

Integrative Biology and Sexual Selection

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Sexual selection by female choice has been defined operationally as a change in male fitness due to variance in the number of mates, and studies of population biology have demonstrated this effect clearly. We argue that sexual selection is a richer phenomenon than this narrow definition implies, involving the interaction of sensory and perceptual mechanisms with signals, all of which can be influenced by an organism's hormonal and experiential milieu. The interaction between signals and receivers is further modulated by physiological processes, social context, and the physical environment. Thus, an approach to sexual selection that integrates mechanistic factors is essential for comprehensive understanding. Merging population biology with mechanistic studies, however, might not be sufficient. This is because the precise forms of the receivers and signals are the products not only of selection on current variability, but also of their evolutionary histories. We cannot imagine how researchers can hope to understand not only the "message" conveyed by a signal but the particular phenotypes that convey and receive this message without reference to history. We urge that our field advance beyond operational definitions and toward an organismal and historical understanding of the processes and mechanisms that underlie sexual selection.

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Biology is a field that embraces a variety of approaches, interests, techniques, and concepts. This variation may be categorized into different levels of analysis¹ sometimes represented as the simple dichotomy of problems addressing proximate and ultimate causation.^{2,3} Within the field of evolutionary biology, an additional dichotomy relates to the evolutionary origin versus the maintenance of traits. These dichotomies are sometimes presented in a manner sug-

gesting that they have no dependence on one another: physiologists investigate proximate causes, whereas evolutionists are concerned with ultimate ones; phylogeneticists address the origin of traits, but population biologists measure their current fitness effects. In the short term and for the narrow question, these levels can effectively be used separately. One need not have an understanding of what goes on in the "black box" to measure how selection acts on variance in its performance. The premise of integrative biology, however, is not merely recognizing the different approaches within biology, but acknowledging a synergism in their interaction. We believe that such synergism is especially relevant for studies of sexual selection, although certainly not limited to them. Here, we use some examples from sexual selection to argue for the virtues of synergistic integrative biology; we develop this and related themes more generally elsewhere. Specifically, we argue that (1) sensory systems (including peripheral, central, and cognitive components) always have a greater response to some stimuli than to others (sensory biases), (2) intraspecific mating preferences emerge from the interaction of

signals and sensory biases, (3) these biases can sometime evolve in contexts not related to intraspecific mate choice, and (4) these effects can persist in descendent taxa, thus setting the stage for sensory exploitation, in which the evolution of male courtship traits can be influenced by preexisting sensory biases. It is due to these inextricable links among population biology, mechanistic biology, and evolutionary history that we argue for the necessity of an integrative approach to understand the general biology of sexual selection.

POPULATION BIOLOGY AND SEXUAL SELECTION

One of the central issues in sexual selection concerns the forces that have resulted in the evolution of male traits that enhance mating success. Such traits can increase a male's attractiveness to females, but (this is the "paradox of the lek") they might also decrease his survivorship by increasing exposure to predators, energetic expenditure, or stress on the immune system.^{4,5} The complexities of this problem can be illustrated by asking a simple question of the peacock's tail, a popular exemplar in the field.⁶ Why?

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If we were to restrict this question to one of population biology, the answer might be that males with more elaborate trains have a net lifetime fitness advantage over less well-endowed males. Specifically, these males are more attractive to females, and this advantage results in greater male mating success that more than compensates for any costs of decreased survivorship. Although that answer might be true, is it complete? If the question posed only addresses the impact of male trait variance on male trait fitness, then the answer is yes. Referring to the two dichotomies above, this analysis addresses the ultimate cause of the elaborate male trait by identifying the factors that are currently implicated in its evolutionary maintenance. This example can be further pursued by asking why females would prefer such a trait. Of the variety of hypothetical explanations, one might be “good genes.” For example, in some peacock populations, females who choose more elaborate mates produce offspring with enhanced survival.⁷

MECHANISTIC BIOLOGY AND SEXUAL SELECTION

The population biology answer, however, might not be adequate to the researcher more generally interested in sexual selection and who wishes to approach the problem more mechanistically. Here we have seen the recent introduction of some mechanistic considerations into sexual selection studies. For example, what is it about the train that excites the female? Is it the added visual stimulation of a larger stimulus or the specific stimulation resulting from more “eyes” on the train? This is an example in which proximate and ultimate causes can be nicely separated. Regardless of the sensory and perceptual mechanisms at the bases of the preference, the “message” to the female might be that some males possess better genes for survival. Understanding the sensory mechanism would certainly yield a more complete understanding of sexual selection in this species, but the interpretation of the selection forces favoring female preference for this sexually selected trait would not be altered

by peering into the black box. This is not always the case: sometimes proximate and ultimate explanations can be more complexly interwoven.

A hallmark of many sexually selected traits is increased signal complexity.^{4,8} A basic property of sensory systems is that they can habituate to repeated presentation of a sensory stimulus; this response is so predictable that it is used as a bioassay to understand animal perception.⁹ Both Hartshorne¹⁰ and Searcy¹¹ have suggested that one of the advantages of large repertoire size in the song of song birds is that the enhanced signal complexity releases the receiver from habituation, thus providing to the signaler a benefit in both territorial interactions with males and in attracting females. What if these researchers are correct, and sensory habituation were to underlie the sexual selection advantage that males accrue through female choice? Our ultimate explanation from a population biology study of why males sing as they do might not change. But what of the understanding of why females prefer signal complexity? In this case the proximate and ultimate explanations might coincide. Few would seriously posit that sensory habituation, a neural property widespread among animals, evolved because it resulted in female songbirds choosing males with larger song repertoires. Of course, this is not to suggest that sensory and perceptual properties do not evolve. They do; the neuromodulation of habituation/ sensitization, for example, can vary substantially among closely related taxa.¹² In principle, it is a testable hypothesis that threshold for auditory habituation in song birds evolved in response to a selective advantage accrued to females in choosing males with greater signal complexity. However, in the absence of any evidence for such a claim, one must at least ask what is the appropriate null hypothesis.

The sensory and perceptual systems of females will shape male signal evolution in other ways as well. Both visual and auditory systems, for example, are limited in the range of wavelengths they perceive, and this sets the bounds within which signals can be effective. Frogs, for example, are not known to communicate in the ultraviolet or the

ultrasonic; this might be due to constraints on the mechanisms of signal production, but more likely results from the envelope of effective signal parameters defined by the receiver. This example might seem trivially true, but then why should it be controversial to suggest that sensory biases within this envelope might also select for the forms of signals that are most salient in eliciting responses?

There are situations in which understanding the mechanism of mate choice might alter our views of ultimate causation in sexual selection; this is especially true when pleiotropic effects are involved.¹³ Male water mites (*Neumania papillator*) produce water-surface vibrations by drumming with the front legs to attract females.¹⁴ Yet in this and closely related species, individuals of both sexes feed on copepods, which are located by detecting water surface vibration produced when this prey locomotes—vibrations that are suspiciously similar to the male mite’s sexual signal. Detection of waterborne vibration might be favored by prey detection (in both sexes) or by mate detection (in females); the same general sensory mechanism is involved in both functions, and thus both might select for similar signal forms (certain pattern of vibration). To ascertain the selective forces maintaining female preferences for drumming males, one must consider the multiple functions of vibration detection and the range of stimuli to which the receiver system can respond. Various combinations of positive, negative, or neutral effects could interact for a net positive fitness effect for those phenotypes that detect and approach such stimuli.¹⁴

As with the water mite example, most sensory and perceptual systems serve a suite of socially and ecologically crucial functions. The degree to which brain functions, for example, can be compartmentalized or modularized has been debated in neuroscience.^{15,16} To the extent that such sensory abilities implicated in mate choice serve other functions, we would expect that selection on the sensory system to perform one function might influence how it performs another. Such an effect might be apparent in the water mite example above. Is

it merely coincidence that the similar signals that lead a female to prey also lead her to a mate? Or is it more likely that because the vibration-detection system was favored to cause the animal to approach this particular pattern of wave vibration in one context (either prey or mate localization), the mites are predisposed to use similar cues that might be reliable in the other context? Which came first? If prey localization were antecedent, then would we also expect that males might have tapped into this type of signal when attempting to attract females? In-depth understanding of the sensory ecology of these mites would lead to predictions as to the phenotypes that may plausibly evolve as adaptations under sexual selection.

EVOLUTIONARY HISTORY AND SEXUAL SELECTION

Understanding mechanisms of mate choice might reveal how the sensory system responds to certain stimuli in different instances; this usually will not reveal the evolutionary sequence in which the current signal-receiver dyad was assembled. This concern has motivated an additional approach to population biology (fitness consequences) and sensory biology (mechanisms) in the study of sexual selection—phylogenetics (historical patterns). By incorporating phylogenetics, the recurring question of “why” takes on a more historical aspect.¹⁷ Why do male peacocks have elaborate trains rather than elaborate bowers? Because they are not bower birds, we assume. Rather than a complex song repertoire? Probably because they are not song birds. The evolutionary pathways traversed by these kinds of birds excluded some phenotypes and favored others as plausible possibilities.

It has always been difficult to understand the evolution of novelties or key innovations, such as communication systems that are unusual for a particular taxon. For example, most moths produce pheromones in mate attraction (females attracting males). In some species of ctenuchid moths, males call with a series of ultrasonic clicks as they approach females and females respond acoustically.^{18,19} Could knowledge of

mechanisms and history predict why some species of lepidopterans, a group that typically relies on olfactory and visual modalities to explore their world, would evolve a mate attraction system based on ultrasonic sounds? Perhaps. The ctenuchids are within the Arctiidae, a group of moths that have evolved an ear that functions in detecting the echolocation signals of approaching bats and a sound-producing organ that functions in predator avoidance. Ctenuchids are aposomatic and day-flying, features that reduce bat predation. Relaxation of predation pressure seems to have resulted in the acoustic system of ctenuchids losing its antipredator function and gaining a second function in courtship. Although ultrasonic communication between the sexes might seem a quite implausible phenotype for lepidopterans in general, it is plausible for arctiids.

A phylogenetic perspective can also illuminate more plausible phenotypes by uncovering some general principles among diverse organisms. Acoustic signals in vertebrates can involve one of three independently derived organs: the larynx (in tetrapods), the syrinx (in birds), and the swim bladder (in fishes). The underlying neuronal circuitries responsible for the rhythmic output of these organs, however, share their origin. Bass and Baker²⁰ suggest that novel pattern-generating circuits involved in vocal and electromotor systems have originated from the same Hox-gene-specified compartments of the embryonic hindbrain that gave rise to rhythmically active cardiac and respiratory circuits during the protochordate-vertebrate transition. Thus, any broad themes in acoustic and electrical communication among vertebrates might be due to signal parameters being selected to send similar messages, to signals facing similar constraints imposed by receivers across modalities and taxa, or as Bass and Baker might suggest, is evidence of a shared ancestral similarity in some of the underlying neural substrate for signal production. Similarly, characteristics of the signals that are divergent among groups, such as birds, frogs, and mammals, could result from the acoustic worlds of these animals generating different selection forces, or from the involvement of sound

production in their differing ventilation systems.²¹ We do not favor a priori one explanation over the others; rather, we favor an integration of as many sources of information as possible that generate additional and testable hypotheses for understanding the complexity of biological systems.

A more formal, fine-grained historical analysis can also be applied to sexual selection. To test the sensory exploitation hypothesis²³ (i.e., that male *Neumania papillator* used vibration as a courtship signal because it was favored by a preexisting sensory bias that evolved in the context of hunting), Proctor²² determined the most parsimonious historical pattern by which hunting and courtship behavior of closely related species of mites evolved. The behavior described for hunting copepods is found within the group containing *N. papillator*. It appears that this method of localizing prey existed before males used water-surface vibrations as a courtship signal. Proctor's²² phylogenetic analysis is consistent with the contention that males have evolved traits that exploit the female's sensory biases. It has sometimes been suggested that sensory exploitation addresses trait origin versus maintenance, but this example shows that need not be the case. If as suggested, male water mites evolved water-surface vibrations as a sexual signal to exploit the female bias to these signals (a bias that originated for and is currently maintained, at least in part, because of advantages accrued in foraging), then origin and maintenance become less divisible. The ultimate cause (evolution of prey localization in the ancestor) led to a proximate cause (vibration detection), which subsequently influenced another ultimate cause (the evolution of signals that enhance male mating success).

INTEGRATIVE BIOLOGY AND SEXUAL SELECTION

Proctor's^{14,22} studies nicely illuminate the strength of an integrative approach. Her initial studies of population biology showed that sexual selection favors males who use leg-drumming, which results in water-surface vibrations, to attract females. A more detailed understanding

of the mechanisms of the communication system reveal that the receiver responds to similar mechanical cues in both hunting and mate location. Finally, the histori-

cal analysis argues that response to this stimulus evolved in the context of hunting, which then set the stage for the evolution of the courtship signal. None of

these approaches in isolation would have provided the same insights into how sexual selection influenced signal evolution in this taxa. This is an example in which synergism resulting from an integrative approach is clear (Fig. 1).

To some persons, an emphasis on the role of history in sexual selection has implied a nonadaptationist agenda. This is not true and might result from another misleading dichotomy, "constraint versus adaptation." Instead, we argue that knowledge of the evolutionary pathways traversed by a lineage provides insights into phenotypes that might plausibly evolve in response to selection. Hypotheses such as sensory exploitation,²³ sensory bias,²⁴ and receiver psychology²⁵ do not suggest that females suffer a net fitness disadvantage by responding to such signals (also see Dawkins and Guilford²⁶)—perhaps exploitation is a misleading term. Receivers, like signals, can evolve in response to selection. By combining mechanistic and historical analyses, we can make strong inferences about the plausible phenotypes of each component, which then each influence its counterpart in the communication dyad.

The immensity of the biological endeavor requires that we use artificial constructs to gain some understanding of its complexity. Thus, we have different disciplines and fields as well as different levels of analysis. That the constructs are artificial make them no less useful. Nevertheless, they are artificial, and when they represent boundaries of disciplines not to be trespassed, these constructs limit not only our approaches but any knowledge that might emerge from a synergism of combining approaches. Expanding knowledge within narrow fields is valuable because it adds to the "parts catalog" of life.²⁷ Reductionism has had a rich and successful history as a research strategy in biology, and we do not intend to eschew its importance. Integrative biology, however, is essential because it allows us to understand how the parts were, and are, put together to form complex living systems.

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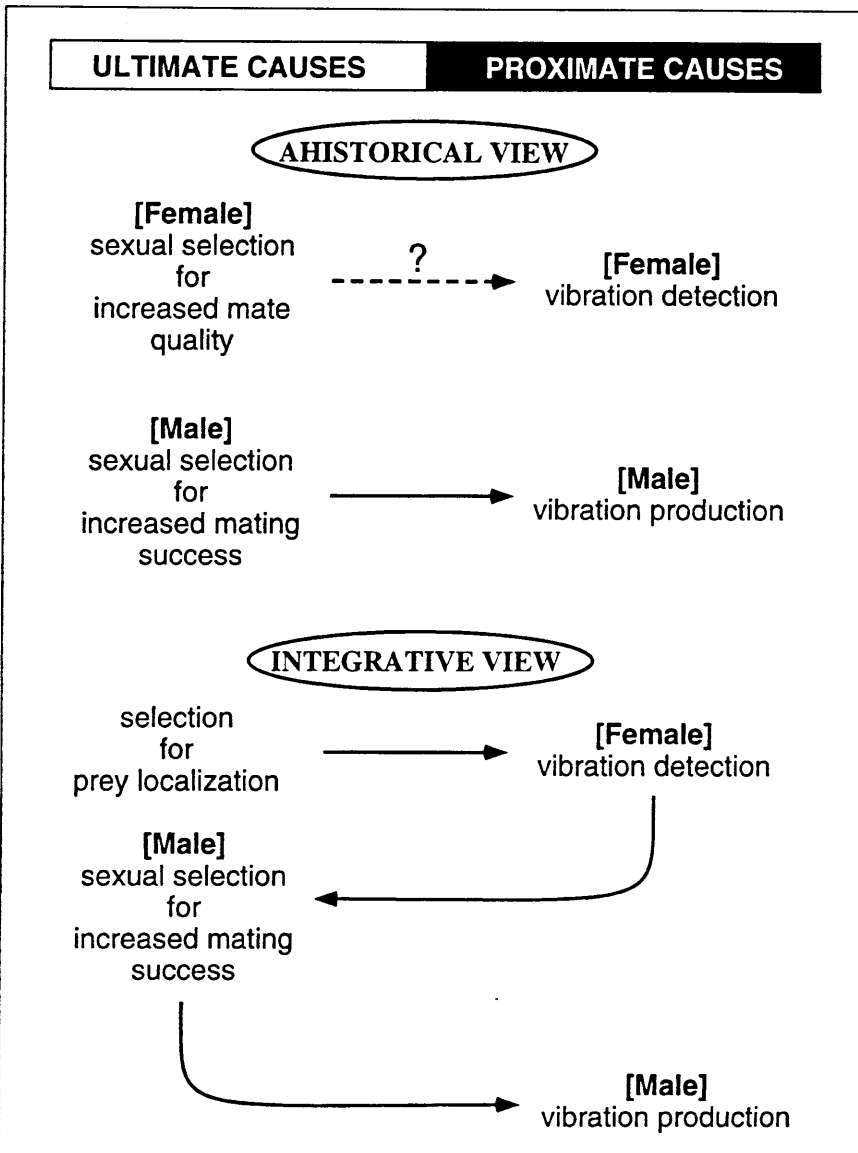


Figure 1. Two approaches to sexual selection in water mites. The ahistorical view, which here combines population and mechanistic biology, shows that males increase their mating success by producing water-surface vibrations (proximate cause) because females are attracted to such stimuli (proximate cause). The male signal seems to have evolved under sexual selection (ultimate cause), but this analysis leaves open the question as to why females would harbor such preferences (ultimate cause). An implicit assumption often made in such studies is that the female preference has evolved under selection for increased fecundity or to transmit genes for enhanced survivorship. The integrative view, which adds a historical analysis to the previous analyses from population and mechanistic biology, alters our view of the evolution of this communication system. The ultimate cause of female preference for water-surface vibration, it is argued, evolved under selection for prey localization. This then set the stage for sexual selection to favor males producing such signals because they attract females.

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