

UNIVERSITY OF CALIFORNIA

Los Angeles

Multimodal Integration in Uncertain Environments: A Quantitative Model and Field
Experiments with Yellow-bellied Marmots (*Marmota flaviventris*)

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biology

by

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2015

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ABSTRACT OF THE DISSERTATION

Multimodal Integration in Uncertain Environments: A Quantitative Model and Field
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by

Nicole Elizabeth Munoz

Doctor of Philosophy in Biology

University of California, Los Angeles, 2015

Professor Daniel T. Blumstein, Chair

Animals are confronted with abiotic cues, conspecific signals, and signals eavesdropped from heterospecifics that create some degree of uncertainty as to the state of their world. They must reduce uncertainty to make optimal decisions. Animals can improve the accuracy with which they make decisions by combining stimuli from different modalities, a phenomenon I term “multimodal integration”. However, in some situations an animal does not benefit from this increase in accuracy and the animal does better to ignore certain stimuli. Despite a body of literature that documents such situation-dependent integration, to date, a quantitative approach to understand the conditions in which integration is favored is lacking. My dissertation develops a framework for thinking about the functional significance of integrating stimuli in multiple modalities. First, I conceptually bring

together the ideas of uncertainty, costs of mistakes and prior expectation of the state of the world in order to explain why more information sources are not always better. I then present a quantitative model that parameterizes uncertainty, the costs of mistakes, prior expectations and the costs of attending to stimuli in predicting whether or not an animal should integrate sequential stimuli in different sensory modalities. The model applies to multimodal stimuli in that different levels of uncertainty can be specified for each stimulus. This feature importantly captures the property of sensory modalities to be independently affected by uncertainty. For example, the sound of noisy traffic will not likely affect your ability to see a friend walking towards you. Finally, using yellow-bellied marmots (*Marmota flaviventris*), I field test the extent to which three of the model's parameters affect integration of olfactory-acoustic predator stimuli. I found that the benefit of alert behavior and uncertainty of the second (acoustic) stimulus does indeed affect integration. Overall, this dissertation establishes a foundation for a new line of inquiry into situation-dependent integration, which will help us understand the evolution of cognitive systems, communication networks, animal signals and the ways in which individuals interact with the abiotic world.

The dissertation of Nicole Elizabeth Munoz is approved.

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TABLE OF CONTENTS

LIST OF TABLES.....	vii
LIST OF FIGURES.....	ix
ACKNOWLEDGEMENTS	xiv
VITA.....	xvi
CHAPTER 1	
General Introduction	1
CHAPTER 2	
Multisensory integration in uncertain environments	13
Introduction.....	13
Clarifying definitions.....	13
Multisensory Perception as a Mechanism.....	15
Predictions from a Cost-benefit Analysis of Multisensory Integration.....	15
<i>Future Directions</i> 16	
Conservation Applications of Research on Multisensory perception.....	16
Conclusions	17
References	17
CHAPTER 3	
Optimal integration: the conditions under which animals should integrate multiple sensory modalities	19
Abstract	19
Introduction.....	20
Methods.....	24
Results.....	31
Applications of the model.....	33
General discussion	39
Conclusion	43
Supplementary material	54
References	57

CHAPTER 4

Testing a model of multimodal integration in yellow-bellied marmots

(*Marmota flaviventris*): integration of predator cues is situation dependent.....61

Abstract	61
Introduction.....	62
Methods.....	64
Results & discussion	68
General discussion	71
References	85

LIST OF TABLES

Table 1. Experimental studies of antipredator behavior employing multimodal cues classified according to a taxonomy modified from Partan and Marler (1999).....14

Table 3-1 Definitions45

Table 3-2 Summary of assumptions46

Table 3-3 Notation definitions.....47

Table 4-1 Results from linear mixed effects models of the proportion of time allocated to foraging in response to the near-to and far-from burrow conditions for Experiment 1. Significant *P*-values are highlighted in bold.75

Table 4-2 Pairwise comparisons of stimulus types (coyote urine only, vocalizations only or the bimodal urine-vocalization stimulus) for Experiment 1.....76

Table 4-3 Results from linear mixed effects models of the proportion of time allocated to foraging in response to the high-noise or low-noise condition in Experiment 2. Significant *P*-values are highlighted in bold.....77

Table 4-4 Pairwise comparisons of stimulus types (coyote urine only, vocalizations only or the bimodal urine-vocalization stimulus) for Experiment 2.....78

Table 4-5 Results from linear mixed effects models of the proportion of time allocated to foraging when foraging at bait with longer handling time or shorter handling time in Experiment 3. Significant *P*-values are highlighted in bold.....79

Table 4-6 Pairwise comparisons of stimulus types (coyote urine only, vocalizations only or the bimodal urine-vocalization stimulus) for Experiment 3.....80

LIST OF FIGURES

Figure 1. Classification system of multisensory stimuli based on behavior responses to stimulus components in isolation and in combination15

Figure 2. A bimodal predator stimulus (A 1 B) reduces uncertainty about the risk of predation compared with either isolated unimodal cue. (a) Antagonism is expected when a bimodal stimulus informs prey that a predator does not pose an immediate danger (see Hazlett and McLay 2005; Thompson et al. 2008). (b) Enhancement is expected when a bimodal stimulus informs prey that a predator poses an immediate danger (see Smith and Belk 2001; Partan et al. 2010).16

Fig. 3-1 Distributions of stimulus magnitudes S_i when no predator is present (NONE) or when a predator is present (PRED). Uncertainty is defined by the extent to which distributions overlap. a) 10% overlap of distributions (i.e., $U_i = 0.1$). b) 90% overlap of distributions (i.e., $U_i = 0.9$). Image credits to clipartbest.com (hare) and shutterstock.com (lion).....48

Fig. 3-2 Favorability of integration (A) for a migrating prey that experiences changing ecological situations. The prey must discriminate predators from non-threats. The prey can either hide (optimal for predators) or forage (optimal for non-threats). The prey typically smells before seeing predators. a) In the summer breeding grounds, $B_{PRED} = 10$, and $B_{NONE} = 5$ (dashed line). The prey's diet becomes restricted to food with greater handling time,

which decreases the benefit of correctly foraging, $B_{NONE} = 1$ (solid line) and the favorability of integration increases. This is because, relative to B_{NONE} the benefit of hiding increases, which means it becomes increasingly important for the prey to accurately assess if a predator is present. When the prey's energy reserves are low, the benefit of foraging outweighs the benefit of hiding because the prey risks starving to death, $B_{NONE} = 60$ (dotted line). Therefore, making accurate antipredator decisions becomes less important and the favorability of integration decreases. b) The prey experiences a different type of predator that inflicts a higher degree of injury; the benefit of hiding greatly outweighs the benefit of foraging, $B_{PRED} = 60$ (dotted line) and the favorability of integration increases. This is because making accurate antipredator decisions becomes increasingly important. As the benefit of hiding from a predator decreases (dashed and dotted lines), so does the favorability of integration. c) and d) show the same cases as a) and b), respectively, except the prey experiences a greater concentration of predators ($P_{PRED} = 0.7$). As the frequency of predators increases, it becomes increasingly important for the prey to make accurate antipredator decisions, the favorability of integration increases.....49

Fig. 3-3 Favorability of integration (A) for two populations of a single bird species. Females typically hear before seeing males. The female has to discriminate conspecifics from heterospecifics. She each either attempt to mate (optimal for conspecifics) or forage (optimal for heterospecifics). Females typically hear before seeing males. One population lives along a stream and, due to the noise of flowing water, experiences high acoustic uncertainty ($U_1 = 0.7$, dashed line) compared to the other ($U_1 = 0.3$, solid line). $B_{CONSP} = 10$ and $B_{HETERO} = 2$ in both populations. a) A male sings a song that likely came from a

conspecific ($S_1 = \mu_{CONSP}$). Females along the stream are less likely to integrate acoustic-visual stimuli than females away from the stream. b) A male sings a song that likely came from a heterospecific ($S_1 = \mu_{HETERO}$). Females along the stream are more likely to integrate than females away from the stream. This is because after hearing the song, a female's expectation that the male is a conspecific has decreased to a greater extent than females along the stream. Since females near the stream have a higher expectation that the male is a heterospecific, it is more important for these females to be able to discriminate conspecifics and heterospecifics. However, regardless of the population's location, the favorability of integration is lower when the female hears a song ($S_1 = \mu_{HETERO}$) that the male was a conspecific decreased to a greater extent than for females along the stream. All other parameters are the same as in a). c) and d) show the same as a) and b), respectively, except the P_{CONSP} decreases. As in the antipredator context, the favorability of integration is lower for lower P_{CONSP} . e) All males along the stream become sick, which decreases the reproductive benefit of females, $B_{CONSP} = 3$. Females now gain so little from being able to discriminate conspecifics and heterospecifics, so value of information when integrating (V_2) decreases ($P_{CONSP} = 0.6, U_1 = 0.7, U_2 = 0.2, B_{NONE} = 2, K_1 = 0$ and $K_2 = 3$). f) The order in which females receive stimuli is important to integration. This graph compares the favorability of integration when the female first hears a male ($U_1 = 0.7, U_2 = 0.2$; solid line) vs. first sees a male ($U_1 = 0.2, U_2 = 0.7$; dashed line). All other parameters are the same as in a). When the first stimulus the female hears is more accurate at discerning conspecifics and heterospecifics, the female is more likely to integrate.51

Fig. 4-1 Spectrograms (top) (349.70 Hz, 512 point FFT) and waveforms (bottom) of a coyote vocalization embedded with either “no noise” (left), low noise (middle) or high noise (right). Signal-to-noise ratio for each is given at the top of each figure. The “no-noise” exemplar was used in generating the low- and high-noise exemplars. Spectrogram grid resolution: 5.38 Hz, 5.805 ms, 50% overlap. The clipping level was -68 dB.81

Fig. 4-2 Results of Experiment 1. Mean proportion of time spent foraging when marmots foraged a) near to (1 m from) the burrow or b) far (3.5 m) from the burrow. Each distance represents a different level of B_{PRED} . Brackets indicate significantly different pairwise comparisons. Marmots only integrated when foraging far from the burrow, where B_{PRED} is greater, as inferred from significantly different responses to the bimodal stimulus compared to urine alone and vocalizations alone. Error bars show 95% confidence intervals.82

Fig. 4-3 Results of Experiment 2. Mean proportion of time marmots spent foraging when a) coyote vocalizations were less noisy or b) more noisy. Different noise level corresponds to different levels of U_2 (Munoz and Blumstein, in review). Brackets indicate significantly different pairwise comparisons. Marmots only integrated when coyote vocalizations were more noisy. Error bars show 95% confidence intervals.83

Fig. 4-4 Results of Experiment 3. Mean proportion of time marmots spent foraging when food handling time was a) long or b) short. Brackets indicate significantly different pairwise comparisons. Different handling times correspond to different levels of B_{NONE} . Marmots did not integrate under either situation. Error bars show 95% confidence intervals.....84

ACKNOWLEDGEMENTS

I want to thank my advisor, Daniel T. Blumstein. During my time at UCLA he has motivated me to be a productive member of the scientific community. Through our engaging conversations, for which he was always available, I have learned to not get lost in the details of our work and to step back to look at the “bigger picture”. I will not forget his mentorship. I would also like to thank my committee, Jamie Lloyd-Smith, Aaron Blaisdell, and Peter Nonacs. Their feedback and constructive criticisms have been invaluable.

I owe much appreciation to all of the Marmoteers who have helped in trapping and marking animals in the field. I single out Matthew Petelle, Adriana Maldonado, Julien Martin, Raquel Monclús, Tiffany Armenta and Amanda Lea because of the countless hours I have spent with them in the field. I am grateful for their physical and intellectual assistance. I thank the Rocky Mountain Biological Laboratory, Jennifer Reithel and Ian Billick for logistical support in helping to make my fieldwork possible and for fostering a stimulating academic community.

I am extremely grateful for having a supportive and encouraging family. My parents Juan and Nahir, my brothers, Juan and Daniel, and sister-in-law, Anna Coyer, have been confidants and soundboards for my scientific, existential crises throughout my duration at UCLA.

My dissertation was funded by the UCLA Department of Ecology and Evolutionary Biology, The UCLA Graduate Division’s Cota Robles Fellowship, and a National Science Foundation Graduate Research Fellowship.

Chapter 2 is a reprint of a published paper - Munoz, N.E., and D.T. Blumstein. 2012. Multisensory perception in uncertain environments. *Behavioral Ecology* 23: 457-462. My

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CHAPTER 1

GENERAL INTRODUCTION

Animals are confronted with abiotic cues, conspecific signals, and signals eavesdropped from heterospecifics. Prey use multisensory stimuli to assess predation risk and make antipredator decisions. For instance, Brown and Magnavacca (2003) report that tetras (*Hemigrammus erythrozonus*) primarily use chemical cues to assess predation risk but will rely on visual cues when chemical cues are absent or ambiguous. Additionally, Hazlett and McLay (2005) report that crabs (*Heterozius rotundifrons*) extend their legs, an antipredator behavior, for longer in response to either a chemical or visual predator cue alone. When presented simultaneously, chemical-visual cues cause crabs to extend their limbs for a shorter duration (Hazlett and McLay 2005). Predators use multisensory stimuli to make hunting decisions. The combination of a visual and vibratory stimulus increases the speed at which predatory jumping spiders (*Phidippus clarus*) respond to playbacks of the sexual display of a male wolf spider (*Schizocosa ocreata*) (Roberts et al. 2007).

Females of many species use multimodal sexual signals in choosing mates (Candolin 2003). For instance, female wolf spiders (*Schizocosa uetzi*) preferred males that courted using vibrations compared to males that did not (Hebets 2005). By contrast, the presence a visual display of leg waving and hair ornamentation did not affect females' choices (Hebets 2005). However, the combination of male visual and vibratory stimuli led to greater receptivity in females compared to the vibratory stimulus alone (Hebets 2005). This result indicates that females are integrating male multimodal mating stimuli.

While necessarily incomplete, the preceding body of literature documents the occurrence of multisensory integration. However, to date, these studies have primarily

been grounded from the perspective of signalers with an emphasis on the evolution of multimodal *signals*. The functional significance of multimodal *integration* by receivers remains largely unexamined (Munoz and Blumstein 2012; Partan 2013). Thus, the question of “Why [should signalers] use multiple cues?” (Candolin 2003; Hebets and Papaj 2005; Partan 2013) that is often asked in reference to the evolution of multicomponent signals, can be turned around and asked from the perspective of individuals perceiving stimuli: “Why should receivers integrate multiple stimuli?”

The accuracy with which the animal’s perception reflects reality directly relates the animal’s ability to make optimal decisions. For the most part, animals are faced with some degree of uncertainty as to the state of their world (Dall and Johnstone 2002). Given that stimuli in multiple modalities can increase the accuracy of the animal’s estimate of its world (Dall et al. 2005; Hebets and Papaj 2005; Partan and Marler 2005), multimodal integration, or the combining of information from multiple senses, can be framed as a solution to uncertainty (Dall and Johnstone 2002; Munoz and Blumstein 2012; Ben-Ari and Inbar 2014; Kunc et al. 2014). Despite the apparent usefulness of having access to multiple stimuli, sometimes animals do not use all available stimuli in making a decision.

Examples of situation-dependent integration suggest that the animal sometimes does best to ignore certain stimuli. Integration has been shown to depend on the individual’s reproductive state (Kasurak et al. 2012), a population’s habitat (Partan et al. 2010) or a species’ type of mating system (Cross and Jackson 2009). These studies discussed situation-dependent integration primarily on a proximate level. Female gobies (*Neogobius melanostomus*) integrated vibrational-olfactory sexual stimuli from males only when reproductive (Kasurak et al. 2012). Kasurak et al. (2012) discuss this result in terms

of a possible plasticity of structures responsible for integration across reproductive states. Squirrels (*Sciurus carolinensis*) in urban habitats exhibited greater response to the visual-only stimulus and greater multimodal enhancement to an audio-visual conspecific alarm stimulus compared to squirrels in rural habitats (Partan et al. 2010). Partan et al. (2010) discussed a cognitive shift from acoustic to visual stimuli in noisy environments (Partan et al. 2010). Multimodal integration was studied across four species of jumping spiders (Cross and Jackson 2009). In three of the species, males compete for females (*Portia fimbriata*, *Portia africana* and *Jacksonoides queenslandicus*). In the fourth species, in addition to male-male competition, female-female competition for mates exists (*Evarcha culicivora*). Only in *E. culicivora* did a conspecific male odor enhance visual-based conflict within females (Cross and Jackson 2009). This last study, by noting that the value of recognizing females is more important in *E. culicivora* compared to the other species, explained situation-dependent integration on a functional level. A deficiency of investigation into situation-dependent integration and, within those few studies, a lack of placing situation-dependent integration in functional terms demonstrates a need for a cohesive framework for understanding the evolutionary significance of multimodal integration.

This dissertation aims to fulfill this knowledge gap and stimulate a field of study that examines the implications of multimodal environments from the perspective of the receivers. Given the interplay between signalers and receivers, this branch of study will not only contribute to understanding of the evolution of multimodal communication but also aid in understanding all ways in which animals interact with all aspects of their environments including abiotic stimuli and eavesdropping.

In Chapter 2 I review the literature to date and built a conceptual framework for making predictions as to the types of situations in which an animal should integrate or not integrate (Munoz and Blumstein 2012). This framework is founded on the reality that environments are uncertain. Chapter 2 argues that an interplay of many variables, including an animal's current perception of the world, the costs of mistakes and extent of environmental uncertainty generate a complex backdrop that makes predicting whether or not an animal should integrate difficult based on intuition alone (Munoz and Blumstein 2012).

Given the complexity of many environmental variables, in Chapter 3 I develop a quantitative model that makes concrete and testable predictions as to, given a set of circumstances, whether or not an animal should integrate. I present the model in terms of a prey's antipredator behavior, however, I later discuss its application to a mate-assessment situation. The prey notices an object that can be either a predator or non-threat, and the animal can do one of two behaviors. Foraging is optimal when a non-threat is present and hiding is optimal when a predator is present. The prey receives an energetic benefit when foraging in the open. While hiding, the prey can also forage but with lower returns. If the prey fails to hide when a threat is present, the prey still escapes but is injured and must energetically invest in healing itself. The prey has a prior expectation of the likelihood that the object is a predator. Typically, because the prey forages with its head down, the prey smells before seeing a potential threat. On average, predators emit an odor with a greater concentration of sulphurous compounds and are visibly larger. The world is uncertain in that either stimulus could have originated from either a predator or non-threat. Therefore,

the likelihood of a stimulus magnitude originating from a non-threat or predator have distributions that partially overlap.

We modeled different sensory modalities by specifying different degrees of uncertainty associated with each stimulus, because uncertainty in each modality is likely independent of another (e.g., acoustic noise is unlikely to affect a visual stimulus). We defined uncertainty as the extent to which the non-threat and predator distributions for a give stimulus overlap. We assumed normal distributions. There is also a cost associated with processing information of each stimulus.

Given the uncertainty of each modality, the average benefit of making correct decisions, the individual's prior assessment of the likelihood of a predator, and the per-stimulus cost of using a stimulus, the animal calculates the "value of information" (Stephens 1989) of stimulus i (V_i), which is the difference in payoffs between using a stimulus and ignoring a stimulus. If $V_i \geq 0$ then the prey uses the stimulus, which means incorporates information into its expectation the object is a predator or non-threat, thereby improving the chances that the prey will correctly forage or correctly hide. If $V_1 < 0$ then the animal ignores the first stimulus. If $V_1 \geq 0$ then the prey, upon receiving second stimulus, calculates V_2 of the second stimulus. If V_1 and $V_2 \geq 0$, then the animal is said to integrate the two stimuli. This condition is, to date, the first ever quantitative definition of "multisensory integration".

The model has utility in making clear, testable predictions as to whether or not an animal is more or less likely to integrate under changing environments. Consider a grazing prey. Since odors tend to be more uncertain than visual stimuli for terrestrial animals, $U_1 = 0.4$ and $U_2 = 0.1$. The prey receives a benefit $B_{PRED} = 10$ for correctly hiding when a predator

is present. In the prey's summer breeding grounds, the prey receives a benefit $B_{NONE} = 5$ for correctly foraging when a non-threat is present. Based on experience, the prey knows that 0.3 of objects are predators. As it migrates to warmer wintering grounds, the prey's typical foraging items become scarce and the prey must forage on items with longer handling times. Since the prey must spend more time foraging to receive the same energetic gain as obtained with its summer diet, the benefit of foraging decreases, which we modeled as $B_{NONE} = 1$ and held all other parameters constant. This decrease in B_{NONE} leads to an increase in the favorability of integration. This is because, relative to B_{NONE} the benefit of hiding increases, which means it becomes increasingly important for the prey to accurately assess if a predator is present. Therefore, the prey will likely improve the accuracy of its antipredator decision by integrating.

The model can also be applied to situations other than predation risk-assessment scenarios. Consider two populations of an avian species where males sing from their territories. In this example a female is trying to assess whether a male is a conspecific or heterospecific in its decision to initial copulation. Conspecifics produced songs with a higher acoustic frequency and have longer tails. Females typically first hear and then see males. A female can either attempt to mate with the male (optimal for a conspecific) or continue foraging (optimal for a heterospecific). One population is typical in that males have territories away from moving water and acoustic uncertainty is $U_1 = 0.3$. However, in the second population, individuals are restricted to territories along the edge of a stream. For females along the stream edge, noise from flowing water increases acoustic uncertainty to $U_1 = 0.7$. Based on experience, females in both populations know that 0.6 of males are conspecifics ($P_{CONSP} = 0.6$) and the cost of attending to an acoustic stimulus is negligible (for

simplification, since we have assumed the cost of attending to acoustic stimuli is negligible, the female will always use acoustic stimuli). We modeled a visual stimulus assuming that females are highly adept at visually distinguishing conspecifics based on tail length than acoustic frequency so $U_2 = 0.2$, and is the same in both populations.

A female hears a song having acoustic frequency equal to the average frequency from a conspecific male in that population, $S_1 = \mu_{1,CONSP}$. Even though a conspecific is highly likely to have produced that song, there is still a possibility that a heterospecific sang that song [$P(CONSP|\mu_{1,CONSP}) > P(HETERO|\mu_{1,CONSP})$]. Due to higher uncertainty of acoustic stimuli, for the females near the stream the probability that a heterospecific did in fact produce that song is greater in comparison to the population far from the stream. The degree to which the female's updated prior, P_{CONSP}' , reflects the truth (i.e., becomes more like 0 or becomes more like 1) increases with decreasing U_1 . More distinct stimuli will give females a better indication as to the type of male. Therefore, for females along the stream, P_{CONSP}' is only marginally increased compared to females away from the stream. All else being equal, since females close to the stream are not more certain as to the singing male's identity, further improvement as to the accuracy of the female's assessment will still produce a higher rate of errors compared to females away from the stream. Therefore, females from the population near the stream, after hearing a song likely produced by a conspecific males are more likely to ignore tail length and only use acoustic frequency when making a decision as to whether to attempt copulation or forage.

In Chapter 4, I present results of three field experiments with yellow-bellied marmots (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory (Gothic, CO, USA) that partially validate the model. I examined whether or not three model parameters

(the benefit of hiding when a non-threat is present, the uncertainty of the second stimulus and the benefit of foraging when a non-threat is present) influence integration. Since marmots allocate their time foraging based on the level of perceived threat, we equated “hiding” with higher levels of vigilance and “foraging” with lower levels of vigilance. In these experiments I used coyote urine and coyote vocalizations as olfactory and acoustic stimuli, respectively. The urine (or water) was applied to a cotton ball and placed near the entrance of a marmot burrow along with bait. For 1 min after an individual began foraging at the bait, I quantified the proportion of time spent foraging. At the end of the minute I played back the acoustic coyote stimulus and quantified the proportion of time spent foraging for the first 15 s after playback. Thus, the proportion of time marmots spent foraging was measured for three stimulus categories: olfactory alone, acoustic alone, or the multimodal olfactory-acoustic stimulus. Following the framework by Partan and Marler (1999), the criterion for integration is when the proportion of time spent foraging to the multimodal stimulus is different compared to the response to urine alone and vocalizations alone.

In Experiment 1 I simulated a low and high benefit of high vigilance when a predator is present by baiting marmots either near to or far from the burrow, respectively. When marmots are farther from their burrow and fail to respond to a predator, they are more likely to suffer greater injury. Therefore, the benefit of being highly vigilant (B_{PRED}) is greater for marmots farther from the burrow. I found that marmots only integrated when foraging far from the burrow but not when foraging close to the burrow. In Experiment 2 I generated low and high levels of uncertainty by embedding the coyote vocalizations in low and high levels of white noise. I assumed a greater level of noise increased the uncertainty

of this, the acoustic, stimulus (U_2). Marmots integrated when vocalizations were highly noisy, but not under the low-noise condition. In Experiment 3 I manipulated the benefit of low vigilance when a non-threat (B_{NONE}) is present by mixing bait with different volumes of pebbles. Effectively, a greater proportion of pebbles increased the handling time of bait since marmots have to sift through more pebbles to access to the bait. Thus, marmots have to spend more time foraging in order to obtain a given energetic gain, thereby decreasing B_{NONE} . The model predicts that integration should be more likely when handling times are greater. In this experiment, marmots did not integrate under either foraging condition. However, this lack of support may occur if the other parameters of the experiment did not lie within the space of the model where changes in B_{NONE} lead to noticeable change in the likelihood of integration. It is possible that if I had tested more disparate levels of B_{NONE} that we could have detected a change in integration response..

Empirically, differences in integration response may be observed wherever differences in environment occur. Given that integration is situation dependent as defined by my model and empirically demonstrated (both in past studies and this dissertation), individuals (as in Kasurak et al. (2012) and my experiments with marmots), populations [as in Partan et al. (2010)], or species [as in Cross and Jackson (2009)] may exhibit different integration responses. When considering changing environments this model can be applied to predict the extent to which integration abilities might change over ecological time (if integration ability is plastic) or the extent to which the ability to integrate might evolve or be lost in species.

Understanding the factors responsible for the diverse types of multimodal integration responses and the evolution or loss of integration abilities is challenging. It

requires an understanding of an animal's state variables, and the past and present environment in which an animal lives. Collectively, these factors map onto the benefits an individual receives for performing a given behavior in a given situation, contribute to the uncertainty of stimuli, give an individual a prior estimate of the likelihood of an event, and impose physiological costs of processing stimuli. By developing a framework for investigators to make and test predictions based on these factors, the approach I developed in my dissertation aims to stimulate a new line of inquiry into the functional significance of multimodal integration. An abundance of studies showing that animals use multimodal information in decisions regarding, for example, mate selection, antipredator behavior, hunting and habitat selection. The versatility of this framework to readily accommodate these areas of study demonstrates its potential for stimulating a plethora of hypothesis-driven empirical studies. A focus on the cognitive processing by receivers not only complements the already strong field of multimodal signaling, thereby enhancing understanding of the evolution of communication networks, but also aids in understanding the ways in which animals interact with their abiotic environments.

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Forum: Invited Review

Multisensory perception in uncertain environments

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Animals must use cues from smells, sounds, and sights to reduce uncertainty about the environment. Despite the ecological relevance of multisensory perception in helping animals cope with uncertainty, empirical support from natural systems is rarely placed within an adaptive framework. The field of psychophysics provides a model for the study of cognitive processes by studying behavior. Using this as a foundation, we develop a framework that can be used to understand the evolutionary significance of multimodal perception. We develop predictions about the conditions under which multiple stimuli combine differently. A key outcome of our analysis is that the ecological context can influence the processes by which animals perceive multisensory stimuli. In addition to its theoretical importance, this framework predicts that anthropogenic activities can affect how animals perceive their environment, which may have profound ecological consequences. [*Behav Ecol* 23:457–462 (2012)]

INTRODUCTION

Animals must use information transmitted by smells, sounds, and sights to make decisions that reduce their uncertainty about the environment (Sih 1992; Dall and Johnstone 2002; Dall et al. 2005). The field of psychophysics analyzes perception by measuring changes in behavior with changes in stimulation (Shettleworth 2010). Under such an approach, changes in behavior indirectly indicate changes in cognitive processing and integration (Curio 1975; Meredith and Stein 1983; Leger 1993). An advantage of psychophysics is that we gain an understanding of which stimuli have behavioral consequences. However, multisensory perception is rarely placed within an adaptive framework. Here, we present a framework that predicts the conditions under which we expect different mechanisms of multisensory perception. For example, multiple predator stimuli lead prey to increase, decrease, or not change their antipredator effort (Table 1).

Borrowing heavily from terminology used to understand the function of multimodal signals (Partan and Marler 1999), we develop a framework to explain the various ways in which animals combine multiple stimuli. We frame multimodal perception as a solution to the problem of making decisions with some degree of uncertainty (Dall and Johnstone 2002). Given that supplemental cues across modalities reduce uncertainty, we expect enhancement when the costs of missed opportunities are high and antagonism when the costs of wasted time and energy are high. We expect dominance and equivalence when the cost of acquiring more information is high.

Three key points emerge from our analysis. First, we suggest that to study the adaptive utility of multisensory perception, we must consider environmental uncertainty. Second, despite the potential for a multicomponent stimulus to reduce uncertainty

relative to a single-component cue, animals may not necessarily utilize all components of a multisensory cue. Third, multiple stimuli may combine differently under different ecological contexts, thus the study of animal perception will benefit by examining the effect of multiple stimuli under various cost-benefit landscapes.

We hope that as future studies on a variety of taxa are placed within this framework that we will develop a better understanding of the evolution of multisensory perception. We will use many examples from the antipredator literature (Table 1) because avoiding predation risk is something that virtually every species must do (Nonacs and Blumstein 2010) and because the balance between managing predation risk and engaging in other activities such as foraging and reproduction sets the stage for different cost-benefit conditions (Lima and Bednekoff 1999), which is the foundation of our framework. However, our framework should also apply to any ecological situation, such as communication, other predator-prey interactions (Roberts et al. 2007; Cross and Jackson 2009; Bassett and Montgomery 2011), interactions with abiotic aspects of the environment (Johnson and Borgo 1976), or cued phenotypic plasticity (Kasumovic and Brooks 2011). Our review will begin with a clarification of terms and conclude with a discussion of conservation applications.

CLARIFYING DEFINITIONS

Multisensory perception: a psychophysics approach

We define “perception” as the product of reception, integration, and processing of stimuli. Under a psychophysics approach, observed behavior is the product of these processes (Meredith and Stein 1983; Shettleworth 2010). Thus, if we observe different stimuli generating different behaviors, we can conclude that the different stimuli were perceived differently (Proops et al. 2009; Shettleworth 2010). For our purposes, we use the term “multisensory stimulus” to define stimuli that are contextually similar and are aligned temporally and spatially as found in nature. For instance, when doves take

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Received 31 August 2011; revised 14 November 2011; accepted 29 November 2011.

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Table 1

Experimental studies of antipredator behavior employing multimodal cues classified according to a taxonomy modified from Partan and Marler (1999)

Taxa	Component A; response(s) to A	Component B; response(s) to B	Response(s) to composite A + B	Stimulus category	Reference
Mosquito fish (<i>Gambusia affinis</i>)	Chemical (water conditioned with predators); response: increased inspection distance	Visual (movement patterns of predator); response: same as A	Further increase in inspection distance	Enhancement	Smith and Belk (2001)
Mosquito fish (<i>Gambusia holbrooki</i>)	Chemical (water conditioned with predators); response: no change in avoiding stimulus	Visual (predator fish); increased avoidance behavior	Avoidance behavior equal to B response	Dominance of visual cue	Ward and Mehner (2010)
Roach (<i>Rutilus rutilus</i>)	Chemical (water conditioned with either pike or perch); response: 1) Pike—increase in open-water refuge; 2) Perch—increase in covered refuge	Visual (pike or perch predator); response: 1) Pike—increase in covered refuge; 2) Perch—increase in open-water refuge	For congruent stimulus combinations: 1) Pike—increase in covered refuge; 2) Perch—increase in covered refuge	1) Pike—dominance of visual cue; 2) Perch—dominance of olfactory cue	Martin et al. (2010)
Crabs (<i>Heterozius rotundifrons</i>)	Chemical (crushed conspecifics); response: increase in alarm behaviors (decreased leg extension and increased time spent motionless)	Visual (shadow); response: same as A	Decrease in alarm behaviors (increased leg extension and decreased time spent motionless)	Antagonistic	Hazlett and McLay (2005)
Gray squirrels (<i>Sciurus carolinensis</i>)	Visual (conspecific tail flicks); response: elevated threat-sensitive behavior	Auditory (conspecific alarm calls); response: same as A	Further increase in antipredator behavior equal to the sum of response A and B	Enhancement	Partan et al. (2009)

flight quickly, their wings flap and the wings may produce a whistle (Barrera et al. 2011), and individuals may respond to either the movement, the whistle, or both stimuli.

We speak of stimuli as conveying information, thereby changing perception, to the extent that stimuli influence behavior (Guilford and Dawkins 1993). Although stimuli are often correlated with physical characteristics in the environment, we do not presume that behavior is based on knowledge of a specific aspect of the environment. For example, California ground squirrels (*Spermophilus beecheyi*) respond more strongly to the rattling sounds from larger rattlesnakes (Swaisgood et al. 1999). Whether squirrels are responding to body size per se or to the acoustic properties of the rattle, a different response to different rattles indicates that the rattles are perceived differently.

The costs of uncertainty

We define environmental uncertainty as ambiguity due to imperfect information about the state of the environment (e.g., Sih 1992; Dall and Johnstone 2002; Esber and Haselgrove 2011). Uncertainty may be characterized by stimulus intensity and/or the signal-to-noise ratio (Dall et al. 2005) or by variation in the predictiveness of a stimulus (Esber and Haselgrove 2011). All stimuli are associated with some inherent degree of uncertainty due to their physical properties and characteristics of the environment (Brown and Cowan 2000). Environmental uncertainty can lead to costly errors in decision making, which suggests that cognitive systems should be adapted to cope with uncertainty (Stephens 1989). Imperfect information about an event can lead to errors, in that animals will engage in activities that are not matched to the probability of an event (Sih 1986). Errors include underestimating the likelihood of an event, which may

lead to missed opportunities, and overestimating the likelihood of an event, which may lead to wasted time and energy.

The benefits and costs of multisensory perception

Multisensory perception can assuage the consequences of uncertainty. Two characteristics of multimodal stimuli illustrate this point.

First, each modality has its own set of limitations. For example, chemical cues from a predator are difficult to localize but are often difficult for a predator to manipulate. Therefore, chemical cues may be better suited for gaining information about a predator's hunger state and recent prey preferences (Brown and Cowan 2000). Visual cues may be particularly useful for locating a predator, however, predators can easily manipulate their intention by changing their posture or behavior patterns, for example (Brown and Cowan 2000). By combining 2 chemical cues, only uncertainty about a predator's hunger state is reduced. By combining chemical and visual cues, prey gain knowledge about the predator's hunger state and intention.

Second, a unique property of multimodal stimuli compared with multiple unimodal stimuli is that each sensory channel can offer independent estimates of events or objects (Møller and Pomiankowski 1993; Ernst and Banks 2002). For example, a noisy audio stimulus is one with a low signal to noise ratio and hence includes some degree of uncertainty. Noise in one modality may be unrelated to the noise in another modality. Indeed, psychological research has demonstrated that cognitive systems integrate stimuli according to the signal-to-noise ratio of each modality (Ernst and Banks 2002; Ghazanfar et al. 2005; Fetsch et al. 2009). Ernst and Banks (2002) conducted

an experiment where humans estimated the height of an object based on visual and tactile stimuli. Tactile stimuli became more important in height estimation as the noise in visual images increased (Ernst and Banks 2002). Further evidence suggests that biasing perception away from uncertain modalities may be common. California ground squirrels living in areas with higher levels of anthropogenic auditory noise displayed elevated levels of vigilance to the playback of auditory alarm cues, suggesting an increase reliance on visual cues (Rabin et al. 2006). In another study, gray squirrels (*Sciurus carolinensis*) living in areas with higher urban auditory noise responded more to the visual component of an auditory-visual alarm signal from conspecifics compared with squirrels in rural environments, indicating an increased reliance on visual cues (Partan et al. 2010).

Together, these examples explain why we are particularly interested in examining multimodal stimuli as opposed multiple stimuli within a single modality as a mechanism to reduce uncertainty. However, our framework can also be applied to multiple unimodal stimuli.

Uncertainty reduction through stimulus acquisition and processing requires time and energy (Sih 1992; Dall and Johnstone 2002; Dall 2010) and can be distracting (reviews in Dukas 2002; Chan and Blumstein 2011). Wolf spiders (*Schizocosa uetzi*) presented with bimodal courtship signals were more likely to be captured by human “predators” compared with spiders that were presented with a single stimulus (Hebets 2005). Thus, in addition to the costs of uncertainty, we must also consider the costs of multisensory perception.

MULTISENSORY PERCEPTION AS A MECHANISM

Throughout our analysis, we use terms from the framework of Partan and Marler (1999, 2005) to describe perception of multimodal stimuli (Figure 1). Partan and Marler’s framework provides a foundation to study the evolution and function of multimodal signals by categorizing multimodal stimuli based on the behavior evoked by signal components in isolation and in combination (Møller and Pomiankowski 1993;














Stimulus	Response	Stimulus	Response	Category
A		A + B		Equivalence
		A + B		Enhancement
B		A + B		Antagonism
		A + B	 and 	Independence
A		A + B		Dominance
B		A + B	 or 	Modulation
		A + B		Emergence

Figure 1
Classification system of multisensory stimuli based on behavior responses to stimulus components in isolation and in combination (Partan and Marler 1999).

Partan and Marler 1999, 2005; Candolin 2003; Hebets and Papaj 2005). If separate components evoke the same response, the components are said to be redundant. Redundant stimuli can evoke a more intense response (enhancement), the same response (equivalence), or a response of lower intensity (antagonistic). Antagonism, a distinct category not made explicit by Partan and Marler (1999), is supported by a body of literature that has focused on antipredator behavior (Zuberbühler et al. 1999; Hazlett and McLay 2005; Thompson et al. 2008), and we include it in Figure 1. In the case of nonredundant stimuli, each component of a bimodal stimulus evokes different responses. Nonredundant stimuli can elicit both unimodal responses simultaneously (independence) or only one of the unimodal responses at equal (dominance) or different (modulation) intensity. Nonredundant stimuli may also lead to a completely new behavior (emergence).

In our framework, perceiver’s cognitive processes are subject to change over evolutionary and ecological time. Instead of asking why signals contain multiple components across modalities, we ask why receivers combine multisensory stimuli in different ways. The categorization of receiver responses in Figure 1 can be thought of as mechanisms that enable animals to make adaptive decisions. Consider the California ground squirrels that increased antipredator behavior in response to rattles from larger snakes (Swaisgood et al. 1999). Though we do not know if squirrels respond to body size per se, a sensitivity to rattles from different sized snakes is the mechanism that allows squirrels to reserve intense antipredator effort for those snakes capable of striking further and faster. Similarly, a perceiver whose response increases when presented with a multimodal versus unimodal stimulus could be increasing its response to one of the signal components in the presence of the second or could be combining the stimuli in an additive fashion. Regardless of the specific psychophysiological processes, we view the increase in perceiver response as a mechanism.

In the next section, we predict the conditions under which we expect to see enhancement, antagonism, equivalence, and dominance. We focus on these 4 categories as they have the greatest representation among the nascent field of multisensory perception.

PREDICTIONS FROM A COST-BENEFIT ANALYSIS OF MULTISENSORY INTEGRATION

Enhancement: minimizing missed opportunities

The problem of uncertainty can lead animals to miss opportunities such as finding a mate or evading a predator. Animals can reduce uncertainty by gathering information from cues in the environment (Dall and Johnstone 2002). An elevated response to multiple cues is adaptive when the number of cues corresponds to the likelihood of an event.

Within the predatory-prey literature, the sensory complement hypothesis states that multiple cues relating to predation risk combine in an additive manner, evoking increased alarm responses (Lima and Steury 2005). Within the context of the sensory complement hypothesis, enhancement is the mechanism that minimizes mortality when predators are nearby. We found 2 studies where a cross-modal predator stimulus evoked enhanced antipredator behavior (Smith and Belk 2001; Partan et al. 2009) such that 2 simultaneous predator cues were perceived as more risky than either cue alone.

Antagonism: minimizing wasted time and energy

In some cases, we see antagonism, a diminished response to a composite stimulus compared with either unimodal component in isolation. Antagonism is expected when multimodal cues indicate a decreased likelihood of an event, thereby

allowing time and energy to be redirected toward other fitness-enhancing activities.

Antagonism with respect to exploratory behaviors was found in sagebrush lizards (*Sceloporus graciosus*). Sniffing, a chemical exploratory behavior, and head-bobbing, which also increases information because it in turn engages an opponent in head-bobbing, are behaviors that reduce uncertainty about a rival (Thompson et al. 2008). When visual and olfactory cues from a rival male were presented simultaneously, resident males decreased the intensity of these behaviors (Thompson et al. 2008). This implies that the time and energy engaged in exploratory behaviors are costly and by being able to acquire more complete information about their rival lizards saved energy.

Crabs (*Heterozius rotundifrons*) showed no response to predator chemical cues but decreased the length of time spent in a catatonic defensive position relative to predator tactile cues when presented with both cues simultaneously (Hazlett and McLay 2005). The simultaneous presentation of both cues may have indicated another type of predation risk such that crabs should change their antipredator tactic by spending less time in a defensive posture and seek refuge (Hazlett and McLay 2005).

Alternately, the pattern of responses could be explained if multiple cues indicated an overall reduction in the likelihood of predation. Because prey should perceive uncertain situations as riskier (Sih 1992; Blumstein et al. 2004), a decrease in antipredator effort is expected when multiple predator cues are available if the cues indicate reduced risk. Under this reducible uncertainty hypothesis, multiple cues may constrain the location or motivation of a predator and indicate that the predator does not pose an immediate threat.

The distinction between the reducible uncertainty hypothesis (antagonism) and the sensory complement hypothesis (enhancement) can be explained by how multiple cues specify aspects of the environment (e.g., information about risk) compared with a single cue (Figure 2). The sensory complement hypothesis is expected when multiple cues indicate elevated

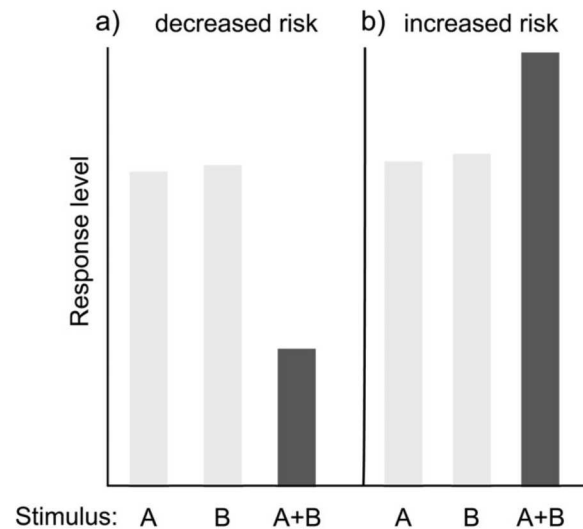


Figure 2
A bimodal predator stimulus (A + B) reduces uncertainty about the risk of predation compared with either isolated unimodal cue. (a) Antagonism is expected when a bimodal stimulus informs prey that a predator does not pose an immediate danger (see Hazlett and McLay 2005; Thompson et al. 2008). (b) Enhancement is expected when a bimodal stimulus informs prey that a predator poses an immediate danger (see Smith and Belk 2001; Partan et al. 2010).

risk relative to a single cue. The reducible uncertainty hypothesis is expected when multiple cues indicate reduced risk relative to a single cue.

Equivalence and dominance: a solution when reducing uncertainty is too costly

As in the case of enhancement and antagonism, animals can reduce uncertainty by sampling the multisensory environment (Dall and Johnstone 2002). However, when the costs are particularly high, combining multisensory stimuli may not be favored (Bernays and Wcislo 1994; McNamara and Houston 2009; Marewski et al. 2010; Santangelo et al. 2010). Under such conditions, we predict that a bimodal response will equal the response to one of the unimodal components in isolation. In terms of the framework of Partan and Marler (1999), such a pattern of responses is called either dominance or equivalence depending on whether isolated components evoke the same (equivalence) or different (dominance) responses. These responses may be adjusted over evolutionary time, as seen when a species specializes on a particular resource type (Bernays and Wcislo 1994), or over ecological time, as seen when predators pay attention to features of only a single prey type when prey are cryptic (Dukas and Ellner 1993).

FUTURE DIRECTIONS

Our framework predicts the conditions under which we should expect different mechanisms of multisensory perception based on the relative costs of uncertainty and multisensory perception. Uncertainty can lead to the costs missed opportunities and wasted time and energy (Sih 1992). To test the predictions resulting from our framework, we need to examine systems where the relative costs of uncertainty differ. For example, under some conditions, missed opportunities may be more costly than wasted time and energy. Predation risk presents an ideal context within which to test predictions from our framework. Predation risk, and therefore the system of costs and benefits, is wonderfully amenable to experimental manipulation (e.g., Lendrem 1983; Brown 1988; Holbrook and Schmitt 1988), and it is possible to study populations with different histories of exposure to predators (Blumstein 2006; Ferrari et al. 2007; Lahti et al. 2009). In a predation context, underestimating risk leads to the “missed opportunity” of failing to respond to a predator. Overestimating risk leads to wasted time and energy on antipredator effort that could be spent on other fitness-enhancing activities.

Thus, to begin to understand the adaptive significance of multisensory perception, we urge future studies to move beyond simply categorizing multisensory perception. Instead, we suggest that researchers should design studies that examine how the relative costs of missed opportunities and wasted time and energy influence the dynamics of multimodal perception.

CONSERVATION APPLICATIONS OF RESEARCH ON MULTISENSORY PERCEPTION

Urbanization is often characterized by the introduction of chemical pollutants, novel structures, and the sounds of both humans and traffic, which can affect species’ survival (Chan and Blumstein 2011). Studies by Rabin et al. (2006) and Partan et al. (2010) examined the influence of anthropogenic activities on behavior from a multisensory perspective and illustrate the applied significance of understanding the interplay between uncertainty and multimodal perception. In situations with anthropogenic auditory noise, auditory predator cues contributed less to a prey’s perception of risk as indicated by an increased effort to obtain visual cues (Rabin et al. 2006)

and elevated responses to visual cues (Partan et al. 2010). Impact studies often precede a planned anthropologic action that may change the environment. Incorporating into these studies investigations on how noise introduced by human actions impacts a population by measuring shifts in multisensory perception will be crucial for a more comprehensive measurement of environmental impact.

The management of threatened or endangered species may also benefit from studies that directly test how multisensory perception differs in different ecological contexts. Multisensory stimuli are important for habitat selection, prey recognition, predator avoidance, and mate selection. The inability of animals to recognize these stimuli on their release has been attributed to a low success in translocations and reintroductions despite implementing prerelease training programs (Stamps and Swaisgood 2007). The success of translocations and reintroductions can be enhanced by understanding how uncertainty influences multisensory learning and retention of stimulus recognition.

CONCLUSIONS

We emphasize that uncertainty is an important consideration to the study of multisensory perception. Within our framework, the costs of uncertainty (missed opportunities and wasted time and energy) and the costs of uncertainty reduction may account for different perceptive mechanisms. The current state of multisensory studies within behavioral biology is to characterize perceiver responses. In taking the next step toward a greater understanding of the evolution of multisensory perception, a challenge for future research will be to measure the pattern of responses across different cost–benefit landscapes to test these predictions. Furthermore, the development of quantitative models could significantly improve predictions of when we expect various mechanisms of perception.

FUNDING

National Science Foundation (NSF) (Graduate Research Fellowship Program and Competitive EDGE Science, Technology, Engineering and Math to N.E.M. and NSF-IDBR-0754247 to D.T.B.) and the UCLA Graduate Division and Department of Ecology and Evolutionary Biology (Eugene V. Cota-Robles Fellowship) to N.E.M.

We thank Julien Martin, Peter Nonacs, Peter Narins, and 2 anonymous reviewers for comments on a previous version of this review.

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CHAPTER 3

Optimal integration: the conditions under which animals should integrate multiple sensory modalities

Abstract

Animals are often confronted with potential information from a variety of modalities and while there is a large proximate literature demonstrating that these different sources of information may be integrated to form a unified percept, there is no general framework to predict the situations in which multimodal integration is favored. The combining of multiple stimuli has the benefit of increasing the accuracy of an animal's perception of the world, thereby leading to an increased chance that the animal will make the correct decision. We developed a quantitative model to explain why unimodal decision making might be favored over multimodal decision making. We introduce our model in terms of an antipredator context where a prey can either forage (optimal when a predator is absent) or hide (optimal when a predator is present). The prey has prior knowledge of the likelihood that a predator is present. The prey receives two, sequential stimuli in two modalities that indicate the presence of a predator. Since the world is uncertain, a stimulus does not definitively indicate that a predator is present. We modeled different sensory modalities by specifying different uncertainties of each stimulus. In some situations, the benefit of increased accuracy in knowing a predator's presence (or absence) afforded by another stimulus is not sufficient to warrant integration, so the prey ignores the stimulus.

Introduction

Animals extract potential information (Table 3-1) from abiotic cues, conspecific signals, and through heterospecific eavesdropping. Information is essential to making optimal decisions. However, an animal is rarely completely certain of the true state of the world (Dall and Johnstone 2002; Dall et al. 2005). Uncertainty is thought to, in part, drive the evolution of multimodal sexual signals because they can increase the likelihood that messages are received, correct for errors in detection of signals, or increase information content (Guilford and Dawkins 1991; Hebets and Papaj 2005; Partan and Marler 2005). Despite an acknowledgement of importance in considering a receiver's environment to the evolution of signals (e.g., Partan and Marler 2005), the literature to date lacks an appreciation of the fact that receivers are not passive agents in their environments and that their cognitive processing systems are also subject to selection. Few studies have explored the idea that the ability to integrate multisensory stimuli may depend on an individual's internal state or surrounding environmental conditions, and analysis of the situations in which an animal should or should not integrate multisensory information is rarely discussed (Munoz and Blumstein 2012; Partan 2013). Such studies are imperative to understanding the evolutionary significance of multimodal integration. In this study we develop a quantitative framework that makes testable predictions, which can be empirically tested, in order to begin unraveling why animals may or may not integrate multisensory stimuli. We suggest that this approach can be applied within or between individuals, populations or species.

Given widespread uncertainty, in order to increase the accuracy of an animal's estimate of its world one may initially assume that an individual will always attend to all available stimuli when making a decision as to how it should behave. Indeed, multisensory integration is one method for dealing with environmental uncertainty (Munoz and Blumstein 2012). We define multisensory integration as the combining of information from multiple sensory modalities that influences decision making (Munoz and Blumstein 2012) (we develop a precise, quantitative definition below). Numerous empirical studies document the occurrence of multisensory integration in many taxa and contexts. Behaviorally, it is assessed by comparing responses to the isolated, unimodal stimuli to the combined, multimodal stimulus (Partan and Marler 1999). The types of stimuli an animal can integrate include conspecific signals, heterospecific eavesdropping stimuli, and abiotic stimuli. Cross-modal integration has been documented in decisions regarding sexual selection (see Heberts and Papaj 2005; Partan and Marler 2005 for reviews), antipredator behavior (Brown and Magnavacca 2003; Hazlett and McLay 2005; Lohrey et al. 2009; Partan et al. 2010; Ward and Mehner 2010), foraging (Sternthal 1974; Rowe and Guilford 1996, 1999; Siemers 2013), host suitability (Völkl 2000), hunting (Roberts et al. 2007; Cross and Jackson 2009a; Harley et al. 2011; Halfwerk et al. 2014), detection and/or assessment of social rivals (Narins et al. 2005; Thompson et al. 2008; de Luna et al. 2010; Bretman et al. 2011; Taylor et al. 2011), navigation (Graham et al. 2010), distinguishing heterospecifics from conspecifics (Cross and Jackson 2009b), heterospecific individual recognition (Smith and Evans 2008; Proops et al. 2009; Kondo et al. 2012), and the onset of breeding activities (Voigt et al. 2011).

Despite the apparent usefulness of having access to multiple stimuli, sometimes animals do not use all available stimuli in making a decision. Integration has been shown to depend on the individual's environmental context such as reproductive state (Kasurak et al. 2012), a population's habitat (Partan et al. 2010) or a species' type of mating system (Cross and Jackson 2009b). These studies discussed situation-dependent integration primarily on a proximate level. For instance, female gobies (*Neogobius melanostomus*) integrated vibrational-olfactory sexual stimuli from males only when reproductive (Kasurak et al. 2012). Kasurak et al. (2012) discuss this result in terms of a possible plasticity of structures responsible for integration across reproductive states. Squirrels (*Sciurus carolinensis*) in urban habitats exhibited greater response to the visual-only stimulus and greater multimodal enhancement to an audio-visual conspecific alarm stimulus compared to squirrels in rural habitats (Partan et al. 2010). Partan et al. (2010) discussed a cognitive shift from relying on acoustic to visual stimuli in noisy environments (Partan et al. 2010). Multimodal integration was studied across four species of jumping spiders (Cross and Jackson 2009b). In three of the species, males compete for females (*Portia fimbriata*, *Portia africana* and *Jacksonoides queenslandicus*). In the fourth species, in addition to male-male competition, female-female competition for mates exists (*Evarcha culicivora*). Only in *E. culicivora* did a conspecific male odor enhance visual-based conflict within females (Cross and Jackson 2009b). This last study, by noting that the value of recognizing females is more important in *E. culicivora* compared to the other species, explained situation-dependent integration on a functional level.

The preceding examples of situation-dependent integration indicate that an interplay of several factors underlies the payoffs of integrating and ignoring stimuli. We

previously developed a conceptual framework to help understand why multi-modal integration is not ubiquitous (Munoz and Blumstein 2012). The precision with which a stimulus indicates the state of the world relates to how often an animal will make mistakes. The frequency at which the animal makes each type of mistake (e.g., Type I vs. Type II) is determined by the costs of each mistake. Based on previous experience (ecological and/or evolutionary), the animal also has some expectation as to the likelihood of a given event. When using a stimulus, the animal also suffers an internal cost associated with processing stimuli (e.g., in the form of physiological investment or energetic costs). These factors can change depending on the animal's situation. For example, a population of birds near a stream will receive conspecific vocalizations with greater uncertainty due to the noise of flowing water. If an animal is starving, mistakenly missing a foraging opportunity may greatly outweigh the cost of a missed reproductive opportunity; if the animal is well fed then the opposite might be true..

Here we formalize the framework outlined in Munoz and Blumstein (2012) by developing a quantitative model to 1) explain why unimodal decision making might be favored over multimodal decision making, 2) identify key factors that favor multimodal integration, and 3) make clear predictions regarding the extent to which various factors influence integration with the aim of providing testable hypotheses to guide future research. We then discuss applications of our model to various ecological problems.

Methods

Modeling framework

When the world is uncertain, sometimes it might not pay for an individual to attend to a stimulus (Bradbury and Vehrencamp 1998, 2000). Here, we formally expand upon this idea and investigate a situation where an animal receives two sequential stimuli in different sensory modalities (see Table 3-2 for a complete summary of assumptions). Specifically, we are interested in the extent to which environmental uncertainty, background level of predation risk, and the costs of mistakes influence whether or not a prey will integrate 2 stimuli in different sensory modalities.

For the purposes of developing our model, we use an example of a foraging prey (notation descriptions in Table 3-3). The world is in one of two possible states, predator present (PRED) or no predator present (NONE). Based on prior experience over its lifetime or through evolution, the prey knows the probability of a predator being present, P_{PRED} . The prey can engage in one of two behaviors, either forage (F) or hide (H). Since the prey is not certain as to the presence of a predator, the prey will sometimes make mistakes. Depending on the state of the world and whether the prey is foraging or hiding, the prey receives one of four payoffs, $W_{behavior,STATE}$, which are positive. The prey always manages to escape a predator, but the predator will inflict injury if the prey fails to hide. $W_{F,NONE}$ and $W_{H,PRED}$ are the payoffs of behaving appropriately either when a predator is absent or present, respectively. $W_{H,NONE}$ and $W_{F,PRED}$ are the payoffs of mistakes either when a predator is absent or present, respectively. The prey receives a net energetic gain $W_{F,NONE}$ when foraging in the open. When foraging in the open and a predator is present, injury inflicted by the predator reduces the net gain (because the prey must energetically invest in healing

itself) such that $W_{F,PRED} < W_{F,NONE}$. While hiding, the prey can still forage but with lower gains and regardless of whether a predator is present or not such that $W_{H,PRED} < W_{F,NONE}$. If a non-threat is present and the prey hides, the prey quickly realizes, emerges, and resumes foraging in the open and receives an average energetic gain compared to hiding when a predator is present, but this gain is less compared to when the prey forages in the open such that $W_{H,PRED} < W_{H,NONE} < W_{F,NONE}$. We assumed these payoffs do not change between the first and second stimuli.

The prey's initial behavior is determined by the prey's prior estimate and the benefits of hiding and foraging in each state. In the absence of a stimulus, the prey sets a cutoff probability, P_c , which is optimal when the following condition holds (Bradbury and Vehrencamp 1998)

$$\frac{P_c}{1 - P_c} = \frac{W_{F,NONE} - W_{H,NONE}}{W_{H,PRED} - W_{F,PRED}}$$

In the absence of any stimuli, if $P_{PRED} \leq P_c$ then the prey will always forage and it receives an average payoff of $(1 - P_{PRED})W_{F,NONE} + P_{PRED}W_{F,PRED}$. If $P_{PRED} > P_c$ then the prey will always hide and it receives an average payoff of $P_{PRED}W_{H,PRED} + (1 - P_{PRED})W_{H,NONE}$.

When the prey ignores a stimulus, its behavior (foraging or hiding) does not change from its initial behavior. Therefore, $\overline{P_{O_{ignore}}}$ depends on P_c :

If $P_{PRED} \leq P_c$ then,

$$\overline{P_{O_{ignore}}} = (1 - P_{PRED})W_{F,NONE} + P_{PRED}W_{F,PRED}$$

If $P_{PRED} > P_c$ then,:

$$\overline{P_{O_{ignore}}} = P_{PRED}W_{H,PRED} + (1 - P_{PRED})W_{H,NONE}$$

Throughout, we use “stimulus” to refer to a *feature* within a sensory modality which can assume a set of magnitudes, S_i (Fig. 3-1). We have used the subscript i to index the order of stimuli. For the purposes of introducing our model, we use “body size” as an example of a stimulus. If the prey “uses” the stimulus, then it incorporates information about body size into its decision to forage or hide. When using a stimulus, the prey receives an average payoff $\overline{PO}_{i,use}$. The animal should use stimulus i only when $\overline{PO}_{i,use} \geq \overline{PO}_{i,ignore}$. The difference between these two average payoffs is also known as the value of information, V_i (Stephens 1989; Bradbury and Vehrencamp 1998), which must be positive for the prey to use the stimulus.

The prey correctly decides to forage with some probability, $P_{i,correct\ reject}$. The animal also makes a correct decision if it hides, which occurs with probability $P_{i,hit}$. The probabilities of mistakes are the probability of foraging when a predator is present, $P_{i,miss}$, and the probability of hiding when in fact a non-threat is present, $P_{i,false\ alarm}$.

The average payoff of using a stimulus equals the average payoff of doing each behavior in each state weighted by the probability that the world is in that state minus the energetics, processing and/or physiological costs, K_i , of processing information. Thus,

$$\overline{PO}_{i,use} = (1 - P_{PRED})(P_{i,correct\ reject}W_{F,NONE} + P_{i,false\ alarm}W_{H,NONE}) + P_{PRED}(P_{i,hit}W_{H,PRED} + P_{i,miss}W_{F,PRED}) - K_i.$$

Since $P_{i,correct\ reject} = 1 - P_{i,false\ alarm}$, and $P_{i,miss} = 1 - P_{i,hit}$ the preceding can be rewritten as

$$\overline{PO}_{i,use} = P_{PRED}P_{i,hit}(W_{H,PRED} - W_{F,PRED}) - (1 - P_{PRED})P_{i,false\ alarm}(W_{F,NONE} - W_{H,PRED}) + P_{PRED}W_{F,PRED} + (1 - P_{PRED})W_{F,NONE} - K_i.$$

The value of information, $\overline{PO}_{i,use} - \overline{PO}_{i,ignore}$, for a using a stimulus when $P_{PRED} \geq P_{i,c}$ is then

$$V_i = P_{PRED}P_{i,hit}B_{PRED} - (1 - P_{PRED})P_{i,false\ alarm}B_{NONE} \\ + P_{PRED}B_{PRED} \left(1 - \frac{(1 - P_{PRED})B_{NONE}}{P_{PRED}B_{PRED}}\right) - K_i$$

and when $P_{PRED} < P_{i,c}$ is

$$V_i = P_{PRED}P_{i,hit}B_{PRED} - (1 - P_{PRED})P_{i,false\ alarm}B_{NONE} - K_i$$

$B_{PRED} = (W_{H,PRED} - W_{F,PRED})$ is the net benefit of hiding when a predator is present.

$B_{NONE} = (W_{F,NONE} - W_{H,NONE})$ is the benefit of foraging when a non-threat is present.

An object with a body size S_i corresponds to a predator with a certain probability, $P(S_i|PRED)$, and to a non-predator with a certain probability, $P(S_i|NONE)$. We assumed these probability distributions are continuous and normal with a standard deviation equal to one unit on an arbitrary scale (Table 3-2). We assumed that the prey has knowledge of these distributions

$$P(S_i|PRED) = \frac{1}{\sqrt{2\pi}} \exp\left[-0.5(S_i - \mu_{i,PRED})^2\right]$$

$$P(S_i|NONE) = \frac{1}{\sqrt{2\pi}} \exp\left[-0.5(S_i - \mu_{i,NONE})^2\right]$$

Body size indicates if the object is more likely a predator or non-predator because the average body size of predators, μ_{PRED} , and non-threats, μ_{NONE} , are different (Fig. 3-1). Here, we have assumed that, on average, predators are larger than non-predators: $\mu_{i,PRED} > \mu_{i,NONE}$ (Fig. 3-1). However, sometimes predators are smaller than non-predators and *vice versa*. On our arbitrary scale for S_i , the grand mean of body sizes equals zero (as will be shown below, only the difference in means between predators and non-threats is important). The extent to which the world is uncertain depends on $\mu_{i,PRED}$ and $\mu_{i,NONE}$. As

$\mu_{i,PRED}$ and $\mu_{i,NONE}$ become more similar the overlap between the NONE and PRED distributions increases, thereby increasing the probability of making mistakes.

We assumed that when the prey uses a stimulus, it makes foraging decisions following signal detection theory in which the prey receives the maximum average payoff when it sets a cutoff at some stimulus magnitude, $S_{i,c}$ (Green and Swets 1966; Oaten et al. 1975; Brilot et al. 2012). If the prey receives a stimulus with magnitude $S_i \geq S_{i,c}$ the prey will always hide. If the prey receives a stimulus with magnitude $S_i < S_{i,c}$ the prey will forage. Consequently, we calculated $S_{i,c}$ from the relationship that at the optimal $S_{i,c}$ the average payoff of foraging, $\overline{PO}(F)_i$, equals the average payoff of high vigilance, $\overline{PO}(H)_i$. The average payoff of a given behavior is the payoff of the behavior in each state weighted by the probability that the world is in a given state. Therefore,

$$\overline{PO}(F)_i = P(PRED|S_{i,c})W_{F,PRED} + P(NONE|S_{i,c})W_{F,NONE}, \text{ and}$$

$$\overline{PO}(H)_i = P(PRED|S_{i,c})W_{H,PRED} + P(NONE|S_{i,c})W_{H,NONE}$$

Alternately, at $S_{i,c}$ the following is true

$$B_{PRED} P(PRED|S_{i,c}) = B_{NONE} P(NONE|S_{i,c})$$

where $P(PRED|S_{i,c})$ and $P(NONE|S_{i,c})$ are the probabilities of the presence of a predator and a non-predator given a stimulus of magnitude $S_{i,c}$, respectively. From Bayes' Theorem,

$$P(PRED|S_{i,c}) = \frac{P_{PRED}P(S_{i,c}|PRED)}{P(S_{i,c})}$$

and similarly for $P(NONE|S_{i,c})$. $P(S_{i,c})$ is the sum of the probability of $S_{i,c}$ in each state, weighted by the probability that the world is in that state.

$$P(S_{i,c}) = P_{PRED}P(S_{i,c}|PRED) + (1 - P_{PRED})P(S_{i,c}|NONE)$$

Therefore, upon specifying B_{PRED} , B_{NONE} , μ_{PRED} and μ_{NONE} , the value of $S_{i,c}$ is known (see Appendix).

$P_{i,hit}$ and $P_{i,false\ alarm}$, which are the areas under the PRED distribution above the $S_{i,c}$ and under the NONE distribution above the $S_{i,c}$, respectively, are given by

$$P_{i,hit} = 1 - 0.5 \left[1 + \operatorname{erf} \left(\frac{S_{i,c} - \mu_{i,PRED}}{\sqrt{2}} \right) \right]$$

and

$$P_{i,false\ alarm} = 1 - 0.5 \left[1 + \operatorname{erf} \left(\frac{S_{i,c} - \mu_{i,NONE}}{\sqrt{2}} \right) \right]$$

where $\operatorname{erf}(x)$ is the error function of x .

Using the preceding equations and upon specifying P_{PRED} , B_{NONE} , B_{PRED} , $\mu_{1,PRED}$, $\mu_{1,NONE}$, and K_1 the value of information of the first stimulus can be calculated (see Appendix for the explicit equation for V_i when $P_{PRED} \geq P_c$ or when $P_{PRED} < P_c$).

If the prey uses the first stimulus (i.e., $V_1 \geq 0$), we can calculate P_{PRED}' from S_1 , $\mu_{1,STATE}$ and P_{PRED} using Bayes' Theorem,

$$P_{PRED}' = \frac{P_{PRED} P(S_1|PRED)}{P(S_1)}$$

where $P(S_1|PRED)$ is the probability of receiving a stimulus with magnitude S_1 when a predator is present. Since we have assumed that the probability of receiving S_1 in each state is a normal distribution with unit standard deviation,

$$P(S_1|PRED) = \frac{1}{\sqrt{2\pi}} \exp \left[-0.5(S_1 - \mu_{1,PRED})^2 \right]$$

$P(S_1)$ is the probability of a stimulus with magnitude S_1 occurring the world, which is the sum of the probabilities of S_1 in each state weighted by the probability that the world is in that state:

$$P(S_1) = P_{PRED}P(S_1|PRED) + (1 - P_{PRED})P(S_1|NONE).$$

The animal then receives a second stimulus having properties $\mu_{2,NONE}$ and $\mu_{2,PRED}$.

Setting $P_{PRED} = P_{PRED}'$, V_2 is then calculated.

When $V_1 \geq 0$ and $V_2 \geq 0$, it is optimal for the prey to use information from both modalities in making a foraging decision, a situation we call integration. Thus, the criterion, $V_1 \geq 0$ and $V_2 \geq 0$, is a formal definition of multimodal integration. The situation can be specific to multiple modalities by specifying different levels of uncertainty for each stimulus. As is typically the case, different sensory modalities are independently disturbed by environmental noise (acoustic noise will not affect a visual stimulus) and/or an individual is generally better at discriminating the world based on stimuli in certain modalities. Two instances of unimodal information use can occur. The first instance is when $V_1 \geq 0$ and $V_2 < 0$, which is when the prey only uses the first stimulus. The second instance of unimodal information use occurs when $V_1 < 0$ and $V_2 \geq 0$. In the latter example, the prey evaluates the second stimulus without updating P_{PRED} . When $V_1 < 0$ and $V_2 < 0$, the prey does not obtain information from either stimuli regarding the presence/absence of a predator.

Graphical methods

We wished to examine different situations where information use switches from unimodal to bimodal. Thus, in presenting our results graphically we frame our results in terms of the

“favorability of integration”, A , which we define as the proportional area of a 2-dimensional parameter area in which V_2 is positive while the other parameters are held constant (Fig. S3-1). Each area consisted of 100 x 100 simulations.

Results

We developed a general model that determines whether or not an animal should integrate two stimuli in different sensory modalities given a set of environmental conditions when making potentially fitness-enhancing decisions. When integrating additional stimuli, the prey increases the accuracy of how the animal perceives the world, and therefore increases the likelihood that the animal makes a correct decision. In some situations, the benefit from making more accurate decisions is not sufficient to warrant integration.

Our model is general enough such that it can be applied to a multitude of different scenarios, including mate selection, rival assessment, or conspecific recognition. For clarity we developed the model in a predation-risk assessment scenario where a prey, must decide whether or not to integrate the stimuli in making antipredator choices. In order to demonstrate the flexibility of our model, later we apply the model to a mate selection scenario.

We modeled two sensory modalities by specifying different degrees of uncertainty for each stimulus, U_1 and U_2 . This is because different modalities are generally independent from one another. For example, wind may diffuse chemical odorants but leave a visual stimulus unchanged. In this case, $U_{odor} > U_{visual}$. Furthermore, an individual likely perceives stimuli in different modalities with different accuracies. To a terrestrial animal, vision may be the most accurate of modalities and therefore have a relatively low uncertainty

compared to other modalities. We also recognize that different stimuli in a single sensory modality can indicate events with different accuracies. For example, the sound of rustling vegetation could correspond to a predator, but wind is also likely to produce a similar sound. Therefore, rustling vegetation may have high uncertainty compared to, for example, a vocalization even though both are acoustic stimuli.

The prey's "environment" to which we refer and as defined in our model is composed of the prey's prior expectation that a predator is present, the uncertainty of the first stimulus (U_1), the benefit of foraging when a non-threat is present (B_{NONE}), the benefit of hiding when a predator is present (B_{PRED}), the prey's cost of attending to the first stimulus (K_1), the magnitude of the first stimulus (S_1), the uncertainty of the second stimulus (U_2) and the cost of attending to the second stimulus (K_2).

Broadly, P_{PRED} increases, B_{PRED} increases, and B_{NONE} decreases the value of information of the i th stimulus (Fig. 3-2 and Fig. 3-3). The cost of using the i th stimulus, K_i , linearly decreases V_i . While U_1 decreases V_1 , the effects of U_1 and U_2 on V_2 is nuanced. The effects of U_1 and U_2 depend on S_1 . Generally, as S_1 tends towards more likely having originated from a predator, then smaller U_1 favors integration. As S_1 tends towards more likely having originated from a non-threat, then larger U_1 favors integration (Fig. 3-3).

We now turn to discussing simple hypothetical situations of risk assessment and mate selection that may be analyzed using our model. These examples illustrate that in some situations the animal does not benefit from additional information obtained from integrating. We emphasize that these examples are hypothetical and are presented to demonstrate how our model might translate to real-world situations. Later we discuss one (of many) empirical method for testing predictions from model.

The first example applies our model to a prey that experiences different environments along its migration route and may or may not integrate when assessing whether an object is a predator or non-threat. The second example shows how our model may be applied to females in different populations in different environments that may or may not integrate when distinguishing between heterospecific and conspecific males.

Applications of the model

In these examples, we assumed the cost of attending to the first stimulus, K_1 , is negligible. K_1 linearly decreases the use of the first stimulus; those instances where the first stimulus is ignored are thus not going to be integrated. This is a simplifying assumption that ensures the first stimulus is always used and allows us to focus on the effect on integration.

Predator vs. non-threat: Changes in the likelihood that an individual prey integrates along a migration route with different environments

Consider a grazing prey that notices an object and must distinguish it as a predator or non-threat (Table 3-2). Since this prey forages with its head down, the prey typically smells before seeing potential predators. Assume the prey cues in on the concentration of sulphurous compounds and body size. On average, predators emit higher concentrations of sulphurous compounds (Nolte et al. 1994) and are visibly larger. The prey can either forage (optimal for a non-threat) or hide (optimal for a predator). If the prey fails to hide when a threat is present, the prey still escapes but is injured. Though the prey typically smells a potential threat first, the acuity with which the prey can distinguish a predator from non-

predator through odor is low ($U_1 = 0.4$) compared to the accuracy obtained from visually assessing body size ($U_2 = 0.1$).

The prey smells something that is highly likely to have come from a predator. However, due to uncertainty there is still a possibility that a non-threat produced the odor. In the prey's summer breeding grounds, foraging in the open when a non-threat is present, the prey receives a net energetic gain $W_{F,NONE} = 7$. When foraging in the open and a predator is present, injury inflicted by the predator reduces the net gain to $W_{F,PRED} = -9$. While hiding, when a predator is present and the prey hides it can still forage but with lower gains such that the prey receives a foraging gain $W_{H,PRED} = 1$. If a non-threat is present and the prey hides, the prey quickly realizes, emerges, and resumes foraging in the open and receives an energetic gain $W_{H,NONE} = 2$. Therefore, the average benefit of correctly hiding when a predator is present $(W_{H,PRED} - W_{F,PRED}) = B_{PRED} = 10$; the prey receives an average benefit of correctly foraging when a non-threat is present $(W_{F,NONE} - W_{H,NONE}) = B_{NONE} = 5$. Based on experience, the prey knows that 0.3 of objects are predators (Fig. 3-2a). As it migrates to warmer wintering grounds, the prey's typical foraging items become scarce and the prey must forage on items with longer handling times. Since the prey must spend more time to receive the same foraging gain as obtained when foraging on its summer diet, the benefit of foraging decreases, which we modeled as $B_{NONE} = 1$ while holding all other parameters constant. As a result, the favorability of integration increases. This is because, relative to B_{NONE} the benefit of hiding increases, which means it becomes increasingly important for the prey (assuming it is well nourished) to accurately assess if a predator is present. Since the prey benefits from an increase in its accuracy of estimating the likelihood of a predator, the favorability of integration increases.

At some point along its migration route, the prey's energy reserves become extremely low. When a missed foraging opportunity could lead to death, the benefit of foraging exceeds the cost of being injured by a predator. We model this situation by setting B_{NONE} to 60 (Fig. 3-2a). As shown in Fig. 3-2a when the prey's energy reserve decreases, the favorability of integration decreases. This is because making accurate antipredator decisions has become less important; the prey can afford to be injured because foraging gains are more beneficial.

The effect is disproportionately opposite if the values of B_{NONE} and B_{PRED} are reversed (Fig. 3-2b). If, for example, the type of predator is capable of inflicting a greater degree of injury, on average the benefit of correctly hiding from a predator (e.g., $B_{PRED} = 60$) will far exceed the benefit of foraging when a non-threat is present (e.g., $B_{NONE} = 10$). As shown by the dotted line in Fig. 3-2b, for $K_2 = 1$ to 20, the prey will always integrate. This is because being sure that an object is in fact a predator is highly important in making an antipredator decision.

When the type of predator in the prey's world changes and the level of injury inflicted upon the prey is minor, then B_{PRED} decreases. Similar to when the prey is low on energy reserves (dotted line in Fig. 3-2a), if the predator is relatively innocuous in that (solid and dashed lines in Fig. 3-2b) the prey is less likely to integrate.

Now imagine that the prey has normal energy reserves (e.g., $B_{NONE} = 5$ and $B_{PRED} = 10$). Along the prey's migration route, the density of predators increases ($P_{PRED} = 0.7$). Regardless of the prey's energy levels or the level of injury inflicted by the predator, the favorability of integration is greater when the density of predators is higher (Fig. 3-2c & d). When an object is more likely a predator, it becomes increasingly important for a prey to

distinguish predators from non-predators because. Consequently, the prey is more likely to integrate additional stimuli to improve the accuracy of its decision. Conversely, the less likely a prey is to encounter a predator, the less important it becomes for the prey to make accurate antipredator decisions; there is no point to being able to assessing whether an object is a predator or not if the object is most likely a non-threat.

Conspecific vs. heterospecific male: differences in the likelihood of integration between female populations in different environments

Consider two populations of an avian species where males sing from their territories (Table 3-2). In this example a female is trying to assess whether a male is a conspecific or heterospecific in its decision to initiate copulation (Fig. 3-3). On average conspecifics produced songs with a higher acoustic frequency and have longer tails. Females typically first hear and then see males. A female can either attempt to mate with the male (optimal for a conspecific) or forage (optimal for a heterospecific). Whenever a female attempts to mate with a conspecific, she receives a reproductive benefit of 12 ($W_{M,CONSP} = 4$). If a female attempts to mate with a heterospecific, she receives no reproductive benefit ($W_{M,HETERO} = 0$; the energy expenditure of attempting copulation and interspecific aggressions are assumed negligible). If the female forages in the presence of either type of male, it receives a reproductive benefit of 2 due to energetic gains of foraging ($W_{F,HETERO} = W_{F,CONSP} = 2$). Therefore, the average benefit of mating with a conspecific ($W_{M,CONSP} - W_{F,CONSP}$) = $B_{CONSP} = 10$; the average benefit of ignoring a heterospecific ($W_{F,HETERO} - W_{M,HETERO}$) = $B_{HETERO} = 2$.

One population is typical in that males have territories away from moving water and acoustic uncertainty is $U_1 = 0.3$. However, in the second population, individuals are

restricted to territories along the edge of a stream. For females along the stream edge, suppose noise from flowing water increases acoustic uncertainty to $U_1 = 0.7$. Based on experience, females in both populations know that 0.6 of males are conspecifics ($P_{CONSP} = 0.6$) and the cost of attending to an acoustic stimulus is negligible. We modeled a visual stimulus assuming that females are highly adept at visually distinguishing conspecifics based on tail length compared to acoustic frequency, so $U_2 = 0.2$ and is the same in both populations.

A female hears a song having acoustic frequency equal to the average frequency from a conspecific male in that population, $S_1 = \mu_{1,CONSP}$. Even though a conspecific is more likely to have produced that song, there is still a possibility that a heterospecific sang that song [$P(\mu_{1,CONSP} | CONSP) > P(\mu_{1,CONSP} | HETERO)$]. The degree to which P_{CONSP}' tends towards 1 (certainty that the male is a conspecific) is larger for smaller U_1 . More acoustically distinct songs will give females a better indication as to the type of male. Therefore, for females along the stream P_{CONSP}' only marginally increases compared to females away from the stream. All else being equal, for females close to the stream, further improvement as to the accuracy of the female's estimate will still produce a higher rate of errors compared to females away from the stream. Therefore, after hearing a song likely produced by a conspecific male, females near the stream are more likely to ignore tail length and only use acoustic frequency when making a decision as to the identity of the male (Fig. 3-3a).

What if instead a female hears a song with a frequency that on average is produced by a heterospecific, $S_1 = \mu_{HETERO}$? A song more likely to have been made by a heterospecific decreases the female's expectation that the male is a conspecific ($P_{CONSP}' < P_{CONSP}$). Since the male is more likely a heterospecific, the female does not need to improve her estimate as to

the type of male. Therefore, the favorability of integration is less when females hear a song likely produced by a heterospecific compared to a song likely produced by a conspecific regardless of the level of acoustic uncertainty. However, due to higher acoustic uncertainty along the stream, P_{CONSP} will decrease to lesser extent compared to the female away from the stream. Therefore, opposite to what was found when $S_1 = \mu_{CONSP}$, females near the stream that hear a song with frequency μ_{HETERO} are more likely to integrate acoustic frequency and tail length than females away from the stream (Fig. 3-3b).

Now consider that the proportion of singing males that are conspecifics decreases such that $P_{CONSP} = 0.2$ (Fig 3c & d). Regardless of a song's acoustic frequency or the level of acoustic noise, the favorability of integration is lower when the proportion of conspecific males decreases. As the proportion of conspecific males decreases it becomes less important for females to distinguish conspecifics from heterospecifics, because the likelihood that a singing male is a conspecific is low.

Also consider the situation where all conspecific males in each population get sick. Assume that females who mate with sick males have a lower reproductive success. Therefore, the benefit of mating with conspecifics, B_{CONSP} , is lower when males are sick. We modeled this by specifying $B_{CONSP} = 10$ for healthy males and $B_{CONSP} = 6$ for sick males (Fig. 3-3e). The benefit of ignoring heterospecifics, $B_{HETERO} = 2$, the density of conspecific males, $P_{CONSP} = 0.6$, and uncertainty of tail length, $U_2 = 0.2$, are the same in both populations. Acoustic uncertainty is still $U_1 = 0.3$ and $U_1 = 0.7$ for females away and along the stream, respectively. The cost of attending to the first stimulus is negligible, and the cost of integrating the acoustic-visual stimulus is $K_2 = 3$. When males are sick, the value of integrating decreases. Since the female receives less benefit from mating with a sick male,

she is not as concerned with being able to accurately assess whether the male is a conspecific or heterospecific.

Order of stimuli affects the favorability of integration

Continuing with the preceding example of the female that must distinguish conspecific and heterospecific males, suppose that vegetation along the stream becomes less dense. In this situation, females receive stimuli in opposite order such that they first see and then hear potential mates. Here, tail length and acoustic frequency have the same uncertainty as before, but the order is reversed ($U_1 = 0.2$; $U_2 = 0.7$; Fig. 3-3f). The favorability of integration is greater if the female were to see a potential mate first. If the first stimulus more accurately distinguishes conspecifics and heterospecifics, then the female is more likely to integrate.

This result can have important implications when considering the investment that males may put into sexual signals that are more likely to be received by females first. If the male is in an environment where females first see the male, the male may invest more in his plumage display in order to ensure that the female also integrate the acoustic features of his song.

General discussion

We have presented a precise definition of the term “multimodal integration”. We defined multimodal integration as occurring when an animal uses both the first and second stimuli in making a decision (i.e., $V_1 \geq 0$ and $V_2 \geq 0$; we discussed both predator risk assessment and

mate assessment contexts). Integration is the use of two or more stimuli in order to improve the accuracy of an individual's decision as to how it should behave. Different sensory modalities are represented in our model through different U_1 and U_2 . This is because different modalities are generally independent from one another. For example, wind may diffuse chemical odorants but leave a visual stimulus unchanged. In this case, $U_{odor} > U_{visual}$. Furthermore, an individual likely perceives stimuli in different modalities with different accuracies. To a terrestrial animal, vision may be the most accurate of modalities and therefore have a relatively low uncertainty compared to other modalities. We also recognize that different stimuli in a single sensory modality can indicate events with different accuracies. For example, the sound of rustling vegetation could correspond to a predator, but wind is also likely to produce a similar sound. Therefore, rustling vegetation may have high uncertainty compared to, for example, a vocalization even though both are acoustic stimuli.

Understanding the factors responsible for the diverse types of multimodal integration responses and the evolution or loss of integration abilities is challenging. It requires an understanding of an animal's state variables and the past and present environment in which an animal lives. These factors can be analyzed through our model. For example, avian populations with females that must distinguish conspecifics from heterospecifics might be in different environments (e.g., island vs. mainland populations) that have different levels of uncertainty (modality and/or stimulus specific noise can be modeled through U_1 or U_2) or have males of differing levels of health (benefit of mating with a conspecific can be modeled through B_{CONSP}). In another example, a migrating prey is likely to encounter changing predation pressures (a prey's expectation of a predator can be

modeled through P_{PRED}) or predator types (degree of injury inflicted by a predator can be modeled through B_{PRED}).

Our model's predications can also be empirically tested. Consider the effect of food handling time on whether or not a prey integrates a multimodal predator stimulus. A prey can be baited to a feed station containing predator urine and subsequently be broadcast predator vocalizations. The proportion of time being vigilant (or foraging if the prey trades off vigilance for foraging) is measured. This type of experiment can be done where the bait is mixed with different volumes of gravel. When the bait is mixed with more gravel, the prey must spend more time sifting through the bait mixture in order to obtain the same energy return as compared to the lower volume of gravel. Therefore, the high-gravel bait mixture effectively generates a greater handling time. A greater handling time means that the benefit of foraging decreases. Integration is less favored when handling time increases (or the benefit of foraging decreases). Integration is assessed by the proportion of time spent foraging as opposed to being vigilant. Following Partan and Marler (1999), the prey is said to integrate when the proportion of time foraging in response to the olfactory-acoustic stimulus is different than the olfactory stimulus alone and the acoustic stimulus alone. Therefore, we expect when foraging at bait mixed with less gravel, we might expect the prey's multimodal response to be different than the olfactory-only and acoustic-only responses.

Given a changing set of environmental conditions, an individual's decision to switch from unimodal to multimodal integration (or *vice versa*) will follow our model's predictions only if the individual has knowledge of the extent to which the environment changed. Sih et al. (2011) provides a thorough review of how animals might have this knowledge in order

to adaptively respond to changing environments. Given the premise that multimodal integration (or unimodal information use) is an adaptive response to an individual's environment, knowledge of a changing environment assumed by our model may be obtained by animals through mechanisms identified by Sih et al. (2011).

Our model can be modified to capture more complex situations. In nature, objects often have several attributes (e.g., size, color, vocalization frequency); each of these attributes can be incorporated by defining S_i as a vector on several axes. Furthermore, more than two stimuli can be examined simply by iteratively applying the algorithm with the new updated probability and stimulus' uncertainty. So far we have assumed stimuli are received on a time scale such that the benefits of correct decisions are constant. However, these benefits may change in rapidly changing environments or when the time lag between receiving a stimulus is relatively large. Our model can also be extended to represent a world that can be in three or more states. For example, a prey's response may depend on whether an aerial predator is present, a terrestrial predator is present or a non-threat is present (e.g., Brilot et al. 2012). Furthermore, behavior decisions may not be bi-modal we have assumed. A prey's decision may be with regards to the level of vigilance it should display, which can vary on a continuous scale depending on the level of threat posed (Lima and Dill 1990). This can be incorporated by specifying a "response function", for example, that varies from 0 (no vigilance) to 1 (constant vigilance) with some function through $S_{i,c}$. These readily modeled situations should be further explored.

Conclusion

We have developed a model predicts the extent to which animals should integrate multisensory stimuli given a set of environments conditions. This model is unique to multimodal situations because of differing degrees of uncertainty specified for each stimulus. Uncertainty and the value of information (Stephens 1989; Koops 2004) have previously been applied to several problems involving a single stimulus. Furthermore, many of these studies adopted a signaler-focused perspective, and centered on the evolution of signals (Hebets and Papaj 2005; Partan and Marler 2005). Since receivers of stimuli are also subjects of selection, we have developed a model that switches focus away from the signaler and towards receivers of multimodal information. When considering changing environments our model can be important to predicting the extent to which integration abilities might change over ecological time (if integration ability is plastic) or the extent to which the ability to integrate might evolve or be lost in species.

We have applied our model to antipredator and mate selection contexts. We hope that, through our descriptions, it has become apparent that our model can predict integration in a variety of ecological contexts and situations. Many studies have shown that animals use multimodal information in decisions regarding, for example, mate selection, antipredator behavior, hunting, rival assessment and habitat selection. The versatility of our modeling framework to readily accommodate these areas of study demonstrates its potential for stimulating a diversity of hypothesis-driven empirical studies. A focus on the cognitive processing of receivers not only compliments the already strong field of multimodal signaling, but can also enhance our understanding of the evolution of signals,

communication networks, and may also aid in understanding the ways in which animals interact with their abiotic environments.

Table 3-1 Definitions

Term	Definition
Stimulus	A feature within a sensory modality such as body size, auditory frequency or odor concentration. A stimulus encompasses the spectrum of magnitudes S_i that said feature can assume.
Uncertainty, U_i	Difference in means of the distributions of S_i (Fig. 3-1). When the difference in means is smaller, the stimulus is more uncertain and the state of the word (e.g., predator vs. non-threat) is less distinguishable. We model different sensory modalities by specifying different U_i for every stimulus.
Receiver environment	Properties of the receiver and/or the receiver's environment that influence how a receiver might respond to S_i . Modeled through $P_{PRED}, U_i, K_i, B_{PRED}, B_{NONE}$.
Using/attending to a stimulus	If an animal "uses" a stimulus, then it incorporates any S_i into its behavioral decision in order to improve the accuracy of its perception of the world. Optimal when $V_i \geq 0$.
Ignoring a stimulus	The animal does not incorporate any S_i into its behavioral decision. Its estimate of the state of is not improved. Optimal when $V_i \leq 0$.
Information	The change in the animal's expectation of the state of the world [after Bradbury & Vehrencamp (1998), p. 389]. If it is optimal for an animal to ignore a stimulus, then the stimulus does not have information.
Multimodal integration	When the animal incorporates information from n stimuli from more than one sensory modality in order to improve the accuracy of its expectation of the world. Optimal when $V_1 \dots V_n \geq 0$ for $n \geq 2$.
Noise	A property of the world that generates stimulus uncertainty.

Table 3-2 Summary of assumptions

Prey assess if a threat is a predator	Female assesses if a male is a conspecific
The prey typically smells then sees a predator.	The female typically hears then sees a male.
World is in one of two states: predator present (PRED) or non-threat present (NONE).	Male is either a conspecific (CONSP) or heterospecific (HETERO).
Prey knows the true likelihood of a predator being present.	Female knows the true likelihood of a male being a conspecific.
Prey can either forage (F) or (H).	Female can either attempt to mate with the male (M) or forage (F).
H is optimal for PRED, and F is optimal for NONE.	M is optimal for CONSP, and F is optimal for HETERO.
If the prey forages when PRED is true, the prey escapes but is injured.	If the female attempts copulation with a heterospecific.
On average, predators are larger than non-threats.	On average, heterospecifics sing a higher acoustic frequency and have longer tails than conspecifics.
Distributions of stimulus magnitudes of PRED and NONE are continuous and normal with a standard deviation of 1 (Fig. 3-1).	Distributions of stimulus magnitudes of CONSP and HETERO are continuous and normal with a standard deviation of 1.
$W_{F,PRED} < W_{F,NONE}, W_{H,PRED} < W_{F,NONE}, W_{H,PRED} < W_{H,NONE} < W_{F,NONE}$	$W_{M,CONSP} > 0, W_{M,HETERO} = 0, W_{F,HETERO} = W_{F,CONSP}, W_{M,CONSP} > W_{F,HETERO}$
Prey has knowledge of U_i, B_{NONE}, B_{PRED} , and K_i .	Female has knowledge of $U_i, B_{HETERO}, B_{CONSP}$, and K_i .
Prey makes antipredator decisions following signal detection theory.	Female makes mating decisions following signal detection theory
All $W_{behavior,STATE}$ are constant.	
Animal updates its prior according to Bayes' Theorem.	
Since processing costs are greater with increasing number of stimuli, $K_i \leq K_{i+1}$.	

Table 3-3 Notation definitions

Notation	Definition
PRED	State of the world when a predator is present.
NONE	State of the world when a non-threat is present.
F	Foraging. Optimal when a non-threat is present.
H	Hiding. Optimal when a predator is present.
P_{PRED}	Prey's estimate of the prior probability that a predator is present.
B_{PRED}	Net benefit of correctly hiding when a predator is present.
B_{NONE}	Net benefit of correctly foraging when a non-threat is present
\overline{PO}_{ignore}	Average payoff of not using a stimulus when making an antipredator decision.
$\overline{PO}_{i,use}$	Average payoff of using the i^{th} stimulus when making an antipredator decision.
K_i	Cost of using the i^{th} stimulus.
$\mu_{i,PRED}$	Mean S_i when a predator is present.
$\mu_{i,NONE}$	Mean S_i when no predator is present.
U_i	A unitless index of uncertainty of the i^{th} stimulus equal to the proportion of overlap between the NONE and PRED distributions of S_i and is a function of $\mu_{i,PRED}$ and $\mu_{i,NONE}$.
S_i	Magnitude of the i^{th} stimulus.
V_i	The value of information is the output variable of model. Equals the difference $\overline{PO}_{i,use} - \overline{PO}_{i,ignore}$. When $V_i \geq 0$ the animal will use the i^{th} stimulus in improving the accuracy of its estimate of the state of the world.
A	Favorability of integration. Equals the proportion of a parameter area, while holding all other parameters constant, in which integration is favored (Fig. A1).

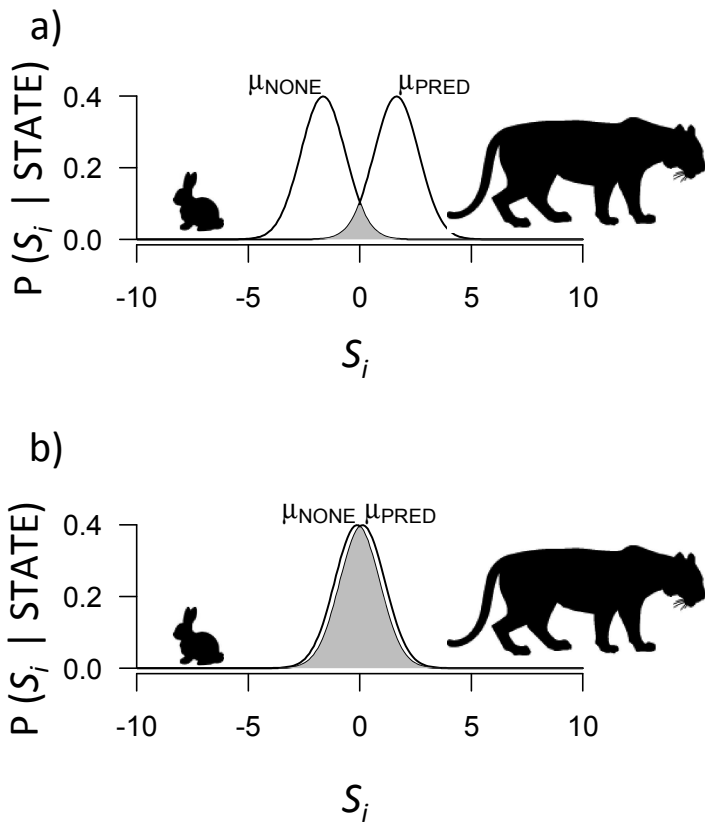


Fig. 3-1 Distributions of stimulus magnitudes S_i when no predator is present (NONE) or when a predator is present (PRED). Uncertainty is defined by the extent to which distributions overlap. a) 10% overlap of distributions (i.e., $U_i = 0.1$). b) 90% overlap of distributions (i.e., $U_i = 0.9$). Image credits to clipartbest.com (hare) and shutterstock.com (lion).

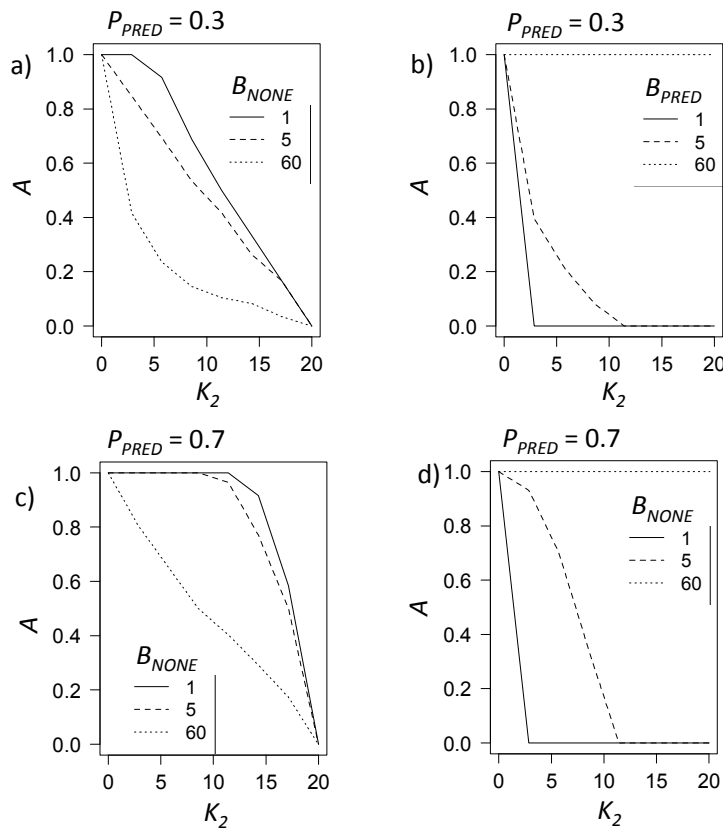


Fig. 3-2 Favorability of integration (A) for a migrating prey that experiences changing ecological situations. The prey must discriminate predators from non-threats. The prey can either hide (optimal for predators) or forage (optimal for non-threats). The prey typically smells before seeing predators. a) In the summer breeding grounds, $B_{PRED} = 10$, and $B_{NONE} = 5$ (dashed line). The prey's diet becomes restricted to food with greater handling time, which decreases the benefit of correctly foraging, $B_{NONE} = 1$ (solid line) and the favorability of integration increases. This is because, relative to B_{NONE} the benefit of hiding increases, which means it becomes increasingly important for the prey to accurately assess if a predator is present. When the prey's energy reserves are low, the benefit of foraging outweighs the benefit of hiding because the prey risks starving to death, $B_{NONE} = 60$ (dotted line). Therefore, making accurate antipredator decisions becomes less important and the

favorability of integration decreases. b) The prey experiences a different type of predator that inflicts a higher degree of injury; the benefit of hiding greatly outweighs the benefit of foraging, $B_{PRED} = 60$ (dotted line) and the favorability of integration increases. This is because making accurate antipredator decisions becomes increasingly important. As the benefit of hiding from a predator decreases (dashed and dotted lines), so does the favorability of integration. c) and d) show the same cases as a) and b), respectively, except the prey experiences a greater concentration of predators ($P_{PRED} = 0.7$). As the frequency of predators increases, it becomes increasingly important for the prey to make accurate antipredator decisions, the favorability of integration increases.

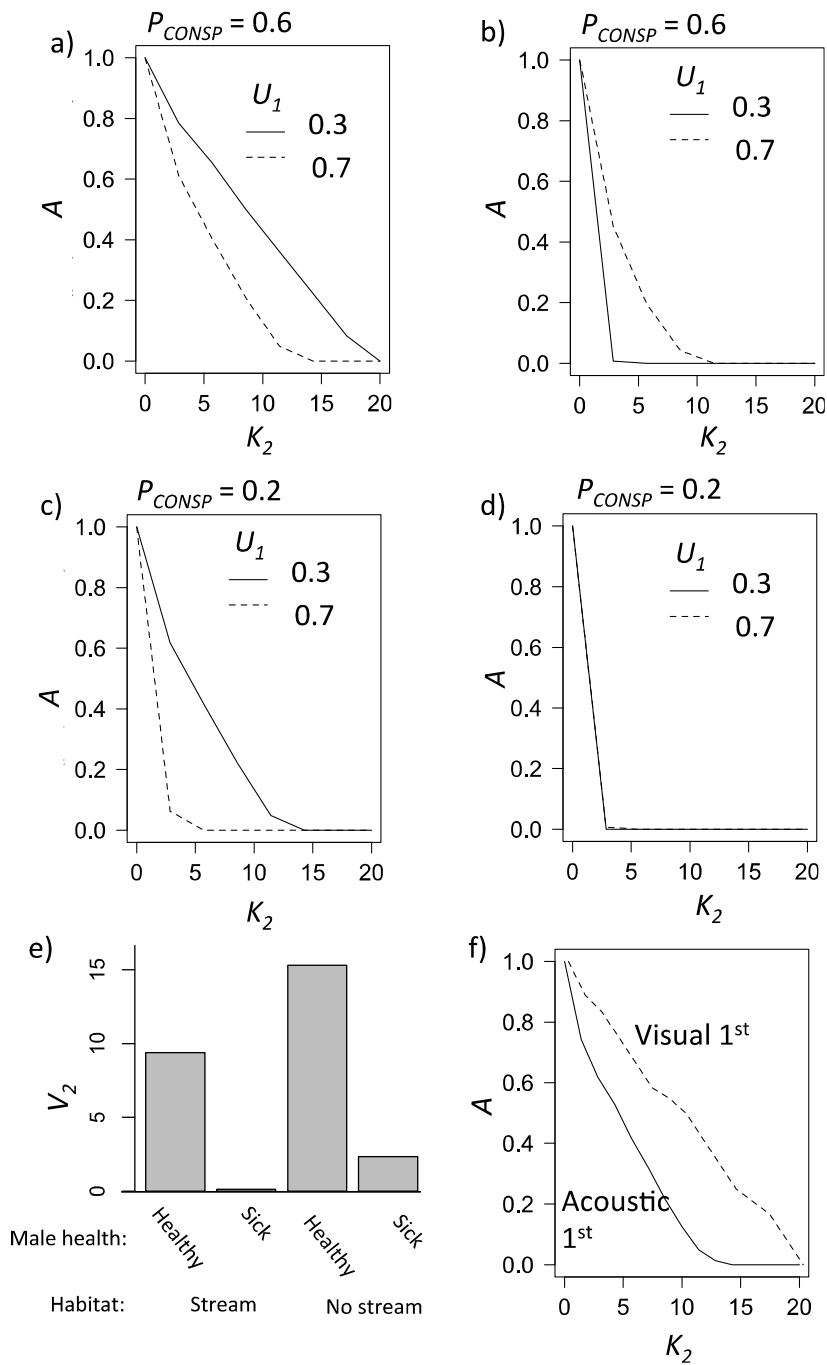


Fig. 3-3 Favorability of integration (A) for two populations of a single bird species. Females typically hear before seeing males. The female has to discriminate conspecifics from heterospecifics. She each either attempt to mate (optimal for conspecifics) or forage (optimal for heterospecifics). Females typically hear before seeing males. One population

lives along a stream and, due to the noise of flowing water, experiences high acoustic uncertainty ($U_1 = 0.7$, dashed line) compared to the other ($U_1 = 0.3$, solid line). $B_{CONSP} = 10$ and $B_{HETERO} = 2$ in both populations. a) A male sings a song that likely came from a conspecific ($S_1 = \mu_{CONSP}$). Females along the stream are less likely to integrate acoustic-visual stimuli than females away from the stream. b) A male sings a song that likely came from a heterospecific ($S_1 = \mu_{HETERO}$). Females along the stream are more likely to integrate than females away from the stream. This is because after hearing the song, a female's expectation that the male is a conspecific has decreased to a greater extent than females along the stream. Since females near the stream have a higher expectation that the male is a heterospecific, it is more important for these females to be able to discriminate conspecifics and heterospecifics. However, regardless of the population's location, the favorability of integration is lower when the female hears a song ($S_1 = \mu_{HETERO}$) that the male was a conspecific decreased to a greater extent than for females along the stream. All other parameters are the same as in a). c) and d) show the same as a) and b), respectively, except the P_{CONSP} decreases. As in the antipredator context, the favorability of integration is lower for lower P_{CONSP} . e) All males along the stream become sick, which decreases the reproductive benefit of females, $B_{CONSP} = 3$. Females now gain so little from being able to discriminate conspecifics and heterospecifics, so value of information when integrating (V_2) decreases ($P_{CONSP} = 0.6$, $U_1 = 0.7$, $U_2 = 0.2$, $B_{NONE} = 2$, $K_1 = 0$ and $K_2 = 3$). f) The order in which females receive stimuli is important to integration. This graph compares the favorability of integration when the female first hears a male ($U_1 = 0.7$, $U_2 = 0.2$; solid line) vs. first sees a male ($U_1 = 0.2$, $U_2 = 0.7$; dashed line). All other parameters are the same as in

a). When the first stimulus the female hears is more accurate at discerning conspecifics and heterospecifics, the female is more likely to integrate.

Supplementary material

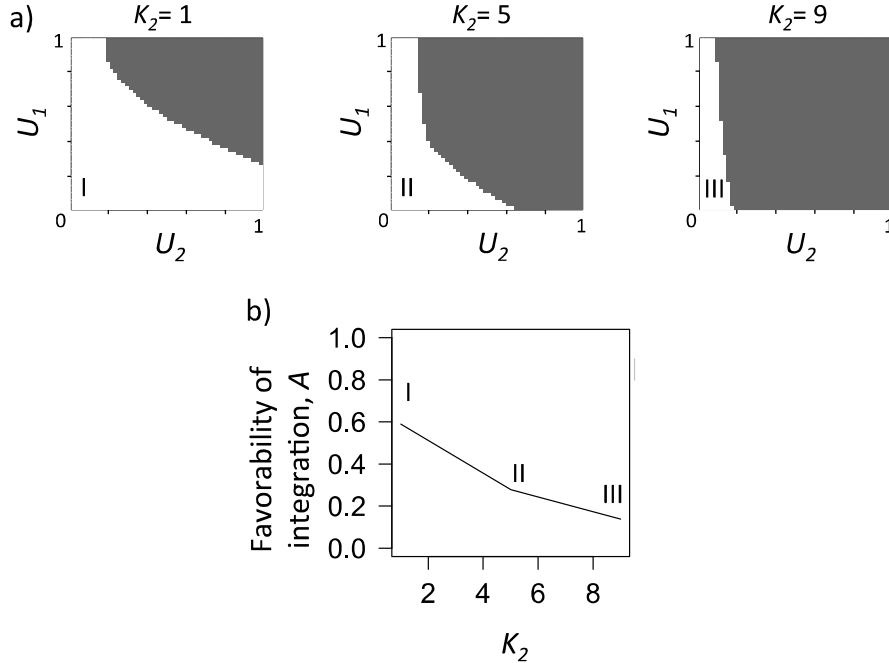


Fig. S3-1 Graphical representation of the calculation of the favorability of integration, A . a) A is the proportion of 2-dimensional parameter space (here, $U_1 \times U_2$) in which the prey will integrate both stimuli (white). In regions where integration is not optimal, the prey only uses the first stimulus (grey). In I – III, $K_2 = 1, 5$ and 9 , respectively; $K_1 = 0$, $B_{PRED} = 10$, $B_{NONE} = 60$, and $S_1 = 1$. b) A as a function K_2 . Roman numerals correspond to plots in a).

Supplementary equations

Equation for the cutoff of stimulus magnitude.

$$S_{i,c} = \frac{\ln(P_{PRED}B_{PRED}) - \ln((1 - P_{PRED})B_{NONE})}{(\mu_{i,NONE}^2 - \mu_{i,PRED}^2)} + \frac{1}{2}$$

The following are the explicit equations for V_i in terms of all input parameters P_{PRED} , B_{NONE} , B_{PRED} , U_i , S_i and K_i ($\mu_{i,NONE}$ and $\mu_{i,PRED}$ are calculated from U_i).

When $P_{PRED} \geq P_c$,

$$\begin{aligned} V_i = & P_{PRED} \left(1 - 0.5 \left[1 \right. \right. \\ & + \operatorname{erf} \left(\frac{\ln(P_{PRED}B_{PRED}) - \ln((1 - P_{PRED})B_{NONE})}{\sqrt{2}(\mu_{i,NONE}^2 - \mu_{i,PRED}^2)} + \frac{1}{2\sqrt{2}} - \frac{\mu_{i,PRED}}{\sqrt{2}} \right) \left. \left. \right] \right) B_{PRED} \\ & - (1 - P_{PRED}) \left(1 \right. \\ & - 0.5 \left[1 \right. \\ & + \operatorname{erf} \left(\frac{\ln(P_{PRED}B_{PRED}) - \ln((1 - P_{PRED})B_{NONE})}{\sqrt{2}(\mu_{i,NONE}^2 - \mu_{i,PRED}^2)} + \frac{1}{2\sqrt{2}} - \frac{\mu_{i,NONE}}{\sqrt{2}} \right) \left. \left. \right] \right) B_{NONE} \\ & + P_{PRED}B_{PRED} \left(1 - \frac{(1 - P_{PRED})(B_{NONE})}{P_{PRED}(B_{PRED})} \right) - K_i \end{aligned}$$

When $P_{PRED} < P_c$

$$\begin{aligned}
 V_i = & P_{PRED} \left(1 \right. \\
 & - 0.5 \left[1 \right. \\
 & \left. + \operatorname{erf} \left(\frac{\ln(P_{PRED} B_{PRED}) - \ln((1 - P_{PRED}) B_{NONE})}{\sqrt{2}(\mu_{i,NONE}^2 - \mu_{i,PRED}^2)} + \frac{1}{2\sqrt{2}} - \frac{\mu_{i,PRED}}{\sqrt{2}}} \right) \right] \Big) B_{PRED} \\
 & - (1 - P_{PRED}) \left(1 \right. \\
 & - 0.5 \left[1 \right. \\
 & \left. + \operatorname{erf} \left(\frac{\ln(P_{PRED} B_{PRED}) - \ln((1 - P_{PRED}) B_{NONE})}{\sqrt{2}(\mu_{i,NONE}^2 - \mu_{i,PRED}^2)} + \frac{1}{2\sqrt{2}} - \frac{\mu_{i,NONE}}{\sqrt{2}}} \right) \right] \Big) B_{NONE} \\
 & - K_i
 \end{aligned}$$

The function $\ln(x)$ is the natural logarithm of x .

The function $\operatorname{erf}(x)$ is the error function of x .

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CHAPTER 4

Testing a model of multimodal integration in yellow-bellied marmots (*Marmota flaviventris*): integration of predator cues is situation dependent

Abstract

Animals acquire information from the environment using multiple modalities, and while there is a large literature describing proximate aspects of multimodal integration, the adaptive value of such integration is largely unstudied. Previously, we developed a quantitative model that predicts whether or not an animal will integrate two sequential stimuli in different modalities given a set of environmental conditions. Here, we apply the model to understand predation risk assessment. To do so, we empirically test whether or not three model parameters (the benefit of alert behavior when a predator is present, the benefit of relaxed behavior when a non-threat is present, and the uncertainty of the second stimulus) affect multisensory integration. In a series of three field experiments we presented yellow-bellied marmots (*Marmota flaviventris*) first with coyote urine followed by a playback of coyote vocalizations. We found that integration is favored when the benefit of alert behavior when a predator is present was greater, as well as under higher uncertainty about the second stimulus. Variation in the benefit of relaxed behavior, at least as we manipulated it, did not produce integration. Together, these results support the importance of key variables in the first quantitative model of multimodal assessment and demonstrate how an animal's environment must be considered when studying mechanisms of integration.

Introduction

Multimodal integration occurs when stimuli from different modalities are combined to create a unified percept. Multimodal integration occurs in several contexts including the assessment of risk (Brown and Magnavacca 2003; Hazlett and McLay 2005; Lohrey et al. 2009; Partan et al. 2009), sexual selection (see Hebets and Papaj 2005 for reviews; Partan and Marler 2005), assessment of competitors (Narins et al. 2005; de Luna et al. 2010; Taylor et al. 2011), and is also used for navigation (Graham et al. 2010) and heterospecific recognition (Proops et al. 2009).

Furthermore, whether or not an animal integrates multimodal stimuli can depend on the individual's environmental context such as reproductive state (Kasurak et al. 2012) or habitat type (Partan et al. 2010). Situation-dependent integration indicates that multimodal integration has functional significance in that in some situations the benefits of ignoring a stimulus are greater than integrating multiple stimuli (Munoz and Blumstein 2012). Thus, the question of "Why [should signalers] use multiple cues?" (Candolin 2003; Hebets and Papaj 2005; Partan 2013) that is often asked in reference to the evolution of multicomponent signals, can also be asked from the perspective of individuals perceiving stimuli: "Why should receivers integrate multiple stimuli?"

Munoz and Blumstein (in review) developed a general, quantitative framework for predicting the situations under which sequential stimuli from different modalities should be integrated, thereby explaining why unimodal decision-making might be favored over multimodal decision-making. Whether or not an animal should integrate can be subject to many environmental factors (Munoz and Blumstein 2012). Incorporating additional stimuli

into an animal's decision increases the accuracy of the animal's perception of the world. However, in some environmental situations, an animal does not benefit from the increase in accuracy of animal's perception of the world that accompanies integration. Munoz and Blumstein (in review) developed a model that parameterizes an animal's environment, broadly speaking, based on the benefits of behaving correctly, the animal's prior expectation that the world is in a give state, uncertainty of each sensory modality, and the costs of attending to each stimulus.

Here, in a predator risk-assessment problem, we empirically test whether three parameters (the benefit of relaxed behavior when no predator is present, the benefit of alert behavior when a predator is present, and the uncertainty of the second of two predator stimuli) do indeed influence multimodal integration. We presented yellow-bellied marmots (*Marmota flaviventris*) first with coyote urine and then broadcast the sounds of coyote (*Canis latrans*) vocalizations to them whereupon we quantified the proportion of time spent foraging. The olfactory and acoustic stimuli were also separately presented to marmots. We used an established paradigm (Stein et al. 1988; Partan and Marler 1999) for assessing multimodal integration based on the responses to each stimulus in isolation compared to the response to the cross-modal combination of both stimuli. If integration occurs, then the multimodal response is different than the response to either unimodal stimulus in isolation.

Methods

General

Through 3 separate field studies, we tested whether or not free-living yellow-bellied marmots integrated predator stimuli from two modalities under different situations that a marmot may experience in its lifetime. Each study examined different environmental features that mapped on to the parameters in a quantitative model by Munoz and Blumstein (in review): the benefit of high levels of antipredator behavior, uncertainty in the second stimulus, and the benefit of low levels of antipredator behavior. The details of each study are given below.

We conducted all experiments around the Rocky Mountain Biological Laboratory in Gunnison County, CO, USA during June – July of 2011-2013. As part of a long-term study, marmots were live-trapped and individually marked with non-toxic fur dye for identification from a distance (Blumstein 2013; Armitage 2014). Protocols for stimulus presentation were adapted from previous studies with marmots that focused on either olfactory (Blumstein et al. 2008a) or acoustic (Blumstein et al. 2008b) predatory stimuli. We chose to use stimuli from coyotes, because they are both relatively common and are a major marmot predator (Van Vuren 1991).

A speaker was placed 10 m from the focal individual's burrow entrance (Advent AV 570, Recoton Home Audio, Benici, CA, USA). Individuals were baited to a feed station where 225 mL of Omalene 300 horse feed (Ralston Purina, St. Louis, MO, USA) was placed at the base of a stake. A cotton ball was attached to the end of stake 10 cm off the ground such that the cotton ball was approximately at the height of a marmot's nose when standing at the station. 100 μ L of coyote urine or water (control) was applied to the cotton ball. We

used 3 urine exemplars, each from a single coyote (Leg Up Enterprises, Lovell, ME USA). The distance at which we place the feed station depended on the particular experiment (see details in each section below).

We waited 30 s after an individual began foraging at the feed station before beginning each trial. In Experiments 1 and 3, 30 s after the start of a trial we played back coyote vocalizations by broadcasting one of three exemplars at 85 dB SPL A (measured 1 m from the speaker with a Sper Scientific Sound Level Meter, Model 840029m Weighting A, peak response). Details of sound levels in Experiment 2 are given below. Trials lasted for 2.5 min and were video recorded. Behavior was scored from video recordings using the event recorder JWatcher 1.0 (Blumstein and Daniel 2007), and we calculated the proportion of time spent foraging, being vigilant (looking quadrupedally and looking bipedally), running and walking.

Individuals received a maximum of 4 treatments, water- X_1 , urine- X_1 , water- X_2 , or urine- X_2 , where X_1 and X_2 are different levels of the parameter we were testing in that experiment (e.g., benefit of alert behavior when a predator is present). We defined the 30 s before playback as the “odor only” condition (or “no stimulus” in the case of water). We used the first 15 s after playback as the multimodal condition (or “audio only” in the case of water). Effectively, dividing trials in this way allowed us to test three odor:audio treatments (water:vocalizations, urine:none, and urine:vocalizations) under 2 different parameter levels (e.g., high and low benefit of alert behavior when a predator is present). This experimental design allowed us to capitalize on the power of a within-subjects study while minimizing the extent to which individuals habituated to our experiment. We assigned treatments according to a pre-defined Latin square.

All analyses were done using R (V. 3.0.2) (R Core Team 2013). In all studies we fitted linear mixed-effects models by maximizing the log-likelihood using the function *lme* in the R package *nlme* (Pinheiro et al. 2013). We specified “individual” as the random factor and the proportion of time spent foraging as the dependent variable. Fixed factors were odor:acoustic stimulus [water:vocalizations (acoustic alone), urine:none (olfactory alone), and urine:vocalizations (multimodal)], age (yearling, adult), sex, audio exemplar (1-3), and trial number (1-4). We present our results in terms of the proportion of time spent foraging, because, given that animals typically forage more under lower predation risk (Lima and Dill 1990), we considered higher levels of foraging as more relaxed behavior (Monclús et al. 2015). In our experiments, marmots traded off foraging with quadrupedal and bipedal vigilance and running towards the burrow [which marmots typically do when evading a threat (personal observation)]. Consequently, time allocated to foraging is also an index of alert behavior; marmots allocating less time to foraging are more alert.

We fitted two separate linear mixed-effects models, one for each level of the parameter we were testing. We tested the significance of fixed effects through Wald tests using the function *anova.lme* in the package *nlme* (Pinheiro et al. 2013). If “stimulus” was a significant factor, then we conducted post-hoc pairwise comparisons of stimulus levels with Tukey contrasts using the function *ghlt* in the package *multcomp* (Hothorn et al. 2008). Following an established framework (Stein et al. 1988; Partan and Marler 1999), we inferred integration if the proportion of time spent foraging in response to the multimodal stimulus was different than the level of foraging to both the coyote vocalizations alone and the urine alone.

Experiment 1: Benefit of alert behavior when a predator is present

This experiment tested the effect on multimodal integration of the benefit to marmots of correctly identifying a predator, B_{PRED} in Munoz and Blumstein (in review). We conducted this study in 2011. We manipulated B_{PRED} based on the distance of the feed station from the burrow. In the lower- B_{PRED} situation, the feed station was set up 1 m from the burrow. In the higher- B_{PRED} situation, the feed station was set up 3.5 m away from the burrow. Based on the average running speed of yellow-bellied marmots (Blumstein et al. 2004), the high- B_{PRED} distance placed marmots at ~ 1 s disadvantage when fleeing to the safety of their burrows compared to the low- B_{PRED} distance. Therefore, we assumed failing to correctly identify a predator when farther away from the burrow will incur a greater cost to the marmot (B_{PRED}), because the expected degree of injury increases with time (because of a higher chance of injury or death when further away).

Experiment 2: Uncertainty of the second stimulus

This experiment tested the effect on multimodal integration of uncertainty of the second stimulus (vocalizations were presented after urine), U_2 in Munoz and Blumstein (in review). We conducted this experiment in 2012. Based on results from the 2011 study (marmots integrated when 3.5 m away from the burrow), we set up the feed station 3.5 m from the burrow. We established two levels of uncertainty in coyote vocalizations based on the level of white noise embedded (using Sound Studio V. 4) in the audio files of coyote vocalizations, high (-5 dB) or low (-20 dB) noise (Fig. 4-1). The overall amplitude of the playback was not adjusted after embedding in noise.

Experiment 3: Benefit of relaxed behavior when a non-threat is present

The experiment tested the effect on multimodal integration of the benefit of relaxed behavior when a non-threat is present, B_{NONE} , in Munoz and Blumstein (in review). We conducted this study in 2013. Based on results from the 2011 study (marmots integrate when 3.5 m away from the burrow), we set up the feed station 3.5 m from the burrow. We manipulated B_{NONE} by mixing the bait with different volumes of pebbles approximately 7 mm in diameter (“Pea Pebbles”, Pavestone, Tyrone, GA). The ratio of bait to pebbles was either 6:1 or 4:3. The volume of the bait-pebble mixture that was set out was such that the volume of actual bait was 250 mL, the same volume of bait in previous experiments. We added pebbles in order to manipulate the handling time of the bait. A lower ratio of bait to pebbles (4:3) meant that, in a given amount of time, marmots obtained a lower foraging return compared to a higher ratio of bait to pebbles (6:1). Therefore, the benefit of foraging is less for the 4:3 mixture compared to the 6:1 mixture.

Results & discussion

Experiment 1: Benefit of alert behavior when a predator is present

When marmots foraged close to (1 m from) the burrow, stimulus type significantly explained variation in the time allocated to foraging ($F = 10.218$, $P < 0.001$; Table 4-1). Marmots foraged significantly less when exposed to predator vocalizations alone compared to predator urine alone (Est. = -0.231, SE = 0.066, $P = 0.001$; Table 4-2; Fig. 4-2a). Marmots allocated significantly less time foraging in response to the multimodal stimulus compared to urine alone (Est. = -0.278, SE = 0.065, $P < 0.001$). The amount of time allocated to foraging was not significantly different between vocalizations alone and the multimodal

stimulus (Est. = -0.047, SE = 0.066, P = 0.759). Therefore, when foraging closer to the burrow, marmots did not integrate the two stimuli.

When foraging far (3.5 m) from the burrow, stimulus significantly affected the proportion of time spent foraging ($F = 12.064$, $P = 0.0001$; Table 4-1). Marmots foraged significantly less to vocalizations alone compared to urine alone (Est. = -0.277, SE = 0.057, $P < 0.001$; Table 4-2; Fig. 4-2b). Marmots spent less time foraging in response to the multimodal stimulus compared to urine alone (Est. = -0.156, SE = 0.055, $P = 0.012$), and marmots spent more time foraging in response to the multimodal stimulus compared to vocalizations alone (Est. = 0.171, SE = 0.058, $P = 0.034$). Therefore, marmots integrated when far from the burrow (higher B_{PRED}) but not close to the burrow (lower B_{PRED}).

Experiment 2: Uncertainty of the second stimulus

When vocalizations were less obscured by noise, stimulus type affected the proportion of time spent foraging ($F = 15.295$, $P < 0.0001$; Table 3). Marmots foraged less after vocalizations compared to urine alone (Est. = -0.286, SE = 0.081, $P = 0.001$; Table 4-4a; Fig. 3a) and foraged less to a multimodal coyote stimulus compared to urine alone (Est. = -0.377, SE = 0.070, $P < 0.001$). The time allocated to foraging was not significantly different between a multimodal stimulus and vocalizations alone (Est. = -0.091, SE = 0.081, $P = 0.500$). Therefore, when vocalizations were less noisy, marmots did not integrate the olfactory-acoustic coyote stimulus.

Stimulus was also a significant factor when vocalizations were more obscured by noise ($F = 16.728$, $P < 0.001$; Table 4-3). When vocalizations were more noisy, marmots foraged less after hearing vocalizations only compared to urine only (Est. = -0.531, SE =

0.093, $P < 0.001$; Table 4-4; Fig. 4-3b). Marmots spent less time foraging in response to a multimodal coyote stimulus compared to urine alone (Est. = -0.206; SE = 0.096, $P = 0.042$), and marmots foraged more after being exposed to a multimodal coyote stimulus compared to vocalizations alone (Est. = 0.325, SE = 0.093, $P = 0.001$). Therefore, marmots integrated the olfactory-acoustic coyote stimulus when vocalizations were noisier (higher U_2).

Experiment 3: *Benefit of relaxed behavior when a non-threat is present*

When handling time was longer, stimulus significantly influenced the time allocated to foraging ($F = 3.702$, $P = 0.035$; Table 4-5). Marmots did not forage significantly different in response to vocalizations only and urine only (Est. = -0.110, SE = 0.085, $P = 0.403$; Table 4-6; Fig. 4-4a). Marmots foraged less in response to the multimodal stimulus compared to urine alone (Est. = -0.236, SE = 0.084, $P = 0.014$). Foraging levels in response to the multimodal stimulus were not significantly different from that elicited by vocalizations only (Est. = -0.126, SE = 0.085, $P = 0.304$).

Under a shorter handling time, stimulus significantly influenced a marmot's decision to forage ($F = 3.946$, $P = 0.028$; Table 4-5; Fig. 4-4b). Marmots foraged less in response to vocalizations alone compared to urine alone (Est. = -0.221, SE = 0.089, $P = 0.035$). Foraging levels in response to the multimodal stimulus were not significantly different from that elicited by urine alone (Est. = -0.192, SE = 0.088, $P = 0.073$) or vocalizations alone (Est. = 0.029, SE = 0.089, $P = 0.945$). Therefore marmots did not integrate when the bait had a lower handling time. Taken together, these results show that marmots neither integrated under conditions of lower nor higher foraging returns.

General discussion

Through a series of three field experiments, we demonstrated that multimodal integration is situation dependent. We tested three parameters from a quantitative model of integration by Munoz and Blumstein (in review): the benefit of alert behavior when a predator is present (B_{PRED}), the uncertainty of the second stimulus (U_2) and the benefit of relaxed behavior when a non-threat is present (B_{NONE}). When testing for an effect of B_{PRED} , we found that marmots only integrated olfactory-acoustic coyote stimuli far from the burrow. When testing for an effect of U_2 , we found that marmots only integrated when the acoustic stimulus was noisier. We did not find an effect of B_{NONE} on integration in marmots. The latter result does not necessarily discount the validity of Munoz and Blumstein's model. The influence of a given parameter depends on the values of other parameters. It is possible that the region in parameter space in which we tested marmots was such that the likelihood of integration does not strongly respond to B_{NONE} . It is possible that if we had chosen more disparate levels in foraging returns that we could have detected a change in integration response.

Other studies have found that multimodal integration can depend on situation. Partan et al. (2010) found that multimodal integration in gray squirrels (*Sciurus carolinensis*) can vary across populations, possibly a result of differences in the levels of acoustic noise. Squirrels in both urban and rural habitats showed an enhanced response to a multimodal alarm stimulus (tail flagging and alarm call) compared to each unimodal stimulus in isolation. However, squirrels in urban habitats, where acoustic noise tends to be greater, exhibited greater multimodal enhancement compared to rural squirrels (Partan et al. 2010). In another example of situation-dependent integration,

reproductive female gobies (*Neogobius melanostomus*) showed an enhanced response to an acoustic-chemical stimulus from a male compared to each unimodal stimulus in isolation; non-reproductive females did not show multimodal enhancement (Kasurak et al. 2012). In the preceding example, while the same individuals were not re-tested, breeding season influenced whether or not female gobies integrated male stimuli.

The interpretation of the level of risk perceived upon integrating urine and vocalizations is difficult to untangle. In both experiments (Experiments 1 and 2), the multimodal response was intermediary to the responses to urine alone and vocalizations alone. One explanation for the pattern of responses to multimodal and unimodal stimuli is that the level of perceived risk may not always be proportional to the number of predator cues. Urine alone did not significantly influence foraging levels. An olfactory stimulus can potentially linger long after the predator has left an area, so, on average, coyote urine may simply have been associated with lower risk. Given that predator odors can remain in an area after the predator has left, some prey have been known to respond less strongly to older odors (Turner and Montgomery 2003; Peacor 2006; Van Buskirk et al. 2014). The urine in this study was sourced annually, but may have aged in a way that did not contain cues that indicated, to marmots, that a predator was currently present. Alternatively, and more likely, marmots had to elect to forage next to the olfactory cue. Thus, they may have already assessed low risk of predator presence once they began foraging and their response was in between the response to a lower-risk (urine only) and higher-risk (vocalizations alone) situation.

Marmots always decreased foraging upon playback of coyote vocalizations. However, only under high risk (foraging far from the burrow), or high uncertainty (noisy

vocalizations), and if urine was present during playback, marmots did not decrease foraging as much compared to if urine was not present during playback. This result suggests that urine, which is perceived less of a threat, may have diminished the level of risk perceived from vocalizations alone. Alternatively, urine may have influenced the degree of perceived risk only if vocalizations were heard.

Another explanation for the pattern of foraging levels that were observed may stem from an antipredator strategy that may be employed by marmots. Marmots typically forage close to their burrows, which allows them to flee to the safety of the burrow if they suddenly are threatened (Blumstein 1998). While hiding in the burrow, a marmot cannot forage (Rhoades and Blumstein 2007). Thus, to acquire as much foraging gain as possible before having to flee to their burrow, at mid-levels of risk, marmots may have higher foraging rates compared to low-level risk. Regardless of the level of risk conveyed by the stimuli, the pattern of foraging levels in response to multimodal coyote stimuli compared to unimodal stimuli demonstrates that marmots integrated stimuli (*sensu* Partan and Marler 1999; Stein et al. 2009) under higher predation risk and when vocalizations were more noisy.

In all experiments, marmots foraged at a urine stimulus for 1 min before vocalizations were played back. One possible explanation for foraging rates decreasing in response to playback is because the bait at the foraging station is gradually depleted and/or marmots became satiated during the course of a trial. We can reject this hypothesis because marmots had higher rates of foraging after being exposed to the multimodal predator stimuli. This finding indicates that the observed effects of playback are likely caused by the stimuli.

We have empirically shown that multisensory integration can be situation dependent at the level of the individual. The results of this study indicate that certain parameters in our model do indeed affect multimodal integration (Munoz and Blumstein Chapter 3). More empirical tests of the Munoz and Blumstein model are necessary to further understand the extent to which integration is an adaptation and the environmental situations that may preclude integration at the level of the individual, population or species. Nonetheless, our current results strongly suggest that the benefit of alert behavior and acoustic uncertainty are important factors in explaining patterns of multi-modal integration in yellow-bellied marmots.

Table 4-1 Results from linear mixed effects models of the proportion of time allocated to foraging in response to the near-to and far-from burrow conditions for Experiment 1.

Significant *P*-values are highlighted in bold.

Fixed factor	Num, den DF	Near to burrow		Far from burrow	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Age	1, 21	0.258	0.617	0.434	0.517
Sex	1, 21	0.033	0.859	4.814	0.040
Audio exemplar	2, 43	3.602	0.036	9.735	0.0003
Treatment number	1, 43	0.034	0.855	1.300	0.261
Stimulus	2, 43	10.218	0.0002	12.064	0.0001

Individual ID was the random effect.

Table 4-2 Pairwise comparisons of stimulus types (coyote urine only, vocalizations only or the bimodal urine-vocalization stimulus) for Experiment 1.

Uni/multimodal stimulus comparison		Near to burrow				Far from burrow			
		Est.	SE	Z	P	Est.	SE	Z	P
Voc. only	Urine only	-0.231	0.066	-3.499	0.001	-0.277	0.057	-4.875	< 0.001
Urine + voc.	Urine only	-0.278	0.066	-4.225	< 0.001	-0.156	0.055	-2.866	0.012
Urine + voc.	Voc. only	-0.047	0.066	-0.708	0.759	0.171	0.058	2.228	0.034

Table 4-3 Results from linear mixed effects models of the proportion of time allocated to foraging in response to the high-noise or low-noise condition in Experiment 2. Significant *P*-values are highlighted in bold.

Fixed factor	Num, den DF	Low acoustic noise		High acoustic noise	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Age	1, 18	0.100	0.755	3.528	0.077
Sex	1, 18	0.078	0.783	0.022	0.884
Audio exemplar	2, 40	1.902	0.163	2.387	0.107
Treatment number	1, 40	10.820	0.002	1.325	0.258
Stimulus	2, 40	15.295	< 0.0001	16.728	< 0.0001

Individual ID was the random effect.

Table 4-4 Pairwise comparisons of stimulus types (coyote urine only, vocalizations only or the bimodal urine-vocalization stimulus) for Experiment 2.

Uni/multimodal stimulus comparison		Low-noise vocalizations				High-noise vocalizations			
		Est.	SE	Z	P	Est.	SE	Z	P
Voc. only	Urine only	-0.286	0.081	-3.517	0.001	-0.531	0.093	-5.702	< 0.001
Urine + voc.	Urine only	-0.377	0.070	-5.369	< 0.001	-0.206	0.096	-2.532	0.042
Urine + voc.	Voc. only	-0.091	0.081	-1.121	0.500	0.325	0.093	3.487	0.001

Table 4-5 Results from linear mixed effects models of the proportion of time allocated to foraging when foraging at bait with longer handling time or shorter handling time in Experiment 3. Significant *P*-values are highlighted in bold.

Fixed factor	Num, den DF	Long handling time		Short handling time	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Age	1, 18	2.875	0.107	0.758	0.395
Sex	1, 18	0.018	0.895	0.049	0.827
Audio exemplar	2, 35	0.357	0.702	1.424	0.255
Treatment number	1, 35	4.891	0.033	3.734	0.061
Stimulus	2, 35	3.946	0.028	3.702	0.035

Individual ID was the random effect.

Table 4-6 Pairwise comparisons of stimulus types (coyote urine only, vocalizations only or the bimodal urine-vocalization stimulus) for Experiment 3.

Uni/multimodal stimulus comparison		Long handling time				Short handling time			
		Est.	SE	Z	P	Est.	SE	Z	P
Voc. only	Urine only	-0.10986	0.085	-1.287	0.403	-0.221	0.089	-2.488	0.035
Urine + voc.	Urine only	-0.23557	0.084	-2.807	0.014	-0.192	0.088	-2.188	0.073
Urine + voc.	Voc. only	-0.12571	0.085	-1.473	0.304	0.029	0.089	0.321	0.945

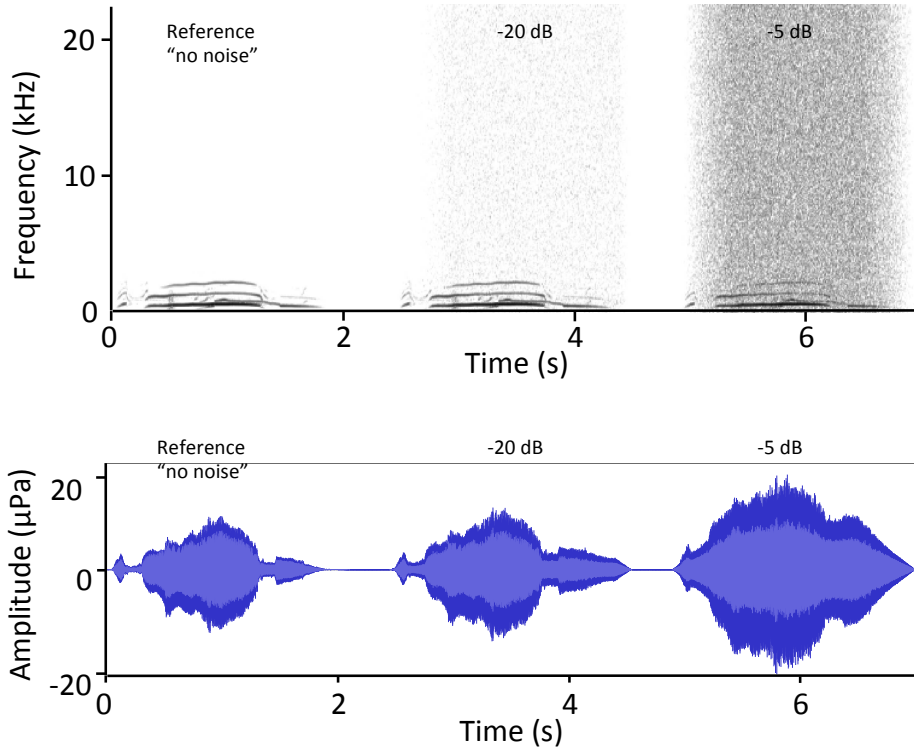


Fig. 4-1 Spectrograms (top) (349.70 Hz, 512 point FFT) and waveforms (bottom) of a coyote vocalization embedded with either “no noise” (left), low noise (middle) or high noise (right). Signal-to-noise ratio for each is given at the top of each figure. The “no-noise” exemplar was used in generating the low- and high-noise exemplars. Spectrogram grid resolution: 5.38 Hz, 5.805 ms, 50% overlap. The clipping level was -68 dB.

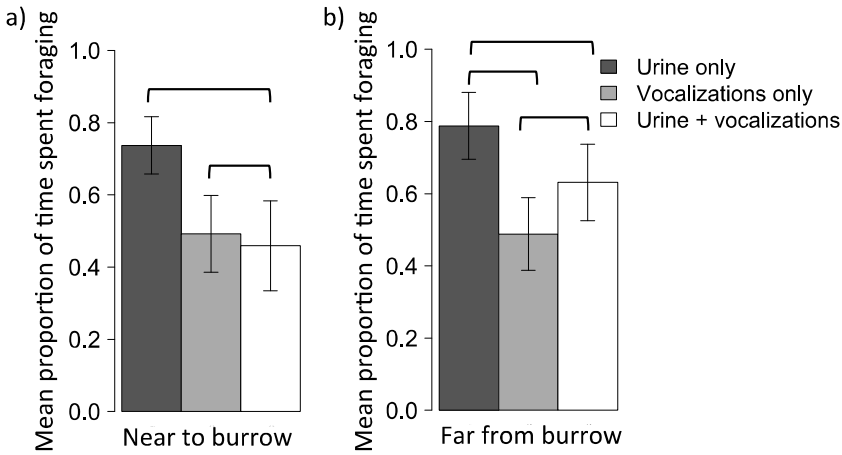


Fig. 4-2 Results of Experiment 1. Mean proportion of time spent foraging when marmots foraged a) near to (1 m from) the burrow or b) far (3.5 m) from the burrow. Each distance represents a different level of B_{PRED} . Brackets indicate significantly different pairwise comparisons. Marmots only integrated when foraging far from the burrow, where B_{PRED} is greater, as inferred from significantly different responses to the bimodal stimulus compared to urine alone and vocalizations alone. Error bars show 95% confidence intervals.

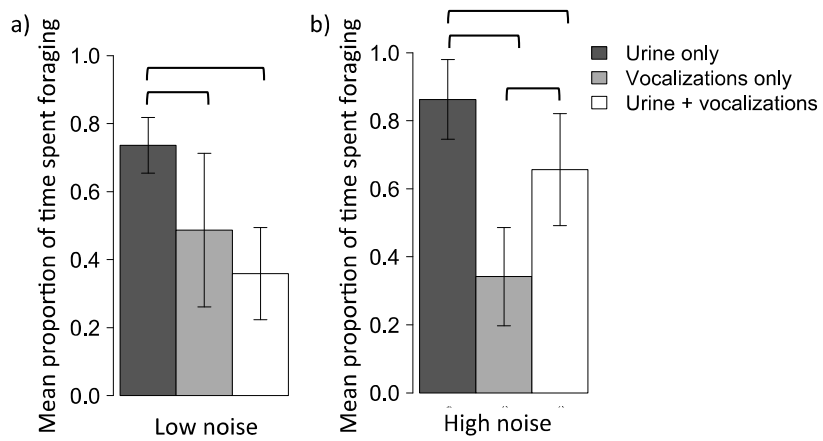


Fig. 4-3 Results of Experiment 2. Mean proportion of time marmots spent foraging when a) coyote vocalizations were less noisy or b) more noisy. Different noise level corresponds to different levels of U_2 (Munoz and Blumstein, in review). Brackets indicate significantly different pairwise comparisons. Marmots only integrated when coyote vocalizations were more noisy. Error bars show 95% confidence intervals.

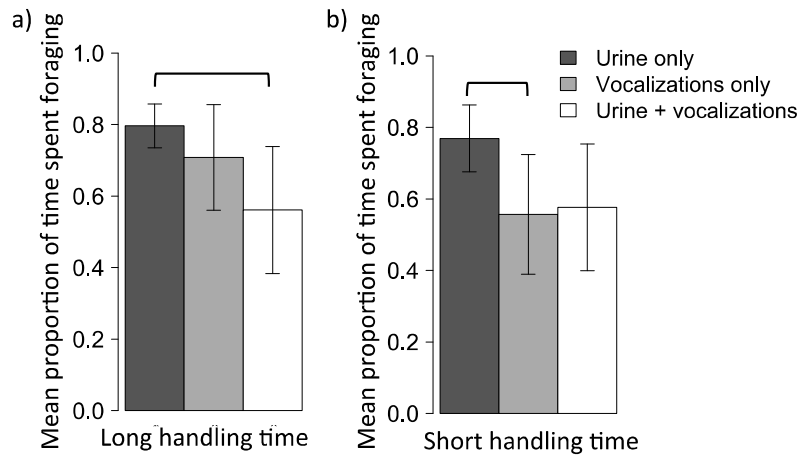


Fig. 4-4 Results of Experiment 3. Mean proportion of time marmots spent foraging when food handling time was a) long or b) short. Brackets indicate significantly different pairwise comparisons. Different handling times correspond to different levels of B_{NONE} . Marmots did not integrate under either situation. Error bars show 95% confidence intervals.

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