NEW DIMENSIONS IN ANIMAL COMMUNICATION: THE CASE FOR COMPLEXITY

Gail L. Patricelli^a and Eileen A. Hebets^b

^aDepartment of Evolution and Ecology, University of California, One Shields Avenue, Davis CA
95616 USA, GPatricelli@ucdavis.edu (corresponding author)

^bSchool of Biological Sciences, University of Nebraska-Lincoln, 402 Manter Hall, Lincoln, NE
68588 USA, ehébets2@unl.edu

1 **ABSTRACT**

2 Animal communication has multiple dimensions of complexity—signals may be variable over
3 time and space; signals may have multiple components interacting with each other and with the
4 receivers’ perceptual and cognitive systems; and signalers and receivers may adjust their
5 behavior with changes in their environment. There is an increasing appreciation that
6 understanding animal communication—especially the diversity of signal form—requires us to
7 examine complexity *per se*. We review recent methods and conceptual frameworks that address
8 the complexity of communication with a specific focus on new developments in quantifying and
9 explaining signal variation, new advances in understanding receiver psychology, including
10 perceptual and cognitive biases, and new unifying frameworks, such as systems theory, which
11 provide a holistic view of complex communication systems.

12

13 **INTRODUCTION**

14 Many of us are drawn to study the evolution of animal communication by the mystifying
15 diversity and breathtaking beauty of animal signals, from the music of the nightingale’s song, to
16 the dances of peacock spiders, to the precision of the worker bees wagging, to the vivid warning
17 colors of poison dart frogs. The traditional approach to understanding complex communication
18 involves breaking the process down into component parts—a signaler producing a signal that has
19 been selected to elicit a response from a target receiver. While an important beginning, there has
20 been a growing appreciation for the importance of addressing complexity *per se* in our study of
21 animal communication [1-4].

Over the last few decades, research has demonstrated that signals can be complex in multiple dimensions, with interacting components in different sensory modalities, variation in form and deployment over time and space, repetition and complex syntax, and conversational exchanges where both parties are signalers and receivers [5-7]. Importantly, we no longer view receivers as passive detectors of signals, or even optimal decision makers, as evidence accrues regarding the critical role of receiver's sensory, perceptual and cognitive processes in influencing signal form [8-12]. We have expanded beyond the dyad of the signaler and receiver to examine the marketplace of interactors and the network of social interactions, which may shape the tactics of all participants [13-16]. Extending even further, we recognize that the environmental context in which communication occurs can shape the evolution of signals and responses at multiple spatial and temporal scales, from brief interactions in the leaf litter to evolutionary change across continents [17-21].

An increased appreciation of the complexity surrounding animal communication has expanded the scope of our questions, encompassing more than honesty and information, allowing us to begin to explain the diversity, form, and function of animal signals. Here we highlight and briefly review some of the contributions from the last two years addressing new dimensions in our thinking about signalers, receivers, and communication systems and we discuss areas in need of further research.

Dimensions of Signal Variability

Whether they involve sounds, smells, colors, dynamic movements, currents, or vibrations, signals often differ over time and space [18,22-25]. This variability can occur for many reasons (**Fig. 1**), including changes in the source signal itself (e.g., changes in pitch or amplitude of

songs produced) or in signaling behavior (e.g. location of singing perch), or changes due to propagation through the environment (e.g. reverberation). It is increasingly clear that signal variation may itself play a role in communication, for example, reflecting motor performance, learning, changes in underlying condition, or tactical adjustments in signaling behavior [26-30]. Researchers have addressed variable signals in several ways—eliminating the variability by averaging multiple measurements to represent each individual, or measuring the variability using metrics such as repeatability, consistency, coefficients of variation (CV), or in the case of signal sequences, transition probabilities. While these approaches remain useful in many cases, several recent reviews discussed below have addressed limitations of these methods, proposing improved methods to quantify individual variability and further explore its possible causes (**Fig. 2**).

Quantifying Variability- To measure and understand within-individual variation in signaling, variation caused by systematic changes in conditions (e.g. experimental treatments, environmental change), must be partitioned from the residual variation. Recent studies offer new tools to address this challenge—Biro and Stamps [27] propose improvements in how we measure repeatability, to better account for changes in behavior over time (**Fig. 2**), whereas Westneat et al. [29] propose a statistical framework based on reaction norms to partition these types of variation.

While studies typically focus on variation explained by experimental treatments or covariates, there is growing appreciation of the interesting biology that may be hidden in the residual variation [26,28,29,31]. Stamps and colleagues suggest a measure adapted from psychology that describes short-term, non-systematic (or at least unexplained) variability in behavior measured under the same conditions—IIV (*Intra-Individual Variability*) [28,31]. There is evidence in

humans and other species that these ‘spontaneous’ endogenous fluctuations in behaviors measured as IIV may respond to selection and change with age, experience, and health [28]. Communicating animals may also benefit from such information, and indeed, receiver preference for consistency in the performance of a signal [e.g. 32,33] may be interpreted as selection for low IIV [28]. Statistically or experimentally controlling for IIV can also help to better isolate predictable causes of within-individual variation in signaling behaviors, such as developmental history, the physiological state of the signaler, or adaptive plasticity in response to social or environmental conditions [27-29,31]. These tools and methods therefore will help to shed new light on how within-individual variability in signals may reveal aspects of signaler quality as well as signaling tactics.

Quantifying within- and among-individual variability in signals is particularly challenging when signals are deployed in complex sequences. Traditional methods addressing this challenge have included Markov chain analyses, permutational approaches, or entropy calculations [34], while recent studies highlight new advances in sequence analysis. For example, Kershenbaum and colleagues [35] call into question the common assumption that signal sequences are Markovian, finding that acoustic sequences in a diverse set of taxa are better explained by non-Markovian dynamics such as the ‘renewal process’, which tends toward repeated elements. Weiss et al. [36] apply network analysis to the sequences of nightingale song types, and a drift-diffusion model was used to explore how the integration of information over time influences receiver decision making in grasshoppers [37]. With these recent developments, as well as increasing sophistication of tools such as machine learning, and models using hidden and semi-Markovian processes [34,38,39], we are compiling a robust and diverse toolkit for the analysis of sequences, appropriate for the diversity of signaling systems that we study and questions that we ask.

Adaptive Plasticity and Variation- Whether signals are repeated or produced in complex sequences, much of the dynamism in variable signals appears to reflect adaptive plasticity in signaling behavior across multiple time scales [13,21]. Several conceptual reviews address the causes and consequences of plasticity in signals and other traits, each with a different emphasis. Snell-Rood [40] and Stamps [31] focus on how early development and adult experience may interact to favor differing degrees and types of behavioral plasticity among individuals and among species, discussing links between plasticity and other big topics in behavioral ecology, such as behavioral syndromes and animal responses to anthropogenic environmental change [41,42]. Vitousek et al. [30] emphasize dynamic feedback between signal expression, behavior, physiology, and the context and outcomes of social interactions. Patricelli et al. [26] synthesize alternative hypotheses for within-individual variability in signals in the context of mate choice, emphasizing tactical adjustments of signaling behavior to maximize benefits and decrease costs, given the social and environmental context of courtship.

To understand the importance of adaptive plasticity in signaling in sexual selection, Patricelli et al. [26] highlight the need for more studies addressing the fitness consequences of variation among individuals in the degree of plasticity [e.g. 43,44-47] and the further development of theory to predict signaling dynamics. Outside of the agonistic context, there is relatively little theory addressing the question of how signalers should plastically adjust persistence and intensity in response to changing costs and benefits of signaling [48-51]. This is an area ripe for further development, adapting models from bargaining or life history theory, or generalizing models from aggressive signaling to mate choice and other communication contexts [13,14,26].

Ultimately, by examining the causes and consequences of within-individual variation in the expression of signals we gain a greater understanding of the scope of natural and sexual selection

in shaping the diversity and complexity of signals. We are excited about the recent surge of interest in this topic, providing new tools and approaches to address this understudied level of variation in signaling behavior.

Dimensions in Receiver Psychology

While we have thus far focused our attention on signalers, inter- and intra-individual variation in receivers is equally important to our understanding of animal communication. Towards this end, two recent reviews aim to reignite interest in the perceptual and cognitive biases in animal communication [52,53], building from the conceptual foundation established by Guilford and Dawkins [8,54] and others [9,55]. Kelley and Kelley [52] use a series of fascinating examples to review the importance of receiver vision and visual illusions, with a strong focus on predator-prey interactions. In contrast, Ryan and Cummings' [53] review encompasses multiple sensory channels, but focuses explicitly on mate choice. Both reviews emphasize the important role of sensory perception and perceptual and cognitive biases in the evolution of animal communication; Ryan and Cummings also warn that many of these and other drivers of signal form may be missed when studies of sexual signaling focus too narrowly on indicators and signal honesty. Since these reviews, a handful of empirical studies, highlighted below, have bolstered their points. The receiver psychology literature has been grown rapidly, with new empirical methods and with new developments in theory; a full review would be impossible in this short space, but here we touch on some of the areas and ideas that we find most exciting.

Perceptual and Cognitive Biases- Conventional studies of receiver bias, in which researchers manipulate signaling phenotypes and assess receiver responses, continue to accrue; and the conceptual foundation of receiver bias, sensory drive theory [17,56], is now being applied to

non-mate choice contexts. As one example, White and Kemp [57] highlight how sensory drive theory can help explain the colors of animal lures. Furthermore, there is increasing awareness that receiver biases can be influenced by complex interactions among dimensions of the communication system, such as sender and receiver behavior, sensory and cognitive mechanisms, and the signaling environment. For example, male great bowerbirds build bowers create forced perspective illusions in females, who stand in the bower during courtship. The field of view imposed by the bower likely increases signal efficacy through chromatic adaptation of females' eyes (which alters color perception) combined with the male's behavior of flashing colored objects into her view [58].

New research on proximate factors underlying biases in receiver sensory and cognitive systems—including genetic, biochemical, neural, and cognitive mechanisms—is combining tools and techniques from traditionally distinct fields of study to address gaps in our knowledge and challenge our assumptions. Recent studies have found that opsin gene expression in the retina, which affects color vision, differs among species, but within a species it may differ with habitat types, populations, developmental conditions, and between males and females [59-62]. Using a combination of electroretinography, morphology, and behavior, Caves et al. [63] find that cleaner shrimp are color blind and likely cannot resolve the colors and patterning of either conspecifics or client fish—critical information for understanding the evolution of morphological patterns in these animals (**Fig. 3A**). Yorzinski and colleagues adapted eye-tracking technology to study visual attention during mate choice in peafowl, finding that females rarely gaze at the entire upper region of the male's train. In addition, they found evidence of interactions between components, with shimmering behavior capturing and holding female's attention on the train (**Fig. 3B**) [64]. To date, some of the most comprehensive work on mechanisms of reproductive

158 decision making is on poeciliid fishes. Cummings and Ramsey [65,66] summarize much of this
159 work, which encompasses behavioral assays, gene expression assays, and pharmacological
160 manipulations towards the goal of understanding what they term the *social cognition of mate*
161 *choice*.

162 As researchers explore sensory capacities outside of our typical human experiences, new
163 channels of communication continue to be discovered. Thermal signaling was discovered
164 between California ground squirrels and rattle snakes [67] and air-particle displacement was
165 shown to predict agonistic interactions in amblypygids (nocturnal arachnids) [68]. Most recently,
166 polarization-mediated communication was described for northern swordtails, *Xiphophorus*
167 *nigrensis* (**Fig. 3C**) [69]. Examples like these, where we become aware of new communication
168 systems hiding in plain sight, dramatically illustrate the power of receiver psychology in shaping
169 animal signals.

170 *Cognition and Comparative Evaluation-* Bateson and Healy [9] argued that receiver decision
171 making in animal communication may be influenced by the number and type of alternatives
172 available for comparison. Such comparative evaluation has recently been shown to influence the
173 preferences of female sparrows [70], fiddler crabs [71], bushcrickets [72] and guppies, where
174 males preferentially court females surrounded by less attractive males [73]. In túngara frogs, a
175 female's binary choice between two stimulus calls is reversed in the presence of a less attractive
176 decoy call [74]. Such findings align well with behavioral economic models that incorporate
177 psychological concepts (e.g. limited cognitive resources, irrationality and sampling biases),
178 rather than traditional animal decision theory, highlighting the importance of incorporating
179 psychological concepts into our understanding of animal communication [9,55,74-76].

180

181 **Unifying the Dimensions of Communication**

182 The conceptual scaffoldings of the highly overlapping fields of sexual selection and animal
183 communication are rife with categorizations and dichotomies—e.g. sensory aspects of receivers
184 versus indicator models [reviewed in 20]; strategic versus tactical signal design [8]; redundant
185 versus non-redundant components [77,78]. To what extent are these categorizations and
186 dichotomies mutually exclusive? To what extent are they useful versus constraining? Exciting
187 new developments are helping to explore the common ground between theory in sexual selection
188 and signaling in other contexts [e.g. 20,57] and to integrate approaches adopted for the study of
189 complex systems into animal communication research [79].

190 Hebets and colleagues argue that the narrow redundant/non-redundant dichotomy in multimodal
191 signaling theory is not only semantically misleading, but has limited our understanding of how
192 signal complexity impacts the robustness and evolvability of behavior [79]. They use data from
193 barn swallows (**Fig. 3D**) [80] to highlight how complex displays may share components across
194 behavioral contexts and how within a context, overall display architecture can have structures
195 simultaneously consistent with both strategic and tactical design [79]. They bring readers from
196 the more traditional one-structure/one-function approach to an intuitive
197 multidimensional/multifunctional approach that offers a more faithful representation of complex
198 animal signaling. They argue for incorporating systems terminology, thinking, and approaches
199 into animal communication research, which integrates the concept of phenotypic integration and
200 moves from more traditional cause-and-effect thinking to synergistic thinking as it emphasizes
201 interactions and linkages [81].

202 *A Systems Approach-* In relating systems terminology and approaches into an animal
203 communication framework, Hebets and colleagues focus predominantly on the first two key
204 properties of system-level understanding [82]—quantifying the structure and dynamics of
205 signaling systems (i.e. how structure/function relationships change over time and across
206 conditions) [79,83]. They translate systems terminology—*redundant* (same structure same
207 independent function), *degenerate* (different structures/overlapping function), *pluripotent* (one
208 structure/multiple functions)—into animal communication scenarios and discuss their
209 consequences for system properties (e.g. robustness, functionality, evolvability) as well as their
210 evolutionary implications [79]. Systems-level understanding, however, also requires the
211 integration of information about the mechanistic underpinnings of system components [82]. In
212 communication systems, this goal is particularly challenging, as mechanistic underpinnings must
213 be determined and integrated both within and between two disparate systems that share varying
214 degrees of underlying machinery (e.g., genes, sensory systems)—signalers and receivers.
215 Ultimately, a system-level understanding will require the rigorous integration of data with
216 mathematical models to achieve a predictive understanding of system design principles [82,84].

217 Despite these challenges, the systems approach has the potential to help modernize animal
218 communication research—aligning it with advances in other scientific disciplines and offering
219 evolutionary hypotheses regarding the relationships between system design principles and
220 system properties. This approach provides a means for cross-taxa, cross-contextual comparisons
221 of animal signaling that can facilitate an evolutionary understanding of the multiple dimensions
222 of animal communication.

223 *Visualization of complex signals* – When considering multiple dimensions in communication
224 systems, visualization is a challenge. ‘Phenotype networks’ are a promising tool to represent the

architecture of complex signals, with signal components as nodes and significant correlations between components as edges (**Fig. 4A**). Network analysis is gaining a foothold in animal communication and has been implemented in studies of birds [36,80,85] and spiders [86]. A network approach allows us to go beyond pairwise metrics to quantify and compare the architecture of signals across individuals and taxa, and potentially, with receiver perceptual networks. Visualization and analysis of phenotype networks can reveal previously hidden patterns of relationships among system components that could lead to novel hypotheses, insights, and future research avenues. A similar holistic method for visualizing complex signal function involves mapping behavioral outcomes into multidimensional space to generate adaptive behavioral landscapes (**Fig. 4B**). This approach borrows from methods commonly used in population genetics and evolutionary biology [overview provided in 79,87,88] and is relevant to testing exciting new models for divergence in sexual signals among populations [89].

Encompassing and integrating the full dimensionality of animal communication into our research remains our most significant challenge. How do we merge a comprehensive, holistic approach to animal communication (e.g. a systems approach) with within-individual variation, perceptual and cognitive receiver biases, and a variable and changing signaling environment? How do we simultaneously quantify, compare, and model the within- and between-system interactions of signalers (e.g. genetic, biochemical and behavioral mechanisms underlying signal production) and receivers (e.g., genetic, biochemical, perceptual and cognitive mechanisms underlying decision making) across signaling environments and behavioral contexts (**Fig. 1**)? Answering these questions will likely keep researchers busy for some time.

Conclusions

The last few decades, and especially the last few years, have seen a great deal of progress in quantifying, explaining, and modelling complexity in animal communication. We urge scientists to continue to expand their conceptual frameworks beyond sexual selection theory, contest theory, mimicry and aposematism, etc. to a communication framework that addresses the commonalities among these contexts. We urge the development of integrated models that can incorporate both sensory and indicator aspects of signal design, as well as adaptive plasticity in their deployment and assessment, and which quantify and analyze communication displays within the perceptual space of receivers. We see great promise in the approaches reviewed here, which embrace these multiple dimensions of complexity in animal communication.

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466 **diversification of sexual signals in similar environments as a first step in speciation.** *Ecology*
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472 **ANNOTATIONS**

473 [26] **Patricelli et al.(2016): Synthesizes alternative hypotheses for causes of within-individual
474 variability in signals in the context of mate choice. These include ‘noise’, current condition
475 indicators, display refinement, and a series of hypotheses addressing tactical adjustments of
476 signaling behavior to maximize benefits and decrease costs, given the social and environmental
477 context of courtship.

478 [27] ** Biro and Stamps (2015): Discusses the use of broad-sense repeatability measures (R) to
479 quantify within-individual variation in traits, including signals. Shows that most studies ignore
480 change over time and have low power for their measures of R, and discusses problems associated
481 with these limitations. Presents suggestions for more robust measures of repeatability in future
482 studies, including the use of different metrics of R for different types of variability (i.e. narrow-
483 sense repeatability).

484 [29] **Westneat et al (2015): Presents a framework for statistically partitioning phenotypic
485 variance at multiple levels based on behavioral reaction norms, with an emphasis on within-
486 individual variance. Discusses processes that may influence within-individual variance, such as
487 the environment, highlighting the significance of ‘residual’ within-individual variation, which
488 may often include interesting biology.

489 [30] **Vitousek et al. (2015): Reviews evidence for dynamic feedbacks between physiological
490 state, signal expression, behavior, and the context and outcomes of social interactions. Discusses
491 the implications of these feedbacks for how signals evolve, how signaling phenotypes are
492 coordinated and how honesty is maintained.

493 [31] **Stamps (2015): Presents a hierarchical framework for categorizing types of plasticities in
494 behavior—Exogenous plasticities (contextual, developmental) and endogenous plasticities
495 (circadian and circannual rhythms, IIV, and age). Discusses methods for measuring individual
496 differences in the degree of plasticity and evidence for such variation in natural systems, as well
497 as the need for research into relationships between the types of plasticities (i.e. whether some
498 individuals are more plastic in multiple contexts).

499 [34] **Kershenbaum, et al. 2014: Demonstrates using data from seven distantly related taxa
500 (including birds, bats, hyrax, whales, and primates) that the vocal sequences of many of these
501 systems are more consistent with non-Markovian renewal processes than with the traditionally
502 assumed Markovian models.

503 [40] **Snell-Rood (2013): Presents a categorization of behavioral plasticity into two major
504 forms: developmental and activational; argues that course-grained environmental variability may
505 favor the former and fine-grained environmental variability may favor the latter. Discusses how
506 knowing the mechanism of behavioral plasticity helps to predict how organisms will respond to
507 rapidly changing and novel environments.

508 [59] *Bloch (2015): Quantifies the expression of four cone opsin genes across 16 species of New
509 World warblers, finding that opsin expression is not only variable across species, but also varied
510 between males and females (i.e. signaler and receivers). In females, the expression levels of one
511 opsin (SWS2) is correlated with plumage dichromatism, suggesting the co-evolution of female
512 visual capacity and male plumage.

513 [61] *Sandkam BA, et al. (2015): Explores population level variation in opsin gene expression in
514 three species of guppy, *Poecilia reticulata*, *P. parae* and *P. picta*. Expression was similar

515 between species in sympatric populations and differed across distinct populations of the same
516 species, suggesting an important role of the environment in influencing receiver perceptual
517 capacities.

518 [65] **Cummings and Ramsey: Summarizes much of the work investigating the mechanisms of
519 reproductive decision making in poeciliid fishes, which is one of the best and most
520 comprehensively studied model systems in this area of research. Encompasses behavioral assays,
521 gene expression assays, pharmacological manipulations, etc, towards the goal of understanding
522 what the authors term the *social cognition of mate choice*.

523 [69] *Calabrese et al. 2014: Develops novel methods to both measure polarization patterns in
524 male and female swordtails and to manipulate the polarization of the light environment and
525 assess female preferences. Finds that the polarized reflectance of females was different than that
526 of males. Females were found to spend more time in the areas with high polarization in
527 illumination, suggesting that mating preferences may be based, at least in part, on male
528 polarization patterns.

529 [74] *Lea and Ryan 2015: Highlights the importance of comparative evaluation in mate choice.
530 Female túngara frogs were given a binary choice between two call stimuli in the presence versus
531 absence of a third call type, a decoy. Two separate experiments altered the location of the decoy
532 – either on the ground between the two binary choice speakers or suspended above the ground
533 such that the call could be heard but was not accessible. In both cases, females demonstrated a
534 reversal of their preference in the presence of a decoy.

535 [79]**Hebets et al (2016): Argues for incorporating systems terminology, thinking, and
536 approaches into animal communication research. Translates systems terminology—*redundant*,

537 *degenerate, and pluripotent*—into the context of animal communication and discusses their
538 consequences for system properties (e.g. robustness, functionality, evolvability) as well as their
539 evolutionary implications.

540 [80] *Wilkins et al. (2014): Uses ‘phenotype networks’ to represent the architecture of complex
541 signals in barn swallows. Here signal components as nodes and significant correlations between
542 components as edges. Allows quantification of complex relationships between components,
543 facilitating comparison between males and females and among species.

544

Figure 1. A schematic of animal communication. Emphasizes factors that can affect signal form on the evolutionary, ontogenetic or behavioral time scales.

Figure 2. Within-individual variation in signals. Hypothetical data illustrating some of the ways in which individuals may vary over time in their signal production (in this case, signal intensity). In all cases, successful signalers (high-fitness; example in blue) produce signals at a higher intensity than unsuccessful signalers (low-fitness; example in orange); the sample mean is a dashed line. **(A)** In this scenario, there is high within-individual variability but no systematic change over time; the degree of variability does not differ between successful and unsuccessful signalers. **(B)** Here, there is systematic change over time and successful signalers are more consistent in their signal production than unsuccessful signalers (i.e. they have lower IIV [intra-individual variability]). **(C)** Here, there is a systematic decrease over time in signal production (for example, due to habituation, seasonal changes in condition, or change in the optimum signal values); successful and unsuccessful signalers differ in consistency as well as slope. Traditional measures of broad-sense repeatability (or consistency) would yield similar results for the high-success signaler in all scenarios, yet this signaler shows higher consistency in scenarios B and C, once the effect of time is removed. Biro and Stamps [26] discuss different measures of repeatability for each scenario. Westneat et al. [28] discuss methods to address heterogeneous within-individual residual variance, as seen in panel C. Patricelli et al. [25] discuss alternative hypotheses about why sexually-selected signals may vary over time and space, with an emphasis on tactical adjustments in signaling behavior.

Figure 3. Study systems for some recent discoveries in animal communication. **(A)** Caves et al. 2016 [62] studied visual systems of several species of cleaner shrimp, including this species

(*Lysmata amboinensis*) shown cleaning a moray eel, finding that they likely cannot resolve the colors and patterning of either conspecifics or client fish (photo copyright CC BY-NC 2.0 by Sudachi, Flickr). **(B)** Yorzinski et al. 2013 [63] used an eye-tracker on peafowl (*Pavo cristatus*) to show that females focus their attention on the lower regions of the male train during mate assessment (photo by Jebulon, copyright CC BY-SA 3.0). **(C)** Calabrese et al. [68] found evidence of communication using polarized light in swordtails (*Xiphophorus nigrensis*)(photo copyright Johnny Jensen, JJPhoto.dk). **(D)** Wilkins et al. 2015 [78] use phenotype networks to represent the architecture of signals in barn swallows (*Hirundo rustica*)(photo copyright Mdf, wikipedia GNU Free Documentation License 1.2).

Figure 4. Methods to visualize complex signals. **(A)** Heuristic phenotype networks illustrating courtship signal architecture through component correlations for two signaling environments (left and right). Data based loosely on preliminary data from the wolf spider *Schizocosa floridana* (Rosenthal 2015). *Node* shape = component type (**circle** = acoustic, **square**= morphological, **triangle** = color). Blue nodes represent significant predictors of copulation success. Edges between nodes represent pair-wise correlations; edge thickness = correlation strength. Quantitative comparisons of network architecture using density coefficients show that system-wide patterns of signal degeneracy (different structure/overlapping function) change across contexts. Network density (our proxy of degeneracy) is higher in the environment on the left (C-values), as visualized by more and thicker connections between components. We might predict then, that effective signaling in that environment is more robust to changing conditions. Differences in function for components 1 and 2 across conditions may provide an example of pluripotentiality – the same components serving multiple functions across signaling environments. **(B)** Complex signals can also be visualized as response surfaces, similar to

590 adaptive landscapes. This surface shows a hypothetical multipeaked response surface for a
591 female based on variation in two male traits. The relative height (strength) of the response peaks
592 at different trait combinations indicate female preference. Mendelson et al. 2014 [87] discuss
593 how complex, multipeaked preference surfaces, such as this example, can favor early divergence
594 among populations in sexual signals (reprinted with permission from Mendelson et al. 2014
595 [87]).

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Signaling Environment

Abiotic Factors

e.g. climate, latitude and longitude, current position of sun, temperature, wind, etc.

Signaler Biology

Signal Form

- Genetic & biochemical architecture
- Relationship with underlying quality, e.g. parasite load, nutrition, developmental history

Signal Production & Deployment

- Learning & memory
- Behavioral plasticity
- Behavioral context, e.g., agonistic, alarm, reproductive

Emitted
signals
&/or cues

**Signal
Transmission**
e.g. attenuation,
distortion,
masking

Arriving
signals
&/or cues

Receiver
feedback:
Arriving
signals &/or
cues

Receiver
feedback:
Emitted
signals &/or
cues

Receiver Biology

Perceptual Capacity

- Genetic & biochemical architecture
- Perceptual & processing mechanisms, e.g. tuning curves

Receiver Response

- Decision-making
- Learning & memory
- perceptual & cognitive biases
- Behavioral context, e.g., agonistic, alarm, reproductive

Biotic Factors

e.g. biome, food availability, predator density, surrounding vegetation, social environment such as conspecific and heterospecific signalers, etc.

Patricelli and Hebets, Figure 3

A

B