselfish (*Stegastes rectifraenum*), and beaugregory (*S. leucostictus*), several studies have demonstrated female preference for algal turf quality, specifically its density, thickness, and filament length (Sikkel 1988, 1995; Hoelzer 1990; Itzkowitz and Slocum 1994; Itzkowitz et al. 1995). These results suggest that the algal farming adaptations of damselfish are under strong sexual selection.

Data on the broader ecological effects of farms for these three species are not available. However, data from other damselfish species show the dramatic effects of farms on reef ecosystems. Algal farms can overgrow existing coral, increase coral prevalence (Casey et al. 2014b; Vermeij et al. 2015), and reduce coral recruitment (Casey et al. 2014a; Gordon et al. 2015). But the effects of farming on primary production are perhaps most notable. A review shows that farms have 1-to-29 times the algal biomass of surrounding substrates and are more productive per gram and unit area (Ceccarelli et al. 2001). Scaling up to the reef scale, by covering approximately 22–70% of reef area, Ceccarelli et al. (2001) estimate that damselfish farms con-

tribute from 35–85% of reef-wide microalgae biomass, respectively, and boosted productivity by 28–66%. What proportion of the ecological effect on primary production can be attributed to sexual selection for farm quality is unknown. Yet, if sexual selection enhances the farm effect, by only a fraction, the impact on reef-wide productivity is substantial.

#### DISTURBANCE AND THE AFRICAN SAVANNA

Elephants are important drivers of ecosystem processes. Much, if not most, of this ecological effect is mediated by tree damage: broken limbs, stripped bark, and uprooted trees. At small scales, tree damage benefits other herbivores (Riginos and Grace 2008; Valeix et al. 2011), small predators (Pringle 2008; Pringle et al. 2015), and can increase plant diversity (Coverdale et al. 2016). However, at regional, or even continental scales, elephant-mediated tree damage can contribute to the rapid conversion of African woodland to grassland (Buechner and Dawkins 1961; Laws 1970; Caughley 1976; Dublin 1995; Duffy et al. 1999; Shannon et al. 2011).

Despite the strength and extent of this interaction, the evolutionary underpinnings of these behaviors remain unclear. Usually viewed as a trophic interaction—elephants topple trees to feed on canopy vegetation—a series of observations suggest this might not be entirely accurate. First of all, bulls account for most tree toppling, suggesting a social or sexual function to tree damage (Guy 1976; Dublin 1995). Furthermore, bulls frequently engage violently with their environment; Poole (1987) recorded an average of one aggressive interaction with a “nonelephant element” once every ten minutes for lone, musth bulls. And, more recently, Midgley et al. (2005) detail support for a sexual function, arguing that tree toppling is derived from male dominance competition, an important component of male reproductive success (Moss 1983; Poole 1989). In essence, support for a sexual explanation of the engineering effects of elephants means that the diverse ecological effects of tree toppling by elephants are consequences of belligerent aggression driven by periodic hyperagres-

sive sexually selected behaviors (musth), which “spills over” to nonelephant features such as trees, utility poles (Midgley et al. 2005), and even other large herbivores (Slo-tow et al. 2000). Together, these observations indicate the behavioral mechanism underlying landscape-scale engineering of Africa’s most treasured and iconic ecosystem is sexual; a notable modification to prevailing ecological perspectives.

#### ECO-EVOLUTIONARY DYNAMICS OF SEXUAL SELECTION: GENERALITIES AND FUTURE DIRECTIONS

Thus far, our survey has attempted to advance the evolutionary ecology of sexual selection by linking traits evolved by sexual selection with ecological processes influenced by them. Although our narrow goal was to illustrate these links with a variety of examples, our broader goal was to facilitate an eco-evolutionary perspective on SSTs. We believe our survey contributes substantially to this latter objective, yet most opportunities for investigating the eco-evolutionary dynamics of sexual selection remain. First, a broad eco-evolutionary model integrating sexual selection does not yet exist. Efforts to include sexual selection in eco-evolutionary dynamics are generally population-based, asking whether evolution by sexual selection favors or disfavors adaptive evolution and increased population mean fitness (Hendry et al. 2018). More specifically, they ask whether condition-dependent sexual selection facilitates adaptation by purging genomes of genetic load (Whitlock 2000; Lorch et al. 2003; Candolin and Heuschele 2008; Whitlock and Agrawal 2009). These fitness-based approaches to eco-evolutionary dynamics are quite different from the trait-based perspective we take here. Indeed, these approaches remain surprisingly isolated despite opportunities for integration and synthesis (Svensson 2018). Consequently, our understanding of whether and how ecological feedbacks arise from sexual selection is fragmentary and incomplete. Below, we highlight several opportunities for future research on the eco-evolutionary dynamics of sexual selection.

All of the topics below have been investigated to some degree but have yet to focus on the effects of SSTs on ecological systems—the phenotype-ecology feedbacks that have made eco-evolutionary perspectives such an appealing model for understanding contemporary ecological dynamics. Our approach here is not to review these models in detail, but to point out where the evolution of SSTs is likely to influence ecological dynamics.

#### INTRAPOPULATION NICHE VARIATION

The eco-evolutionary dynamics of intrapopulation variation has fascinated evolutionary biologists for many decades, however, interest among ecologists is more recent (Araújo et al. 2011; Bolnick et al. 2011; Des Roches et al. 2018). Several recurring patterns of sex-specific ecological niche variation arose during our review. First, divergent sexual phenotypes often have divergent patterns of resource use along habitat and dietary axes (see Supplemental Table 1). Second, intersexual niche variation can sometimes resemble a nested pattern of resource use. For example, male skinks include larger, well-defended prey in their diet as well as smaller items used by females (Vitt and Cooper 1985; Figure 1a). Third, sexual behaviors that cause sexes to aggregate or synchronize reduce the degree of intersexual spatial niche separation. For example, sexual segregation during nonbreeding seasons is followed by coalescence once reproductive opportunities return (Blanco-Fontao et al. 2012, 2013).

In addition, many species exhibit heritable intrasexual polymorphisms in behavior, morphology, and/or physiology (Gross 1984, 1985; Sinervo and Lively 1996; McKinnon and Pierotti 2010). Despite the potential for intrasexual phenotypic variation to influence niche variation, surprisingly few studies actually demonstrate whether such polymorphisms translate to niche variation (viz., Colborne et al. 2013; Lattanzio and Miles 2016; Figure 1b). We do not know why evidence for linkages between intrasexual polymorphism and niche variation resource is so rare. One possibility is that polymorphisms underlying intrapopulation niche variation

go unnoticed without obvious phenotypic indicators such as coloration and size (Svensson et al. 2006; Dall et al. 2012). Indeed, even in the bluegill sunfish, a long-standing model of intrapopulation variation in foraging ecology, a sexually selected male polymorphism with substantial effects on habitat use and trophic niche (Colborne et al. 2013; Figure 1c) went overlooked for decades (Gross and Charnov 1980; Mittelbach 1981, 1983; Werner and Mittelbach 1981; Gross 1982).

Given the striking phenotypic differences among and within sexes we suspect many cases of intrapopulation niche variation driven by sexual selection exist. Despite decades of interest in the evolution of intrapopulation niche breadth by sexual selection (Schoener 1967, 1968; Shine 1989), inclusion of sexual selection in syntheses of intrapopulation variation is relatively rare (Araújo et al. 2011; Bolnick et al. 2011; Des Roches et al. 2018). Why this exemption persists is unclear. Several decades ago, Schoener (1967) suggested large intersexual diet and habitat differences in the lizard, *Anolis conspersus*, might reduce intrapopulation resource competition and allow for higher total population densities. But, as far as we can tell, this logical and testable hypothesis has yet to be evaluated rigorously or extended to intrasexual niche variation. At this point, hypothesizing specific ecological feedbacks arising from evolved inter- and intrasexual diversity is a logical next step in the development of eco-evolutionary theory. It seems clear that future research programs focused on the eco-evolutionary dynamics of population niche variation should investigate the contribution sexual selection makes to the evolution of intrapopulation niche variation.

#### INTRALOCUS SEXUAL CONFLICT AND POPULATION MEAN FITNESS

Here we have shown that the ecological effects of SSTs often arise because of a negative fitness effect on the opposite sex. For instance, infanticide and sexual harassment can reduce population size because they decrease the average female fitness (Rankin and Kokko 2006, 2007). These interac-

tions represent interlocus sexual conflict, antagonistic interactions between individuals arising from divergent evolutionary interests of the sexes (Trivers 1972; Parker 1979; Chapman et al. 2003). Conflicts arise because males often express traits that are antagonistic to the fitness of females. Counteradaptations can result in an evolutionary “arms race” between males and females called sexually antagonistic coevolution. The accumulated negative effects of interlocus conflict on individual fitness can be detrimental for the population.

Intralocus sexual conflict is also likely to negatively impact population mean fitness. Because sexes are under divergent selection, the fitness benefits of expressing sexual traits are sex-specific (Trivers 1972; Parker 1979; Chapman et al. 2003; Rankin et al. 2011). Therefore, expression of SSTs such as ornaments or weapons in females due to an underlying genetic correlation can have negative consequences for female fitness (e.g., Robinson et al. 2006). Pervasive sexual dimorphism suggests that many species mitigate costs of sexually antagonistic selection by evolving regulatory and genetic mechanisms that minimize intralocus sexual conflict (Fairbairn 1997; Dean and Mank 2016; Mank 2017; Wright et al. 2018). However, the resolution of intralocus sexual conflict is often incomplete, resulting in an evolutionary “tug-of-war” in which one or both sexes are displaced from hypothetical fitness optima (Rice 1992; Bedhomme and Chippindale 2007; Kruuk et al. 2008; Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009). Intralocus sexual conflict can therefore be viewed as sources of population-level maladaptation—depressing mean fitness in one or both sexes depending on the relative strength of antagonistic sexual selection (Rice 1992, 1996; Arnqvist and Tuda 2010).

What is important from an ecological perspective is that effects of maladaptive sexual trait expression will affect trait means and vital rates in both sexes—a fitness cost termed “gender load” or “sexual dimorphism load” (Rice 1992; Arnqvist and Tuda 2010). For instance, relatively strong sexual selection for intrasexual weapons and aggression may

be deleterious for male survivorship, but it may also depress female life span and fecundity because of an underlying genetic correlation. Theory and experimental evidence indicate that these effects on population mean fitness are a consequence of unmitigated sexually antagonistic selection, yet data from natural systems are relatively rare (Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009; van Doorn 2009; Maklakov and Lummaa 2013; Adler and Bonduriansky 2014; Berger et al. 2016b). Nevertheless, several field studies provide good empirical support for reduced female fecundity and survivorship due to gender load (Robinson et al. 2006; Foerster et al. 2007; Stulp et al. 2012; Swierk and Langkilde 2013).

There is abundant scope for future exploration of eco-evolutionary dynamics from an intralocus sexual conflict perspective (Svensson 2018). In general, empirical study of intralocus sexual conflict has been restricted to the laboratory, leaving exciting opportunities for extension into natural systems. In our opinion, further empirical work should focus on examining the spatial and temporal variation in gender load, what ecological factors exacerbate or ameliorate gender load, how readily mitigating adaptations evolve, and how inter- and intralocus conflicts interact. But, more generally, an eco-evolutionary framework integrating intralocus sexual conflict needs to be developed before the field can advance.

#### REGULATION OF POPULATIONS BY SEXUALLY SELECTED TRAITS

Despite a recent surge in interest, eco-evolutionary thinking has been around for decades (Schoener 2011). An early example is the “Chitty hypothesis” (CH; Figure 2), an eco-evolutionary model of intrinsic population regulation driven by density-dependent evolution of sexually selected behavior. Briefly, Chitty hypothesized that density-dependent evolution of traits such as male aggression and infanticide could contribute to population regulation (specifically, cycling) in rodents (Krebs 1964, 1978; Chitty 1967). After decades of investigation and controversy, sup-

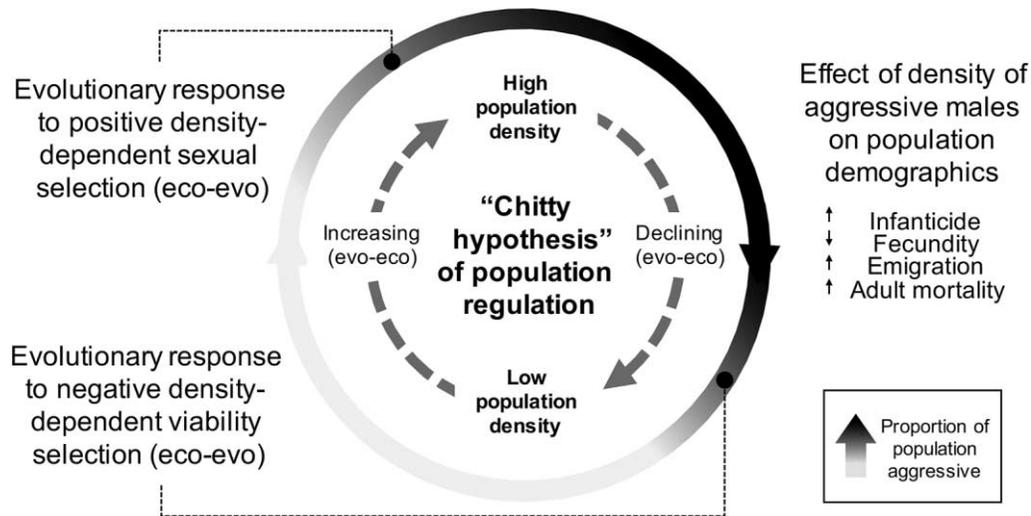


FIGURE 2. INTRINSIC POPULATION REGULATION VIA MICROEVOLUTIONARY CHANGE IN SEXUALLY SELECTED MALE AGGRESSION

The model is adapted from that initially presented in Krebs (1964, 1978). The outside ring depicts the evolutionary change in the proportion of the population with aggressive phenotypes. The inner ring depicts the concurrent change in population density that arises from and drives selection on aggressive phenotypes. “Eco-evo” indicates an evolutionary change arising from ecological change, in this case, the effect of population density on the proportion of the population composed of aggressive phenotypes. “Evo-eco” indicates an ecological change resulting from evolution in the population. Note that evolutionary and ecological cycles are offset indicating a lag effect of density-dependent selection on phenotypic evolution that perpetuates the eco-evolutionary cycle.

port for the CH (and intrinsic control in general) remains weak; alternative models of population dynamics favoring extrinsic factors such as predation and resource supply have generally prevailed (Krebs 2013).

But, in recent years, an increasing interest in the contribution of behavior and sexual conflict to population dynamics has revealed elements of CH in a variety of systems (Kokko and Rankin 2006; Holman and Kokko 2013). First, sexually selected male-male aggression has been shown to be heritable in a variety of systems, including ones in which there is intralocus (Mokkonen et al. 2011) and interlocus sexual conflict (Horth 2003; Horth et al. 2010). Second, sexual selection on aggression is density dependent; Knell (2009) showed that the reproductive fitness advantage of aggression is variable but tends to favor aggressive males at high density—a positive density-dependent reproductive advantage of aggres-

sion. Third, nonsexual selection on male aggression can be negatively density dependent. For example, Horth and Travis (2002) show that survival of aggressive male eastern mosquitofish (*Gambusia holbrooki*) is negatively related to the density of aggressive male morphs. And, fourth, effects of aggressive males on population growth rate can be negatively density dependent. For example, in a damselfly (*Ischnura elegans*) high frequency sexual harassment has negative impacts on female fecundity (Gosden and Svensson 2009). In all of these cases, the negative effects of SSTs on population mean fitness contributes to declining population abundances that limit the fitness benefit of the SST—a core mechanism underlying the CH (Figure 2).

Although evidence for individual elements of the CH have been accumulating for years, a clear illustration that density-dependent evo-

lution of a SST can regulate population dynamics in a single system has remained elusive. However, a recent summary of long-term data on western bluebirds (*Sialia mexicana*) reveals density-dependent selection on male aggression; culminating in what Duckworth and Aguillon (2015) tentatively report as a causal relationship between aggression and population density that causes populations to fluctuate due to density-dependent trait evolution. Specifically, as predicted by CH, selection for male aggression is positively density dependent and fecundity selection on aggressive males is negatively density dependent, presumably from a fecundity-sexual selection tradeoff.

Widespread evidence of intrinsic population regulation by SSTs suggests the eco-evolutionary dynamics comprising the CH may not be uncommon. Indeed, by relaxing the “cycling” component of the CH and looking beyond rodent systems, many of the studies cited here clearly suggest that density-dependent evolution of a SST can generate a negative feedback on population density—an interaction that could perpetuate reciprocal eco-evolutionary feedbacks (Figure 2). Nevertheless, as discussed in Duckworth and Aguillon (2015) and Krebs (1978), separating cause from effect presents substantial challenges to evidencing the CH.

#### GENERAL DISCUSSION

The prevailing approach to the evolutionary ecology of sexual traits is one in which ecological forces depress the viability of the bearer through natural selection (Andersson 1994). Here, we extend this perspective by arguing that SSTs also have effects on ecological systems. We believe four generalities uncovered by our review exemplify these effects. First, *a broad range of traits evolve by sexual selection*. In addition to ornaments and intrasexual weapons, sexual selection targets traits such as locomotion, spacing behavior, and phenology. Second, *ecological consequences of sexual selection can arise indirectly*. Evolution of SSTs such as male body size can have pleiotropic effects on a range of traits due to genetic or developmental correlations. Although

many traits arise merely as byproducts of sexual selection (e.g., intraspecific variation in trophic ecology routinely arises as a byproduct of sex-specific body and/or head size evolution), they nevertheless have diverse and important consequences for fundamental ecological interactions. Third, *behaviors evolved by sexual selection have major impacts on interspecific interactions and population dynamics*. Sexual selection acts on a broad range of traits—many of which are not traditionally recognized as SSTs. Nevertheless, behaviors modified by sexual selection such as infanticide, sexual harassment, and male-male aggression have substantial effects on population dynamics. Fourth, *sexual selection underlies ecological variation at all levels of ecological organization*. Here, we show that SSTs shape interspecific interactions, influence population dynamics, and may influence ecosystem-scale processes. But if SSTs are important, why is there not a widespread appreciation of these pervasive and diverse ecological effects? Several reasons may underlie a historical tendency to overlook the ecological consequences of SSTs.

First, not all intersexual phenotypic diversity is driven by sexual selection; fecundity and viability selection also drive the evolution of intersexual diversity (Hedrick and Temeles 1989). Although theory suggests that disruptive viability selection on nonsexual resources (e.g., food) can contribute to sexual dimorphisms (Slatkin 1984; Bolnick and Doebeli 2003), unambiguous empirical support for this ecological-causation hypothesis is limited (Selander 1966; Schoener 1967; Dayan et al. 1989; Temeles et al. 2000, 2010). Indeed, Fairbairn’s (1997) review of sexual dimorphism suggests that sexual and fecundity selection account for many of the sexual dimorphisms in nature. And, more recently, a review of dimorphisms in fighting traits reveals that the strong male bias in weaponry, and a tendency for herbivores to evolve dimorphic fighting morphology, strongly supports the sexual selection hypothesis as well (Rico-Guevara and Hurme 2019). Furthermore, one of the best-known examples of the ecological-causation hypothesis for sexual dimorphism (bill dimorphism in hum-

mingbirds) has been undermined by data showing that male bill morphology evolves by male-male combat (Rico-Guevara and Araya-Salas 2015; Rico-Guevara and Rubega 2017). It is important to note, however, that sexual selection, fecundity, and ecological-causation explanations for sexual dimorphism are not mutually exclusive (Hedrick and Temeles 1989; Shine 1989; Fairbairn 1997). We speculate that the practical difficulty of parsing the contributions of multifarious selection might have dissuaded empiricists from partitioning fitness into components; thus explaining the historical tendency to underestimate the role of sexual selection in the evolution of intersexual ecological variation.

Second, work on the evolutionary ecology of sexual selection has generally focused on morphological traits such as conspicuous ornaments and signals rather than behavioral or physiological traits—a bias that could divert attention from important eco-evolutionary links between sexual selection and ecology (Irschick et al. 2007). Indeed, elaborate SSTs serving little purpose outside of mate attraction are arguably the most familiar traits evolved by sexual selection. But imagining substantial ecological effects driven by the expression of such traits (e.g., fin redness or spot size) seems particularly challenging. We believe this focus on traits employed solely during sexual display is far too narrow to represent the ecological consequences of sexual selection. Indeed, most (if not all) traits are conceivably shaped by sexual selection if they influence an individual's ability to compete for mating opportunities (Lailvaux and Irschick 2006; Irschick et al. 2007, 2008; Husak and Fox 2008). For example, work on collared lizards (*Crotaphytus collaris*) has revealed strong sexual selection on locomotor performance—something we think many would presume evolves via selection on food acquisition and predator escape performance (Husak et al. 2006). Clearly, recognizing the range of traits subject to and shaped by sexual selection is an important step in drawing causal links between sexual selection and ecological processes. We think an eco-evolutionary perspective should include a variety of traits, determined not by

their presumed roles in sex and mate competition, but rather their measured contribution to reproductive fitness (Husak and Fox 2008). Indeed, just as conspicuous mating signals can be shaped by sexual and natural selection, so can all traits (Sih et al. 2004; Ball et al. 2014).

In conclusion, advancing toward an eco-evolutionary model of sexual selection will require multiple fronts. Mutation-purging models show increasing promise (Lumley et al. 2015; Jacomb et al. 2016; Godwin et al. 2018), as do conflict-based models (Arbuthnott et al. 2014; Chenoweth et al. 2015; Berger et al. 2016a; Rowe et al. 2018). But we feel that the scope of an eco-evolutionary model of sexual selection should extend beyond the amelioration or amendment of genetic loads and focus more on the ecological effects of phenotypes on species interactions and population dynamics. We hope that our focus on the ecological relevance of SSTs will stimulate empiricists to integrate SSTs into eco-evolutionary dynamics—as they have for traits typically shaped by viability and fecundity selection (Hendry 2016). We have little doubt that future work will continue to uncover ecologically diverse effects of sexual selection and we look forward to seeing additional evidence along those lines. But whether SSTs will ever engender the same interest as viability traits remains to be seen. Nevertheless, SSTs such as large body size, bite force, aggression, and infanticide should be on the short list of traits relevant for a wide range of ecological processes.

We also believe that inclusion of SSTs in ecological thinking will become more common as the divide between ecologists and evolutionary biologists is bridged by a more integrative understanding of natural systems.

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