



# Songbird Behavior and Conservation in the Anthropocene

Darren S. Proppe (Editor)



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# Songbird Behavior and Conservation in the Anthropocene

*Editor*

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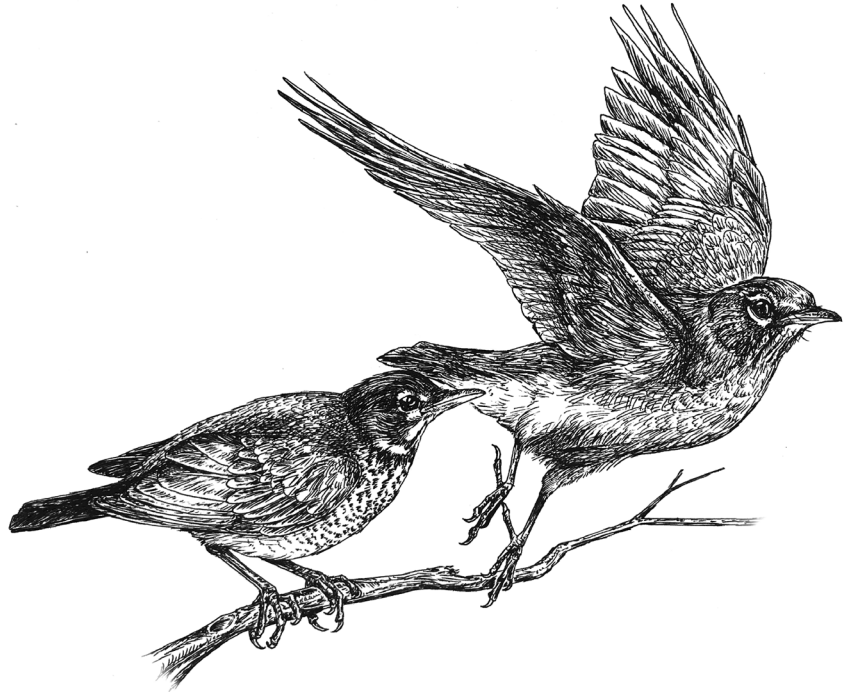
*This book is dedicated to  
my wife and children who gave me the space and time to explore,  
write and edit; to the many authors who put in countless hours to  
write and edit each chapter; and to the songbirds that we aim to protect.*



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## *Preface: How to Utilize this Book*

*Darren S. Proppe*<sup>1</sup>

This volume is dedicated to explaining the role that behavior plays in the function and ecology of free-living songbirds with a particular focus on its importance in conservation and management. Understanding songbird behavior is no small task. Indeed, many have dedicated their careers to studying particular aspects of songbird behavior. In addition, there is a long history of study on the behavior of animals—often located across disparate fields and academic journals. Although the integration of behavior into conservation and management is a relatively new endeavor, many of the underlying processes and systems have been explored in detail. In fact, developing a text that merely explored bird behavior as a scientific study might have been redundant. Donald and Lilian Stokes wrote several volumes on bird behavior in the 1980's [1], and in 2001, David Allen Sibley wrote an excellent and accessible text called *The Sibley Guide to Bird Life and Behavior* [2]. Other texts have extensively addressed the song system [3, 4] and elements of avian migration [5–7]. Still others have examined the impacts of urbanization on birds [8, 9]. In 2014, Dr. John Marzluff published a very informative and easy read for a lay audience called *Welcome to Subirdia* [10]. In part, I cite these texts here to direct

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<sup>1</sup>Research Director, Wild Basin Creative Research Center, St. Edward's University

you to some of the excellent resources that are available. But I also wish to answer a question: Why another book? Our book is distinct from these texts because it explicitly addresses behavior in light of the conservation challenges we face in the human era—the Anthropocene. My goal in editing this book was to provide a ‘one-stop shop’ for those interested in integrating behavior into management or applied research programs. That is not to say that you will find every bit of known information contained within these pages—far from it. Rather, we aim to provide the needed groundwork to understand basic concepts and to recognize where research has led us at the time of publication.

Chapters are broken into particular behavioral topics (e.g., habitat selection, foraging, personality, etc.). In reality, however, animal behavior is not a discrete set of responses that relate only to one topic – or ecological system. Rather, there is much overlap. What an animal eats, for example, is related to energetics and foraging strategies, but also associated with predation and social information. In the same vein, anthropogenic changes will likely alter many behavioral systems. Human-produced noise might impact communication directly, but also impact foraging and sexual selection. As the editor, I have worked with each author team to keep their chapter within the bounds of their particular subset of behavioral systems. But do not be surprised when particular behaviors, or particular anthropogenic stressors are addressed within several chapters. In fact, this repetition of themes should reinforce the notion that behavioral responses operate along a continuum and within a multi-sensory input and response system. To suggest, for example, that predation and habitat selection are not connected, and that personality would not impact both of these systems would be misleading. Thus, chapters are designed to be separate, but overlapping. One positive aspect of interconnected themes is the potential that a few management techniques might go a long way towards preserving many behavioral systems.

To provide a foundational understanding of behavior, each chapter begins with a primer on the stated behavioral topic. Every chapter is written by experts in their particular niche of songbird behavior. Each author team is well published, actively engaged in scientific research, and well-regarded by their peers. However, each author was also instructed to write in a style that is accessible to fellow academic researchers, on-the-ground managers, and engaged community scientists alike (although we know that many of you will wear all of these hats). To get the creative juices flowing, each author has peppered their text with examples where particular species or systems display the behaviors being described. The intentional inclusion of examples was designed to display the phenomenal capabilities demonstrated by songbirds, but also to accelerate the application of information to your system of interest. These examples should also be particularly valuable for managing or conserving species with little published information. For example, Otter et al. (Chapter 5) describe that some lekking species might be more reliant on characteristics of ambient lighting than most birds [11]. Might the system or species that you manage be similar? What elements of your system might elevate, or not elevate, the role of light? Of course, most the time our examples will not directly address your particular species. But this is one of the beautiful elements about studying behavior—there is so much to learn! So, I challenge you to let the text push you to think more deeply, and more creatively, about your organisms and systems.

Once each chapter reviews behavioral fundamentals and the latest research, the authors move on to describe some of the primary threats stemming from the human alteration of native habitats and ecosystems. Perhaps this is the crux of the text. If we are going to successfully maintain diverse songbird populations and communities, we must recognize the threats to their established behavioral systems—which may go way

beyond structural or vegetative changes to habitat. Again, specific examples from the scientific literature abound, allowing the reader to delve much more deeply into the topics they deem most pertinent or interesting. In each case, threats are followed by the presentation of potential solutions. On this front, some authors are fortunate to be able to report on protocols that have already been implemented, or experimental solutions that offer promise. Others must recognize that the solutions are yet forthcoming. But hopefully that is why you are reading this book – to play an active role in developing solutions that can sustain behavioral systems in songbirds, and thus their existence, in a world that is changing with incredible speed. Understanding the required habitats utilized by birds is critical, but failing to integrate the role of behavior into management is likely to produce subpar results. It is my hope that reading this book will lead you to agree, and that it will spur the development of holistic and novel techniques for managing songbirds.

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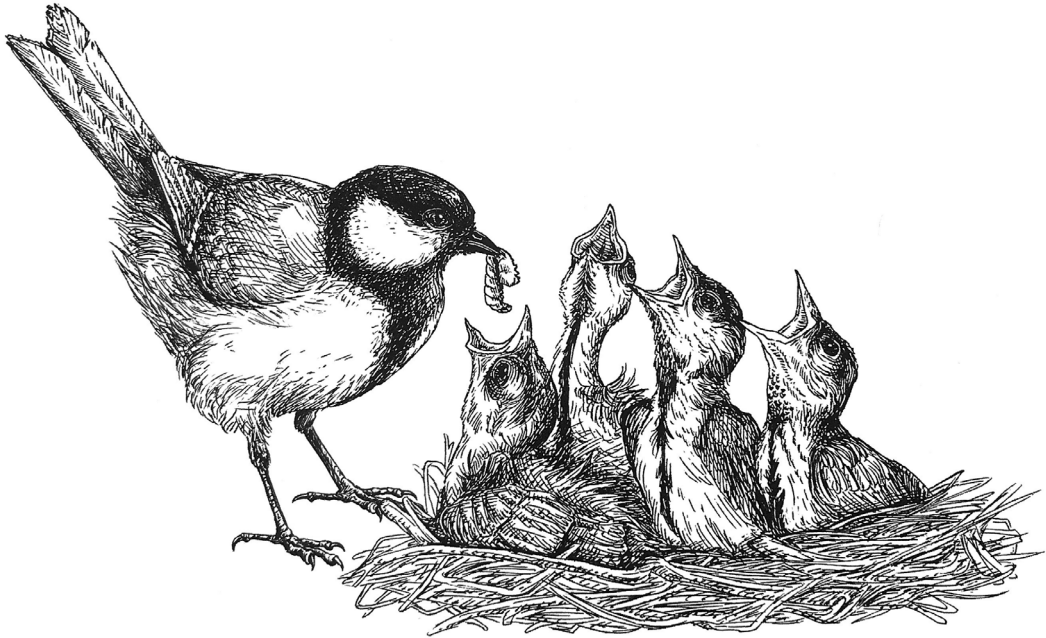
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## Chapter **1**

# *Static Organisms in a Changing System?*

*Darren S. Proppe*<sup>1</sup>

## **Introduction**

Domestic chickens are known for simple, predictable, and often stereotyped behavior. Eat, sleep, eat, sleep, eat, sleep... repeat. Although chickens are not songbirds, I open with this species here as an example of an organism with which many people are familiar; one that vividly portrays the types of behaviors that lead many to believe the actions of organisms are by-in-large static. But for those who have owned and raised chickens, or for that matter any domestic animal, the story is more complicated. Some chickens choose to feed primarily from a food cup while others forage predominantly

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on the ground. Some individuals follow their owners incessantly, while others flee from human presence. Even behavior within an individual is not static. Not long ago, an unfortunate dog attack left one of my chickens severely injured. Although the chicken made a full recovery, her behavior was forever altered. The sound of a dog bark sent this free-ranging chicken in a full sprint back to the safety of the enclosed coop. Before her incident with the dog, she responded to an audible dog bark by merely raising, and sometimes cocking her head. Other chickens in the same flock continued to exhibit only this minimal response to the acoustic sounds of a potential canine predator. They had not experienced a fear-inducing interaction with a dog, and did not socially learn fear behavior from the injured chicken. Thus, they had no learned fear response as a result.

While an experienced chicken owner will likely recognize the presence of among-individual and within-individual variation in behavior, an educated owner also knows that some behaviors *are* largely static. No one expects that domestic chickens will suddenly become migratory. Nor will they begin building nests in trees, or nests at all for that matter. More narrowly, if an owner desires regular egg production, they must provide the right environmental conditions—which includes a relatively confined dry space with soft bedding. In fact, the importance of understanding and accommodating behavior is rarely lost on one who own pets or livestock. Dog owners speak regularly about good or bad behavior, and often elaborate about their pet's personality. Ranchers know which heifer or horse to be wary of, and farmers know which goat or rooster should not be left with children. Despite the clear acknowledgement that behavior plays a role in the care of captive animals, behavior has not received the same attention when it comes to the management of non-captive organisms.

I open this introductory chapter by providing the definition of behavior, and briefly describing the history of behavior as a scientific field of study. Next, I explore learning and cue-response systems as the mechanisms that underlie the behavioral responses we observe. This section is followed by an exploration of stability and flexibility in behavioral systems, with focus on relevant songbird responses to environmental cues and signals. I then place these systems within the context of anthropogenic change – addressing the need to bring an understanding of behavior to conservation and management plans.

## The Foundations of Behavior

Behavior is broadly defined as, (1) the way in which one acts or conducts oneself, especially toward others, (2) the way in which an animal (non-human) or person acts in response to a particular situation or stimulus, or (3) the way in which a natural phenomenon or a machine works or functions [1]. For our purposes, we will focus on animal behavior, meaning that the second definition is most relevant. The beauty, and sometimes the curse, of animal behavior as a scientific study is that it covers a broad range of fields and expertise. For example, much of our initial understanding of learning and behavior was developed by prominent psychologists with an interest in explaining human behavior. More recently, entire branches of the psychological field have become dedicated to understanding the development of behavior and the proximal mechanisms that underlie non-human animal behavior. Lab and field studies often attempt to explain behavior under natural conditions – a particular scenario defined as *ethology*. Topics such as learning and cognition continue to be explored extensively among psychologists [2],

producing many advances that are relevant to biologists focused on behavior and management. Animal behavior has become a focus of study for many ecologists as well, with foundations of the field established in the early to mid-1900's by scientists such as Nikolaas Tinbergen, Konrad Lorenz, and Karl von Frisch [3]. Perhaps one of Tinbergen's most significant contributions to the field was his description of the four questions (or arenas) for the study of animal behavior [4]. *Causation* (or mechanism) and *development* (or ontogeny) of behavior describes many of the topics investigated using captive animals. Ecologists that study behavior tend to focus on Tinbergen's second two questions: *function* (or adaptation) and *evolution* (or phylogeny) of behavior. These latter questions may be thought of as exploring why particular behaviors occur, which is often explained by the correlation between their performance costs and the benefits of their expression. This study of *ultimate* (as opposed to *proximate*) explanations of behavior is often defined as *behavioral ecology* [5].

While Tinbergen's designations have been extremely beneficial for studying and understanding behavior, they have also had the unintended consequence of creating somewhat siloed fields of study. This unfortunate situation is exacerbated by the difficulty of tracking the vast literature found across many field-specific journals, and the sometimes differing study techniques used by biologists, ecologists, and psychologist [6]. To fully understand behavior, and to manage animals accordingly, will require an integrated understanding of all four of Tinbergen's questions. The focus on collaborative management and ecosystem approaches in recent years has led to an exciting and unprecedented integration of information about the development and function of behavior [7–9]. This integration is timely and critical as we now work to sustain populations and communities of songbirds in landscapes that are changing rapidly. No doubt one of the keys to integrating behavior into management for songbirds will be understanding how, and how quickly, behavior can change to accommodate shifting environmental conditions.

## Learning and the Development of Behavioral Response Systems

The development of particular behavioral systems (or responses) is shaped by the same processes of natural and sexual selection that leads to physical traits better suited for particular environments. If behaviors are thought of as responses to particular situations or environments, variation in these responses must exist for natural selection to shape the system. Within this range of responses, there must also be variation in how the resulting outcome impacts fitness (e.g., some responses provide better fitness gains than others). While heritability, a keystone of natural selection, also plays a role in the development and maintenance of many behaviors we observe, learning can also maintain some elements of behavioral systems. The basic cue-response system that leads to standardized behavioral responses, and to changes in behavioral responses, can be represented as a triangle with *cue*, *response*, and *outcome* at the three corners (Box 1). Although each term is singular here, in reality it may take multiple cues to elicit a response, or responses. Here the *cue* represents the environmental stimulus that could trigger a particular response. To understand this in human terms, simply imagine that someone is cooking bacon for breakfast (if you do not like bacon, imagine your favorite food here). As most readers are probably aware, bacon that is being cooked

has a strong, distinctive smell. This smell could be classified as potential cue, which might trigger a *response* from nearby humans. The response to bacon is likely to differ among individuals, but for those that like bacon it is likely to trigger a desire to find and consume bacon. If this response does lead to consumption, the *outcome* in the bacon-lover will be positive—a pleasurable dining experience. Repeated experience with this particular cue-response system would establish a ‘find-and-eat’ response to the smell of bacon. If bacon was the only, or perhaps the most beneficial food source available, the fitness of individuals with the ‘find-and-eat’ response would increase, and the behavior would be selected for. If genetics were to underly this response, selection would increase the prevalence of this response in the population by favoring the responsible genotype. Even without genetic underpinnings, experience and teaching (a phenomenon that is less prevalent, but not absent, in non-human animals) might increase the bacon-philic response. While this example is somewhat silly and underestimates the complexity of behavioral development, it does provide the basic level of understanding needed to grasp the development of behavior (for a deeper understanding see [10, 11]). Our bacon example also allows for a few extensions that can explain how the use of cues and responses can change over time.

If bacon creates an automatic ‘find-and-eat’ response in many of us, that response is said to be an unconditioned stimulus (i.e., no training is needed to evoke this response). But through a procedure called *classical conditioning*, we could actively train individuals to exhibit the same ‘find-and-eat’ response to the sight of a pancake—if the sight of a pancake and smell of bacon are paired across several trials, and always result in the availability of bacon. Eventually, the ‘find-and-eat’ response would be learned and evoked by the sight of a pancake alone (conditioned stimulus; i.e., training was needed to evoke this response). The classic example of this process is Pavlov’s dogs, who were trained to salivate for food in response to the sound of a metronome [12]. In songbirds, a similar process likely underlies the selection for particular habitats or tree species. While selected trees or habitats likely supply better food sources than non-selected locations, it is unlikely that birds directly assess insect populations prior to selection. More likely, experience (or selected genetic preferences) has facilitated an association between the preferred habitat characteristics and food availability [13, 14].

A particular response can also be extinguished by changing the outcome in the cue-response system [15]. For example, some alternative-fuel vehicles use recycled food grease as fuel [16]. The resulting exhaust can have a bacon-like smell. In this case, the ‘find-and-eat’ response to the smell of bacon described above could result in the negative outcome of being exposed to vehicle exhaust or the danger of approaching a moving vehicle. If a particular response is no longer rewarded with a positive outcome, or results in a negative outcome, the response might be extinguished. If bacon smell becomes more commonly associated with vehicles than a preferred food source, the ‘find-and-eat’ response may become extinct. Similarly, most songbirds exhibit a fear of humans, but fear behavior is diminishing in populations that inhabit human-dominated systems (e.g., cities [17, 18]). In this case, repeated neutral or positive (e.g., food provided) interactions with humans in urban systems are likely extinguishing fearful behavior. While the altered cue-response system here might appear benign, the impact of changing the outcome in a cue-response system can come with negative fitness impacts. For example, songbirds are killed regularly by wind-powered turbines during migration [19]. This is potentially due to their attraction to light [20] which also serves as an important cue for migration, or through other established migratory behaviors such as low-altitude flight in large groups [21]. Given enough time and experience, songbirds may learn to associate particular

characteristics of turbines with the danger that they represent (i.e., extinguish attraction). But for a time, there is a *mismatch* between the response and the expected outcome [22, 23]. During this mismatch period, there is a high likelihood that more songbirds will be injured or killed by turbine blades. Simply put, behavioral changes may be too slow to avoid the negative impacts of environmental change (i.e., the outcome).

## Stability and Plasticity in Songbird Behavior

As with most organisms, songbird behavioral systems exhibit a range of plasticity. Some genetically coded behaviors have become *fixed*, which can indicate that strong selection has nearly, if not completely eliminated genetic variability in the loci responsible for producing the particular behavior, and thus eliminated variability in the associated behavior. Other behaviors are crystalized after a short learning period. Some more plastic behaviors are shaped in individuals and populations through experience, and some responses are subject to high levels of within-individual plasticity based on the particular set of environmental conditions. In this section I provide an explanation of, and examples for songbird behaviors that are typically characterized as innate or largely stable, learned, shaped by experience, and plastic. However, much remains to be learned about each system, and these categories should not be considered to be set in stone or mutually exclusive. In addition, plasticity itself may be under selective pressures that can increase or decrease variability over time [24]. I conclude the section by explaining why multiple behavioral responses to the same stimuli often exist within songbird populations and species.

### Innate or Largely Stable Behavior

Immediately after hatch, hungry Cactus wren (*Campylorhynchus brunneicapillus*) nestlings lift their heads upward with their mouth agape at any detection of movement or sound – which most likely represents an adult approaching the nest to feed [25]. Although critical for their survival, this ‘gaping’ behavior does not stem from experience or tutelage. Gaping, which is a trait shared across songbird species, is innate [26]; likely coded within the genes. This is not to say that there is not variability in gaping behavior, but rather that natural selection will strongly favor individuals that exhibit this behavior over those that do not. Gaping and begging correlate with hunger level [27], and parents likely perceive these behaviors to be an honest indicator of a nestlings need for nourishment. In keeping with this hypothesis, experimental work with tree swallows (*Tachycineta bicolor*) and great tits (*Parus major*) indicates that parents increase feeding rates as gaping and begging rates increase [28–30]. A nestling that does not gape, or gapes less often, is less likely to be fed. An unfed nestling is unlikely to survive and carry this trait into the next generation. Although gaping and begging are an honest indicator of hunger that is critical for survival, variation in begging rates among broods may also be indicator of health. For example, great tit nestlings that hatched from eggs laid by a female given supplemental carotenoids, an important but limited antioxidant, begged more intensely than control nestlings [31]. Because carotenoids are associated with nestling health, more intense begging is still an honest indicator of fitness, and increased feeding of these carotenoid-rich chicks is probably a good investment on the part of a parent. Again, selection favors stronger gaping and begging behavior.



Migration, the seasonal movement between spatially distinct habitats, is a common songbird life history trait. The role of genetics and experience in navigation between breeding and wintering grounds has received much attention in the scientific literature, and is addressed more broadly in Chapter 7. However, I want to visit this topic briefly here because elements of migration are thought to be innate [32]. For example, *zugunruhe* refers the restlessness observed in both experienced and naïve birds around the time when migration should occur [33]. Further the direction and distance to the wintering grounds appears to be genetically encoded in first-time migrants. Good confirmation of this came from crossbreeding studies where hybrids from two populations with unique migratory routes and destinations exhibited an intermediate migratory path [34]. Displacement experiments have also found that naive birds are not able to consistently correct the angle or distance of their migratory path to reach the correct wintering ground [35]. In adults, however, experience with a navigational map allows for such corrections to be made [36]. Despite the innate components of migration, plasticity is more common than might be expected. Recent work suggests that juvenile migrants do have some ability to compensate for strong winds and minor displacements [37]. The presence of *zugunruhe* in a resident species of stonechat (*Saxicola torquatus*; [38]) suggests that this species may have been migratory in the past, or could become migratory in the future [39]. Indeed, migratory populations of blackcaps (*Sylvia atricapilla*) in Europe are staying closer to home as conditions on the breeding grounds become more favorable year round [40] despite the presence of genetic differences between migratory and already resident populations in this species [41]. In contrast to gaping and begging, these studies suggest that it is plausible that migratory behavior could appear or disappear in response to changing conditions – a good reminder that innate underpinnings do not preclude rapid change.

Traditional thinking has been that elements of the nestbuilding process are also innate [42]. But, a role of experience has long been recognized, and experimental evidence to support claims of innate behavior were often lacking [43]. Evidence from hand-rearing experiments, field observations, and laboratory manipulations indicate that associative learning, social learning, and imprinting are important contributors to the nest building process [44]. While nest-building is probably not a hard-wired response [45], and thus not innate, the propensity to build nests is nearly ubiquitous across songbird species. This suggests that selection strongly favors nest-building as a strategy for increasing survival in offspring. This is not to say that alternative strategies are not plausible. A few passerines, including several cowbirds species (genus *Molothrus*), have abandoned nest building; instead laying parasitic eggs in the nests of other species [46]. Several non-passerine species, including a large percentage of shorebirds (order Charadriiformes) lay camouflaged eggs directly on the ground. This non-nest building strategy has been successful in many non-passerine bird species [47]. But in passerines, observing a shift from a nest-building to non-building strategy in response to management or environmental change is unlikely to occur. Nests provide many ecological benefits, including; protection from predation, providing a barrier for containment of nestlings, and to some extent buffering the variability in the environment (e.g., wind, rain, temperature) [48]. Nest characteristics, such as thickness, material, and even placement may be modified more quickly based on learning and experience. For example, orange-crowned warblers (*Vermivora celata*) nesting on Santa Catalina Island, California, USA, were more likely to place nests off the ground than their mainland counterparts, and offspring survival increased with nest height [49]. But when an aerial predator (blue jay, *Cyanocitta cristata*) found on the mainland was artificially presented

to the island population during nest building, nests were moved closer to the ground and to more concealed locations.

Other songbird behaviors that exhibit innate components include; predator detection [50] and recognition [51], and some components of vocal production [52] and recognition [53]. In general, innate behaviors should exhibit relatively low levels of plasticity – especially in cases where alternative strategies are not available (e.g., begging). However, this does not preclude change. In the strictest situation, where a genetically encoded behavior has become fixed in a species, change will require genetic mutations that provide variability, and thus, the fodder on which selection can operate. But in most behavioral systems, genetic variation not so tightly constrained. Further, as exhibited through migration, innate behavior is often refined by experience.

### **Learned Behavior—Systematic**

Here I address learned behavior as a systematic process that functions to maintain some level of stability within a range of potential behavioral responses. While experience also contributes to learned behavior, I will more explicitly address this situation in the next section. In songbirds, learning is often classified as open-ended (lifelong learning) or closed-ended (learning occurs during a set period) [54]. This system is often used to describe the development of song. The species-specific songs characteristic of most songbirds are learned only during development – being closed ended. Young birds listen to tutors (silent phase), practice (subsong), and establish adult song (crystallization) [55]. Once songs are crystallized, learning on the macro-scale ceases, although minor modifications to temporal and pitch characteristics can be made in many species [56, 57]. Without tutoring, some elements of song may marginally mimic adult song, which indicates that there may be some genetic components of song development, but these loose mimics are unlikely to function normally [58]. Some species, including those in the suborder Tyranni (i.e., suboscines) are an exception, because they tend to produce adult-like songs without tutoring [59, 60]. On the other hand, some species, such as mockingbirds and other members of the family Mimidae are open-ended learners [61, 62]. Song learning continues throughout adulthood. Still, species-specific characteristics, such as the number of times phrases are repeated, are maintained. In most songbird species, dramatic changes to song types can be made once per generation during the sensitive phase. The limited range of nearby tutors, which is not limited to the paternal parent [63, 64], serves to converge each generation of learned songs toward the species mean. Stabilizing selection is further supported by sexual selection, where females are more likely to pair with males that propagate songs that resemble the species mean [65]. Sexual selection may also serve to maintain more stable visual courtship displays, since females tend to prefer performances that exemplify the idealistic species-specific moves (e.g., highest leap, quickest flight) [66]. In manakins (genus *Manacus*) and other species with extreme courtship displays sexual selection may even drive the development of the physical traits required to perform otherwise atypical body movements including production of sound with other structures on their body like modified feathers [67].

While tutoring and sexual selection might place an outer limit on the rate of change in vocal or visual displays that will be observed within a particular individual or generation, it does not eliminate modification. A multi-decadal study of song types in the white-throated sparrow (*Zonotrichia albicollis*) recently revealed that a novel doublet-ending version of the species-specific song arose in western Canada and replaced the typical triplet-ending version across the much of the continent [68]. Geolocator tracking

indicates that birds from spatially separate breeding regions mix on their wintering grounds, where tutoring is likely facilitating the broadscale vocal change. Experimental work in an isolated population of savannah sparrows (*Passerculus sandwichensis*) reveals the process by which a novel song can be integrated [69]. Researchers tutored five developing cohorts with a novel song exemplar played via loudspeakers. During six years of tutelage with the novel song type, 30 individuals incorporated the novel song type into their repertoires, and several second-generation birds learned the novel song from the previous generation. In this case, however, regulation from sexual selection may have been lessened because developing females were also exposed to the novel song type.

One learned behavior that may be less open to modification is imprinting. Young zebra finches selectively prefer their host nest via olfactory imprinting [70], which may also guide future nest building endeavors. Olfactory imprinting during development may also play a role in kin recognition [71, 72]. After fledging, most songbirds scout their breeding habitat before departure, imprinting on the habitat characteristics to which they will return [73, 74]. Although not confirmed in songbirds, pelagic birds [75], sea turtles [76, 77] and salmon [78] also imprint to the earth's magnetic field during development, allowing for long-distance navigation back to their natal habitats as adults for breeding. Imprinting on olfactory or magnetic cues may also facilitate return trips to the breeding grounds in songbirds. Because imprinted behaviors are solidified during development, they may be relatively non-flexible in adults. In these cases, management during development may be required if an alteration to behavior is desired. One famous example is the imprinting of naïve whooping cranes (*Grus americana*) on an ultralight aircraft as surrogate adult guide, and then using this craft to guide birds along the new migratory route. Since 2001, imprinted adult cranes continue to use this trained migratory path, and are now making their own adaptations to the route [79].

## Behavior Shaped by Experience

In contrast with systematic learning, behavior that is shaped by experience is not always shared across individuals or populations. In humans, our experiences as a youth, our interactions with different cultures, and our exposure to particular traumatic or particularly rewarding events very much impact how we act as adults. Conversely, having a political figure or professional athlete in one's family increases the likelihood of this career path in the next generation – or more broadly, parental values directly and indirectly influence the aspirations of their offspring [80]. Pavlov's dogs, and extensions of classical conditioning make it clear that this process is not limited to the human realm.

Animals, including songbirds, regularly respond to environmental stimuli and these experiences shape future behavior. One particularly poignant example comes from American crows (*Corvus brachyrhynchos*), which are members of the Corvid family, a group of birds known for their cognitive abilities. Researchers from the University of Washington wore masks while trapping and banding crows [81]. When these same masks were worn on campus in future years, crows responded with harsh calls and mobbing, but neutral masks were not treated with equal disdain. Like humans, crows also transferred their disdain for particular masks to their young [82]. In a novel laboratory experiment, food-caching scrub jays (*Aphelocoma coerulescens*) that had pilfered the caches of other jays moved their own cache sites when other jays observed them during their initial cache [83]. However, jays without previous experience pilfering another's cache did not alter their own cache sites. While experience-dependent learning is particularly impressive in Corvids, it is certainly not limited to this family. Many songbird species

become less leery of people when they experience humans regularly [84]. Urban black-capped chickadees (*Poecile atricapillus*) show less neophobia towards novel objects [85] than their rural counterparts, but are less likely to return to a feeder when a house cat model is present [86]. Both differences are likely due to a differing set of past experiences; more benign interactions with novel objects and more adverse interactions with cats in urban-dwelling chickadees.

McGrath and colleagues provided a particularly compelling example of shaping behavior via experience in a field experiment with wild superb fairy-wrens (*Malurus cyaneus*) [87]. Ten individuals were exposed to novel alarm calls accompanied with a gliding predator model. Although none of the birds fled in response to the novel alarm prior to experiment pairing with a predator model, nine of ten individuals fled to the novel alarm after training. These experimental results clearly display the role of experience in shaping critical behavioral responses in songbirds, but they also reveal a potentially important conservation tool - managers may be able to intentionally modify cue-response systems in songbirds via artificial experiences that alter future behavioral responses.

### **Within-individual Behavioral Plasticity**

In many cases, individuals possess the ability to respond and behave differently based on variation in a particular set of external cues. This is broadly known as within-individual plasticity. Foraging demonstrates this concept well in that individuals will select prey species based on the combination of prey availability, energetic gain, and time required to capture and consume prey [88]. This idea, formalized as optimal foraging theory [89], proposes that variation in the aforementioned criteria will lead to a constantly shifting diet composition. For example, great tits offered profitable and unprofitable prey in a lab setting were not selective when both prey densities were low [90]. But when the encounter rate of profitable prey was increased, tits ceased to ingest unprofitable prey. Continued research indicates that optimal foraging is also shaped by competition from heterospecific species [91, 92], and by predation pressure (e.g., landscape of fear [93, 94]). In the urban setting, perceived risk – and therefore foraging behavior – may also be impacted by connectivity, where isolated patchy habitats are less likely to be used by foragers [95].

Plastic behavior may be thought of as possessing a suite of if-then tactics [96]. For the foraging example used above, this might translate to ‘if profitable prey is abundant, avoid unprofitable prey’. Alternatively, ‘if profitable prey is not abundant, consume any available prey’. Tactics can be distinct responses, or represent a range of responses along a continuum. A number of songbird species are cooperative breeders, such that related or unrelated, non-parental individuals will assist in raising offspring. In this case, a young, reproductively capable songbird must select categorically between having a nest of its own or helping at the parental nest. Which tactic is chosen is dependent on the costs and benefits of each option. In the well-studied Seychelles warbler cooperative system [97], the decision to help at a nest is based upon the availability of new territories, the quality of available territories, and the likelihood of finding a mate [98, 99]. The decision to breed or help will be revisited each year, with helping to raise genetically similar offspring selected when the likelihood of producing one’s own offspring is low. Habitat selection is another case where discrete tactics are employed each year in migratory species: settle or do not settle [100]. A number of interacting variables likely play a role in the selection of breeding and wintering habitats [101]; including patch size, vegetation,

and the presence of conspecific and heterospecific species [102, 103]. In this case, vocal conspecific cues have been used to train several species to utilize newly created [104], or alternative [105, 106], habitats. Here conservation objectives might include manipulating behavior by carefully altering flexible cue-response systems.

In contrast to these discrete sets of tactics, a number of studies have demonstrated that songbirds can adjust the frequency of their adult songs along a continuum in response to the level of human produced noise, which tends to be low-frequency. While higher frequency songs that reduce masking by low-frequency anthropogenic noise could arise from selection for individuals that always sing higher-frequency songs, a number of studies indicate that individuals can shift their frequency in relation to current ambient conditions [107, 108]. In this case, individual songbirds may be balancing the need to be heard over elevated ambient noise, with the need to produce vocal cues of quality or dominance. Accordingly, we found that black-capped chickadees increased their frequency throughout the morning as traffic levels (and noise) increased [57]. In addition, chickadees sang at generally lower frequencies on weekends when traffic levels were lower. Here the tactics would likely be ‘if noise level is high, sing at high frequencies to be heard’, but ‘if noise level is low, sing at low frequencies to convey information about quality’. While behavioral plasticity might be a welcome trait in a rapidly changing world, it is important to remember that the range of tactics available is not boundless. Physical and physiological limits will limit capabilities. For example, song production is limited by the vocal tract and beak shape, while foraging will be limited by the ability to handle, digest, and procure sufficient nutrients from available food sources. Further, sexual and natural selection will tend to eliminate extreme diversions from typical, species-specific behavior.

## Different Behavioral Strategies Among-individuals

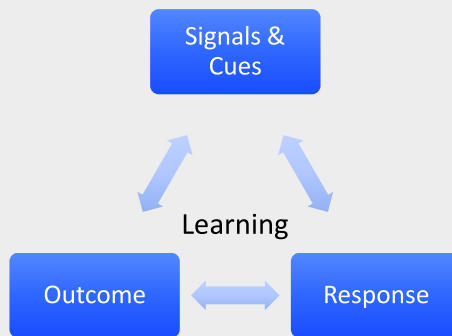
If individual songbirds alter their behavior in ways to maximize gain (benefits-costs), the existence of multiple tactics is not surprising. However, we also observe several behavioral patterns that are consistent within individuals, but differ between individuals. For example, wintering ovenbirds (*Seiurus aurocapilla*) in the West Indies were classified as sedentary [109] (e.g., holding stable territories) or floaters (e.g., holding small or no territories with regular foraging excursions). Only a small portion of the population exhibited a floating strategy, and artificially altering food availability did not produce changes in foraging strategies. So, the question might arise as to which strategy is best, and why both continue to persist. The answer here is that the fitness value of each strategy was dependent upon the environment. In years when food resources were high, sedentary, territory holders had higher body mass – an indicator of health. But, when food was scarce, floaters – who were more likely to search for and exploit novel food resources – had higher body mass. Thus, a fluctuating environment will maintain both behavioral strategies within the population.

Even in a stable environment, multiple behavioral strategies can coexist. In the above example, floaters were always less common than sedentary birds. If the percentage of floaters in the population increases, there will be fewer territory holders. Under this scenario, defending a high-quality territory might become easier since fewer birds are doing so – and selection will favor territory holders. Conversely, if most birds hold territories, defense of new territories becomes costly, and intrusion by a few individuals into territories may go unnoticed. Under this scenario, individuals with a floating

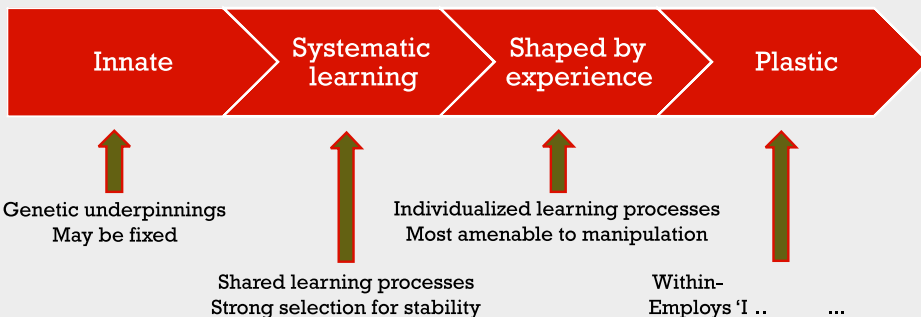
strategy become favored. This is known as frequency-dependent selection, where the most stable situation will favor the existence of multiple behavioral strategies within the population [110]. At times, the relative frequency of multiple strategies can even be predicted. For example, floating should be consistently less common than a sedentary strategy. If a majority, or even a strong minority of individuals utilize a floating strategy, territory holders will likely strengthen their defenses to avoid a substantial loss of resources. This equilibrium of strategies is known as an Evolutionary Stable Strategy (ESS [111]). As with species and genetics, maintaining a diversity of behavioral strategies is often important for maintaining ecosystem function. For example, an environment that eliminates the floating strategy in wintering ovenbirds, will increase risk of population, or even species extinction during years with low foraging resources.

**Box 1** Plasticity in behavior

- Behavior is the way in which an animal acts in response to a particular situation or stimulus
- Behavior is shaped by selection through a *cue*, *response*, and *outcome*



- Modified environments can misalign cue-response systems, potentially resulting in mismatches where behavior becomes maladaptive (e.g., evolutionary mismatch)
- Behavioral systems can also shift to accommodate altered systems to some extent
- Flexibility in a behavioral system depends on the strength of selection and the presence of variation or plasticity in responses



- An evolutionarily stable strategy (ESS) might include multiple behavioral strategies, which are maintained by:
  - Variable habitats
  - Frequency dependent selection

## Managing Behavior in the Midst of Anthropogenic Change

### Why Integrating Behavior is Important

The structure and function of earth's ecosystems are changing rapidly – perhaps more rapidly than at any time in history. The mere fact that ecosystems are changing is neither abnormal nor problematic. How many times have we been astonished to find ancient marine fossils in high deserts [112], or signs of lush ancient forests in frozen ice cores [113]. The issue is not change, but rather, rate of change. In the examples above we are observing the remnants of dramatic changes that occurred over Millennia. Today, we are witnessing equally dramatic changes that occur over only a few years, or sometimes just days. While natural events, such as hurricanes or volcanoes can dramatically reshape landscapes over a short duration, the majority of the changes we are witnessing are anthropogenic – or human produced. Andy Sih and colleagues have labelled this pervasive phenomenon as Human Induced Rapid Environmental Change, abbreviated as HIREC [23, 114]. In its most extreme form, HIREC results in complete habitat conversion – which is typically equivalent to habitat destruction for native organisms. Examples include conversion of forest to housing developments and parking lots, grasslands to monocultures, rivers to dammed reservoirs, etc. In these cases, the fundamental resources required for life are typically removed, or altered to a point that they are no longer accessible to native organisms. Here an understanding of behavior and flexibility in cue-response systems may have little impact on a management strategy. But in many cases, anthropogenic impacts are more subtle. The food web in an urban park, for example, is probably different than a similar preserve located within a larger undeveloped habitat. However, an urban park may retain a number of trophic levels and a different, but functional, food web. Yet, as urbanization increases, these habitats often contain fewer species of nesting songbirds [115]. Why?

Classical concepts from landscape ecology would suggest that managers consider larger-scale spatial variables, such as patch size, landscape configuration, and connectivity with other habitat patches [116–118]. There is no doubt that fragmenting habitat, restricting movement, reducing and isolating resources, etc. will directly impact fitness and population persistence. I am confident that every author in this text would advocate for assessing resource and landscape needs as priority objectives for managing songbird species. But we might also ask the question: Is this enough? For several years, I worked with a team of researchers to attract Henslow's sparrows (*Ammodramus henslowii*) to four reconstructed warm-season grassland prairies in Southwestern Michigan. Each field was ~9–12 hectares in size. Despite the reintroduction of native warm-season grasses, Henslow's sparrows, and several other grassland obligate species, were consistently absent. At first blush, an astute observer might state, "these prairies are too small." Perhaps this is true, and this outcome does emphasize the importance of evaluating landscape variables prior to restoration efforts. But, if the landscape perspective that these habitats are too small is our final answer, the reconstruction of these four ~10 acre fields for the conservation of grassland birds was a wasted endeavor.

Might an understanding of behavior yet open these fields to use by obligate grassland birds? At <0.5 hectares [119], a Henslow's nesting territory could fit easily within these fields with ample room for foraging. Our fields were flush with a diverse insect community, ample water was available in nearby habitats, and grasses provided the cover thought necessary for nest placement and concealment. If the fundamental

resource provisions are in place, perhaps an overlooked cue-response system is not functional – or has prevented the selection of these habitats. Alternatively, interspecific interaction might differ. For example, the greater composition of edge habitat might result in higher populations of avian or terrestrial nest predators. In this particular case, the landowner and managing organization wanted to investigate further. One hypothesis was that conspecific cues were missing. It is not uncommon for birds to use vocal cues that indicate conspecific presence when selecting breeding territories [120, 121]. But, two years of song playback resulted in only one nesting Henslow's sparrow. Not zero, but not the resounding success that has been seen using this technique elsewhere [122].

Dr. Rob Keys, a colleague at a university in Grand Rapids, Michigan, hypothesized that these northern populations of grassland obligate birds were preferentially selecting old fields comprised of non-native, cool-season grasses (as opposed to our fields planted with warm-season grasses). While this would contrast with research from other parts of the range [123], a few anecdotal, but notable, observations supported this hypothesis. First, Henslow's sparrows had been reported more regularly in our field before their conversion to warm-season grasses. Second, a broad survey of other potential grassland sites in the region indicated that locations dominated by cool-season grasses were for more likely to house populations of grassland obligates; including Henslow's sparrows, Bobolinks (*Dolichonyx oryzivorus*), Eastern meadowlarks (*Sturnella magna*), savannah sparrows (*Passerculus sandwichensis*), and grasshopper sparrows (*Ammodramus savannarum*). In 2019, experimental mowing and replanting resulted in territorial establishment by eight individuals from two obligate species (Henslow's and savannah sparrows; unpublished data). An analogous study in the historically forested piedmont region of North Carolina, USA, found that obligate grassland birds showed no preference for warm or cool-season grasses [124]. It is plausible that grassland obligate songbirds now breeding in regions that historically contained minimal native grassland habitat are cueing in on the cool-season grasses found more commonly in abandoned farm fields. If so, 'restoring' cool-season grasslands in these regions that accommodate this potentially altered cue-response system might be of value. Alternatively, facultative grassland bird species, such as the field (*Spizella pusilla*) and song sparrows (*Melospiza melodia*) that arrive earlier in the spring could be preferentially selecting warm-season grasses and excluding obligates from these territories – a case of heterospecific competition. Research on this particular topic is ongoing and it may be too early to alter management regimes, but it illustrates well the point that understanding behavior might lead to tangible shifts in management strategies.

## Potential Anthropogenic Changes to Cue-response Systems

Some cue-response systems in songbirds are clearly more flexible than others. But all are to some extent engrained in individual birds and populations. As such, we must expect that any time human activities alter the environment, there is likely to be an impact on the established behavioral responses, and therefore, on fitness. But what anthropogenic impacts should be monitored beyond the obvious impacts of habitat destruction and modification? To answer this question conclusively requires an intimate knowledge of the species and behaviors present in the ecosystem of interest – indicating that location-specific field studies and natural history scholars will remain paramount as we move through the Anthropocene. However, there are a few common, but often overlooked, disturbance regimes that I will address here. Specifically, I will briefly address sensory



ecology, range shifts and species invasions, and temperature change. Each topic is explored in more depth in the chapters that follow.

Sensory ecology deals with how birds perceive and respond to cues through vision, olfaction, acoustics, taste, touch, and magnetoreception. These topics are explored in depth in the text, *The Sensory Ecology of Birds* [125]. Despite their critical role in eliciting particular behaviors, many of these changes are not quickly perceived by human observers. For example, because most of us have become accustomed to light and sound pollution near our homes and places of work, we are less aware of the potential impact of the noise from airplanes as they regularly pass over otherwise remote habitats [126] or the effect of the pervasive, ever-present glow of the city skyline in exurban landscapes [127]. If we fail to measure, mitigate, and manage the sensory environment, we may create visually pleasing habitats that are devoid of the species we aim to protect. Dominoni et al. [128] nicely describe how sensory ecology can contribute to conservation biology. In their perspective paper, they suggest that sensory pollutants impact cue-response systems in three ways. First, *masking* reduces an organism's ability to detect or discriminate cues. Second, *distraction* interferes with an organism's ability to process cues because other overlapping cues have captured the individual's attention. Third, *misleading* cues result from conflation of sensory pollutants with natural cues, leading to an inappropriate response. The path towards resolution differs for each of these sensory pollution mechanisms. For example, spatial and/or temporal separation between competing cues may be required when distraction is the primary mechanism. As the literature on sensory ecology grows and summative reviews become available [7, 129], I recommend that managers incorporate the latest developments whenever possible.

As the physical parameters that limit songbird establishment shift, we should expect that changes in species ranges and niches will respond accordingly – which will alter which set of species are interacting with each other in any given area. The impacts of climate change on regional and global temperature is one clear example that I will address in the next paragraph. But even small-scale changes to habitats can alter the distribution and interaction levels of heterospecific species. For example, oil extraction in Northern Michigan has perforated forest interiors with small anthropogenic openings. Between these openings, which are referred to as 'pads', the native forests remain largely contiguous. In many cases interior songbird species continue to nest near the edges of these pads. But research by some of my former students indicated that the insertion of small openings and edge habitats has increased the presence of edge-associated avian nest predators near pad sites, which resulted in significantly higher predation rates in an artificial nest study [130]. Competition from novel, non-predatory heterospecific species may also impact native species as ranges shift. The succession of old field habitat to shrub ecosystems in portions of the northern United States has facilitated the recent establishment of blue-winged warblers (*Vermivora pinus*) in locations previously settled by golden-winged warblers (*V. chrysoptera*). Although the mechanisms are not entirely clear, novel overlap in the range of these two species predictably results in the reduction or extirpation of the golden-winged warbler genetic phenotype [131]. Taken together, these studies serve as a reminder that understanding the interactions between predators and competitors is required when maintaining or reintroducing particular species, and that we must take into account the shifting ranges of these heterospecific players in light of anthropogenic changes.

Climate changes may be the most concerning driver of external change to songbird cue-response systems in the near future. Temperature, and associated moisture levels, drive changes in vegetative ranges [132] and phenology [133, 134], insect emergence [135], and may directly alter the physiological parameters that facilitate songbird survival. Thus, changes in temperature and moisture are likely to drive alterations in songbird species ranges and heterospecific interactions, and may introduce foraging mismatches during critical life stages such as migration and nestling provisioning. Although attempting to prevent climate change may be largely futile at the local management level, planning accordingly is critical. For example, the conservation-reliant Kirtland's warbler (*Setophaga kirtlandii*) breeds primarily in early-successional jack pine stands (*Pinus banksiana*), and most of their habitat is managed through intentional planting programs in Michigan, USA [136]. But some climate models indicate that future jack pine stands will exist largely to the north in the Canadian provinces [137]. Management must either recognize the Kirtland's warblers reliance on the shifting jack pine range and act accordingly [138], or consider facilitating use of other habitats [105].

## The Rate of Change Problem

Anthropogenic processes are quickly changing our landscapes. A moderately zoomed out aerial map of almost any location will reveal signs of human development. But ecosystems are not static, and neither is songbird behavior. In the preceding sections, I have outlined several instances where changes in behavior have been observed naturally in response to anthropogenic alteration [49], or as a result of human manipulation [87]. The real question though, is whether songbird behavior can change fast enough to accommodate rapid anthropogenic change. In many cases the answer may be no. Migration research, for example, has indicated that shifting arrival and departure dates do not necessarily mitigate rising temperatures on the breeding grounds [139]. Correspondingly, we found that the arrival temperature at a fall stopover site in Western Michigan increased over the decades despite significantly later arrival times in four commonly captured short-distance migrants [142]. To estimate the impact of anthropogenic change *a-priori*, I recommend assessing the rate of change in, (1) the anthropogenic variable of interest and, (2) in critical behavioral systems. A dynamic and flexible cue-response system might be better pre-adapted to accommodate change than largely innate or heavily selected behaviors. But it is good to remember that all cue-response systems have rate of change limitations and absolute limits to the range of potential changes on the short-term timescale.

## Behavioral Conservation and Management

Where anthropogenic processes threaten to disrupt cue-response systems, managers have two primary options: decrease the rate of anthropogenic change *or* increase the rate of behavioral change in animals by manipulating the learning process. Where possible, decreasing the rate of anthropogenic change is generally the preferred method. This may rightly sound intuitive, but it does contrast with the stark assessment that either human development or functional ecosystems must cease completely. If academics, managers, politicians, and communities can join forces to slow the rate of land transformation and

sensory pollution we may be able to buy time for cue-response systems to redevelop and adjust to novel cues and shifting outcomes. Practical guidelines might include developing neighborhoods and urban landscapes slowly, preserving native vegetation whenever possible, reducing edge or patchy ecotones by maintaining the integrity of the tree canopy, maintaining areas of grass-shrub pollinator supporting patches, minimizing and dimming lighting, abating noise, etc. A parallel principle might also be to contain anthropogenic impacts within limited spatial areas, allowing organisms to accommodate these changes within a larger intact landscape. As a young adult who loved to hike and backpack in the United States, I was taught to leave the trail to urinate. The goal (in addition to privacy) was to spread the human impact across the landscape. As a graduate student in Canada, however, the advice of many in the outdoor community was to urinate directly on the trail – with the goal being to limit human impact to a small portion of the landscape. Urban centers are an example of this concept on a much larger scale. High impact in a spatially compact area. Taking this development principle to heart might also slow the overall rate of change across our native landscapes.

Slow change might also be a pertinent principle for restoration efforts. Is converting large swaths of old field into restored prairie in one instance disruptive to communities that have already established there? Might a few acres at a time better increase diversity? Does a quick removal of all non-native species from a forest decimate vegetative cover to the point that songbirds are not able, or not inclined, to nest in these habitats? Perhaps an incremental invasive removal program will allow birds to continue nesting until natives can take hold, even if productivity is somewhat lower.

As ecologists we often have to recognize that there are many situations where we simply do not have the power to moderate the rate of development. Further, restoration of native habitats or the removal of sensory pollutants may be an impossibility in many circumstances. In these cases, it may be worth asking whether we can increase the rate of behavioral change in songbirds themselves. Specifically, can we use learning paradigms to alter cue-response systems in songbirds to reduced or eliminate maladaptive responses? Manipulating behavior, just like manipulating genetics, may be unappealing to some. Some may consider this to be meddling in biological systems, which can have the potential for unexpected outcomes. But often the alternative is to be a casual observer of slowly (or rapidly) declining populations as evolutionary mismatches fail to resolve themselves quickly enough to facilitate recovery. For example, the recovery of small populations in many species may be inhibited by the Allee effect – which points to a reliance on social interaction for successful breeding [140]. Can managers artificially create the appearance of social groups in the field by manipulating the sensory environment (e.g., visual models and vocal playback)? Could reintroduction programs use similar cues in captive settings paired with live models from similar species? Certainly, the successful development of a new migratory route in a captive-raised group of whooping cranes was a heavily manipulated management regime. Are there other areas, other ways, that we can manipulate behavior to enhance or rescue songbird populations?

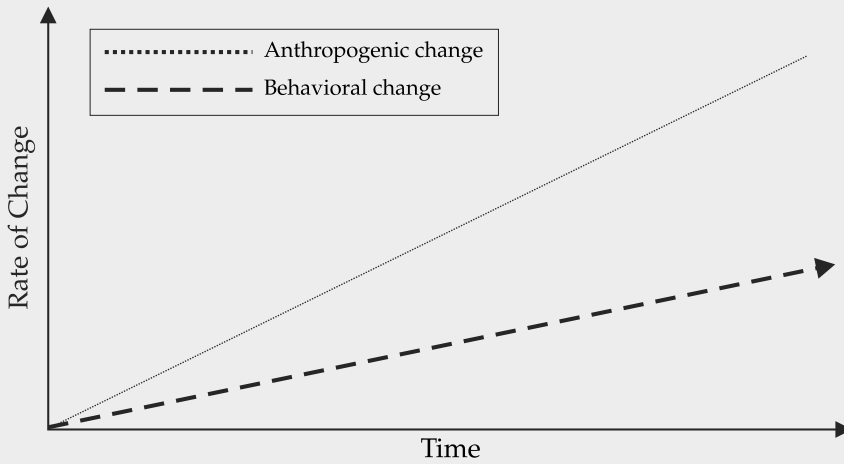
Several years ago, I worked with students to see if we could draw songbirds into forested areas near low-use road in Northern Michigan. Previous data suggested that vehicular noise reduced bird abundance and diversity up to a kilometer from roadsides [141]. But my own observations were that noise levels were quite low beyond a few hundred meters from the roadway. I hypothesized that in these areas where noise

levels were low but not absent, entrenched cue-response systems prohibited settlement because preferred habitats were historically quiet [8]. To over-ride aversion to low-level noise, we attempted to place another cue on the landscape known to enhance site settlement – conspecific song. Although our experimental progress has been slow, we were able to draw several species into roadside habitats using song playback [106]. I close with this example to demonstrate an area where I see promise for using behavioral manipulation to advance conservation goals, but also to demonstrate the complexity and need for caution when manipulating behavior. The first point is that the trained or manipulated behavior (settlement in low-noise areas in this case) must confer a fitness benefit. Or at the very least, it must not result in a fitness decrease (e.g., a population sink). Perhaps there is another impact of low-level noise we are not accounting for (e.g., distraction, increased predators). In our case, if playback draws birds from high-quality areas into an area that is unsuitable, we will likely decrease productivity, and thus population sustainability. Conversely, if non-territory holders (i.e., floaters) settle and breed successfully, populations may increase. We must examine productivity and survivorship before using such a technique on a broader scale. Second, if birds are retrained to use a novel cue-response system, how will it be maintained? The positive outcome in response to the behavioral choice must be reinforced. Our hypothesis was that natal imprinting might facilitate site return by some individuals, and provide conspecific song for addition generations – reinforcing establishment without artificial song playback. But this hypothesis remains untested.

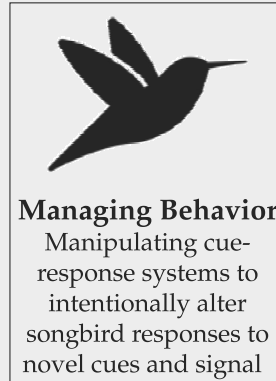
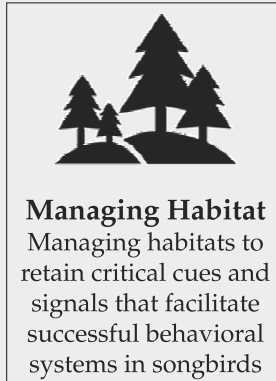
I invite you to consider how you might decrease the rate of anthropogenic changes *and* how you might increase the rate of behavioral change in the systems and species where you work. The challenges we face in the Anthropocene are profound. Those whose job and passion is to see songbirds thrive for generations to come will need to be creative. We must be ready to employ an array of conservation tools – and managing habitats and species in relation to behavior must be among these tools.

#### Box 2 Anthropogenic and Behavioral Change

- Anthropogenic changes will impact birds directly by removing required resources
- Anthropogenic changes will also impact bird behavior by altering cue-response systems
- Ignoring behavioral impacts might lead to subpar management. Two examples, include:
  - Ignoring sensory ecology, which drives behavior and ultimately physical functions
  - Ignoring changes to species ranges, which drives novel heterospecific interactions
- Anthropogenic change moves on a rapid scale
- Changes in songbird cue-response systems may not change rapidly enough to mitigate mismatches before irreversible negative impacts on populations and species are incurred

**Box 2 (Contd.) Anthropogenic and Behavioral Change**

- Where preventing change is not an option, slowing the rate of change might provide benefits by allowing behavioral cue-response systems time to adjust or shift
- Behavioral management falls into two primary categories

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## Conspecific and Heterospecific Interactions

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## Sociality and Antipredator Behavior

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## Conclusion: The Role of Human Behavior in Songbird Conservation

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