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Original Article

Optimal multisensory integration

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Animals are often confronted with potentially informative stimuli from a variety of sensory modalities. Although there is a large proximate literature demonstrating multisensory integration, no general framework explains why animals integrate. We developed and tested a quantitative model that explains why multisensory integration is not always adaptive and explains why unimodal decision-making might be favored over multisensory integration. We present our model in terms of a prey that must determine the presence or absence of a predator. A greater chance of encountering a predator, a greater benefit of correctly responding to a predator, a lower benefit of correctly foraging, or a greater uncertainty of the second stimulus favors integration. Uncertainty of the first stimulus may either increase or decrease the favorability of integration. In three field studies, we demonstrate how our model can be empirically tested. We evaluated the model with field studies of yellow-bellied marmots (*Marmota flaviventer*) by presenting marmots with an olfactory-acoustic predator stimulus at a feed station. We found some support for the model's prediction that integration is favored when the second stimulus is less noisy. We hope additional predictions of the model will guide future empirical work that seeks to understand the extent to which multimodal integration might be situation dependent. We suggest that the model is generalizable beyond antipredator contexts and can be applied within or between individuals, populations, or species.

Key words: **antipredator, decision-making, information, integration, multimodal, multisensory, risk assessment, unified percept, yellow-bellied marmots.**

INTRODUCTION

Animals extract potential information 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 these signals can increase the likelihood that messages are received, correct for errors in signal detection, or increase information content (Guilford and Dawkins 1991; Hebets and Papaj 2005; Partan and Marler 2005). Despite acknowledging the importance in considering a receiver's environment to the evolution of signals (e.g., Guilford and Dawkins 1991; Partan and Marler 2005), less attention has been given to the fact that receivers are not passive agents in their environments and that their cognitive processing systems are also subject to selection (Dukas 2004; Miller and Bee 2012; Ronald et al. 2012; Mesterton-Gibbons and Heap 2014). 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 a growing area of interest (Munoz and Blumstein 2012; Partan 2013; Halfwerk et al. 2019; Ryan et al. 2019). Such studies are essential for developing a better understanding of the evolutionary significance of multimodal integration. In this study, we develop a quantitative framework that makes empirically testable predictions that allows us to ask why animals may or may not integrate multisensory stimuli.

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 important decisions. Indeed, multisensory signaling and integration are methods for dealing with environmental uncertainty (Munoz and Blumstein 2012; Halfwerk and Slabbekoorn 2015; Partan 2017). 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 with 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 Hebets and Papaj [2005], Partan and Marler [2005], and Halfwerk et al. [2019] for reviews), antipredator behavior (Brown and Magnavacca 2003; Hazlett and McLay 2005; Lohrey et al. 2009; Partan et al.

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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; Gomes et al. 2017; Rojas et al. 2018; Rojas et al. 2019), 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), individual heterospecific individual (Smith and Evans 2008; Proops et al. 2009; Kondo et al. 2012), mother-offspring recognition (Wierucka et al. 2018), 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 an 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 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 with 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. 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 (*Evarcha culicivora*), in addition to male–male competition, female–female competition for mates exists. 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 with the other species, explained situation-dependent integration on a functional level.

These examples of situation-dependent integration indicate 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?"

An interplay of several factors may underlie the payoffs of integrating and ignoring stimuli. We previously discussed, on a conceptual level, why multimodal integration is not ubiquitous (Munoz and Blumstein 2012). The precision with which a stimulus indicates the state of the world (either due to the state of the world or the perceiver's cognitive ability to discriminate) 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 error) is determined by the costs of each mistake (formalized and developed below). Based on previous experience, ecological and/or evolutionary, the animal will also have some expectation as to the likelihood of a given event. The animal will also experience some physiological cost to attending to a stimulus. These factors can change depending on the animal's situation or environment. 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 a framework outlined by 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. Finally, to illustrate that the model makes testable predictions that can be evaluated with animals, we ask whether three parameters (the benefit of alert behavior when a predator is present, the benefit of relaxed behavior when no predator is present, and the uncertainty of the second of two predator stimuli) influence multimodal integration in free-living yellow-bellied marmots (*Marmota flaviventer*).

PART I: THEORETICAL MODEL

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 on this idea by modeling a situation where an animal receives two sequential stimuli in different sensory modalities (see Table 1 for definitions and Table 2 for a complete summary of assumptions). In our model, different sensory modalities are represented in our model through the uncertainty parameter 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. 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 with 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 something innocuous such as wind is also likely to produce a similar sound. Therefore, rustling vegetation may have high uncertainty compared with, for example, a vocalization even though both are acoustic stimuli.

The model examines the extent to which stimulus uncertainties, prior probability of a given state, and the costs of mistakes influence whether or not a prey will integrate two stimuli in different sensory modalities. We also include a physiological cost to integration. For the purposes of developing our model, we use an example of a foraging prey (notation descriptions in Table 3). We refer readers to Supplementary Material for an application of the model to mate recognition.

The world is in one of two possible states, predator present (PRED) or no predator present (NONE). The prey has an estimate for the prior probability of the presence of a predator, P_{PRED}, which could have been gathered over evolutionary time or within the lifetime of the prey. The prey can engage in one of two behaviors, either forage (F) or hide (H). Because the prey is not certain as to the presence of a predator, the prey will sometimes make mistakes. The

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Table 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 (Figure 1). When the difference in means is smaller, the stimulus is more uncertain and the state of the word (e.g., predator vs. nonthreat) 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 and 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 $V_1 \ldots V_n \geq 0$ for $n \geq 2$.
Noise	A property of the world that generates stimulus uncertainty.

Table 2
Summary of assumptions for analyzing optimal-integration model

Prey receives stimuli sequentially.
World is in one of two states: predator present (PRED) or nonthreat present (NONE).
Prey knows the true likelihood of a predator being present.
Prey can either forage (F) or hide (H).
H is optimal for PRED, and F is optimal for NONE.
If the prey forages when PRED is true, the prey escapes but is injured.
Distributions of stimulus magnitudes of PRED and NONE are continuous
and normal with an SD of 1 (Figure 1).
$W_{F,\mathrm{PRED}} < W_{F,\mathrm{NONE}}$, $W_{H,\mathrm{PRED}} < W_{F,\mathrm{NONE}}$.
Prey has knowledge of U_i, B_{NONE}, B_{PRED}, and K_i.
Prey makes antipredator decisions following signal detection theory.
All $W_{\mathrm{behavior,STATE}}$ are constant.
Animal updates its prior according to Bayes' Theorem.
$K_1 = 0$.
$0 \leq K_2 \leq 5$.
$-1 \leq S_1 \leq 1$.
$0 \leq U_1, U_2 \leq 1$.
$0 \leq B_{\mathrm{PRED}}, B_{\mathrm{NONE}} \leq 5$.

prey always manages to escape the predator, but the predator will injure the prey if the prey fails to hide. Depending on the state of the world and whether the prey is foraging or hiding, the prey can receive one of four payoffs, $W_{\mathrm{behavior,STATE}}$. $W_{F,\mathrm{NONE}}$ and $W_{H,\mathrm{PRED}}$ are the payoffs of behaving appropriately either when a predator is absent or present, respectively. $W_{H,\mathrm{NONE}}$ and $W_{F,\mathrm{PRED}}$ are the payoffs of mistakes either when a predator is absent or present, respectively. Foraging receives the greatest benefit when a predator is not present, and hiding receives the greatest benefit when a predator is present. We assumed these payoffs do not change in between the first and second stimuli.

In the absence of a stimulus or when the prey "ignores" a stimulus, the prey sets a cutoff probability P_c, which is optimal when the following condition holds (Bradbury and Vehrencamp 1998):

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

The payoff the prey receives when ignoring a stimulus depends on the value of P_c relative to P_{PRED}. When $P_{\mathrm{PRED}} \leq P_c$, the prey always forages with low vigilance and receives the average payoff:

$$\overline{\mathrm{PO}}_{\mathrm{ignore}} = \left(1 - P_{\mathrm{PRED}}\right) W_{F,\mathrm{NONE}} + P_{\mathrm{PRED}} W_{F,\mathrm{PRED}}$$

When $P_{PRED} > P_c$ the prey will always hide and receives the average payoff:

$$\overline{\mathrm{PO}}_{\mathrm{ignore}} = P_{\mathrm{PRED}} W_{H,\mathrm{PRED}} + \left(1 - P_{\mathrm{PRED}}\right) W_{H,\mathrm{NONE}}.$$

Throughout, we use "stimulus" to refer to a *feature* within a sensory modality which can assume a set of magnitudes S_i (Figure 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 POi,use. The animal should use stimulus i only when $\mathrm{PO}_{i,\mathrm{use}} \geq \mathrm{PO}_{i,\mathrm{ignore}}$. 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 $P_{i,\mathrm{correct\ reject}}$. The animal also makes a correct decision if it hides, which occurs with probability $P_{i,\mathrm{hit}}$. The probabilities of mistakes are the probability of foraging when a predator is present, $P_{i,\mathrm{miss}}$, and the probability of hiding when in fact a nonthreat is present, $P_{i,\mathrm{false\ alarm}}$.

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 processing costs in the form of energy expenditure and/or physiological investment in sensory systems (Niven and Laughlin 2008), K_i, of attending to the stimulus. Thus,

$$\begin{aligned}\overline{\mathrm{PO}}_{i,\mathrm{use}} = {} & \left(1 - P_{\mathrm{PRED}}\right)\left(P_{i,\mathrm{correct\quad reject}} W_{F,\ \mathrm{NONE}} + P_{i,\mathrm{false\quad alarm}} W_{H,\mathrm{NONE}}\right)\\ & + P_{\mathrm{PRED}}\left(P_{i,\mathrm{hit}} W_{H,\mathrm{PRED}} + P_{i,\mathrm{miss}} W_{F,\mathrm{PRED}}\right) - K_i.\end{aligned}$$

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

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Table 3
Notation definitions

Notation	Definition
PRED	State of the world when a predator is present
NONE	State of the world when a nonthreat is present
F	Foraging. Optimal when a nonthreat 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 nonthreat is present
$\mathrm{PO}_{\mathrm{ignore}}$	Average payoff of not using a stimulus when making an antipredator decision
$\mathrm{PO}_{\mathrm{i,use}}$	Average payoff of using the *i*th stimulus when making an antipredator decision
K_i	Cost of using the *i*th stimulus
$\mu_{i,\mathrm{PRED}}$	Mean S_i when a predator is present
$\mu_{i,\mathrm{NONE}}$	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 $\mu_{i,\mathrm{PRED}}$ and $\mu_{i,\mathrm{NONE}}$
S_i	Magnitude of the *i*th stimulus
V_i	The value of information is the output variable of model. Equals the difference $\mathrm{PO}_{\mathrm{i,use}}$- $\mathrm{PO}_{\mathrm{i,ignore}}$. 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 (Supplementary Figure S1)

$$\begin{aligned}\overline{\mathrm{PO}}_{i,\mathrm{use}} = {} & P_{\mathrm{PRED}} P_{\mathrm{i,hit}} \left(W_{H,\mathrm{PRED}} - W_{F,\mathrm{PRED}}\right) \\ & - \left(1 - P_{\mathrm{PRED}}\right) P_{i,\mathrm{false\ alarm}} \left(W_{F,\mathrm{NONE}} - W_{H,\mathrm{PRED}}\right) \\ & + P_{\mathrm{PRED}} W_{F,\mathrm{PRED}} + \left(1 - P_{\mathrm{PRED}}\right) W_{F,\mathrm{NONE}} - K_i.\end{aligned}$$

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

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

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

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

$B_{\mathrm{PRED}} = W_{H,\mathrm{PRED}} - W_{F,\mathrm{PRED}}$ is the net benefit of hiding when a predator is present. $B_{\mathrm{NONE}} = (W_{F,\mathrm{NONE}} - W_{H,\mathrm{NONE}})$ is the benefit of foraging when a nonthreat is present.

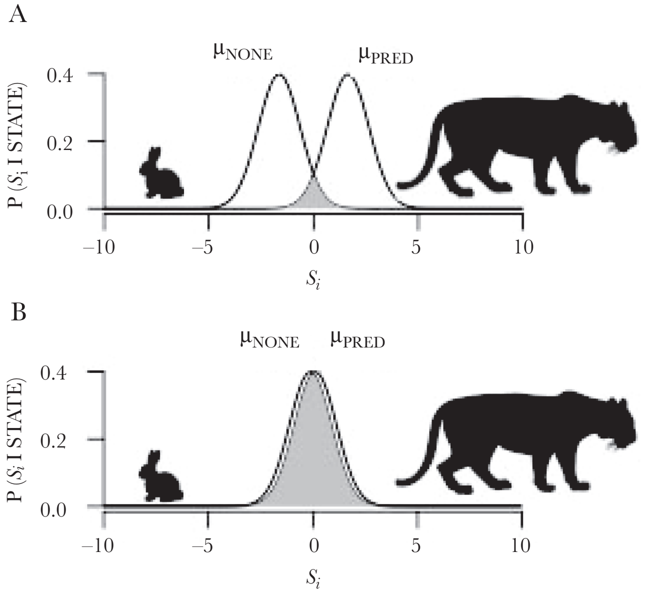

Figure 1
Distributions of stimulus magnitudes S_i when no predator is present (NONE) or when a predator is present (PRED). Uncertainty is defined by the extent to which distributions overlap. We have assumed that $\mu_{\mathrm{NONE}} < \mu_{\mathrm{PRED}}$. (a) 10% overlap of distributions (i.e., $U_i = 0.1$). (b) 90% overlap of distributions (i.e., $U_i = 0.9$). Image credits to clipartbest.com (hare) and shutterstock.com (lion).

An object with a body size S_i corresponds to a predator with a certain probability $P(S_i|\mathrm{PRED})$ and to a nonpredator with a certain probability $P(S_i|\mathrm{NONE})$. We assumed these probability distributions are continuous and normal with a standard deviation (SD) equal to 1 unit on an arbitrary scale (Table 2). We assumed that the prey has knowledge of these distributions

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

$$P\left(S_i \mid \mathrm{NONE}\right) = \frac{1}{\sqrt{2\pi}} \exp\left[-0.5\left(S_1 - \mu_{i,\mathrm{NONE}}\right)^2\right]$$

Body size indicates if the object is more likely a predator or nonpredator because the average body size of predators, μ_{PRED}, and nonthreats, μ_{NONE}, are different (Figure 1). Here, we have assumed that, on average, predators are larger than nonpredators: $\mu_{i,\mathrm{PRED}} > \mu_{i,\mathrm{NONE}}$ (Figure 1). However, sometimes predators are smaller than nonpredators and vice versa. On our arbitrary scale for S_i, the grand mean of body sizes equals 0 (as will be shown below; only the difference in means between predators and nonthreats is important). The extent to which the world is uncertain depends on $\mu_{i,\mathrm{PRED}}$ and $\mu_{i,\mathrm{NONE}}$. As $\mu_{i,\mathrm{PRED}}$ and $\mu_{i,\mathrm{NONE}}$ 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 $\overline{\mathrm{PO}}(F)_i$ equals the average payoff of high vigilance $\overline{\mathrm{PO}}(H)_i$. 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,

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

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

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

$$B_{\mathrm{PRED}} P\left(\mathrm{PRED}|S_{i,c}\right) \quad = B_{\mathrm{NONE}} P\left(\mathrm{NONE}|S_{i,c}\right)$$

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

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

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

$$P\left(S_{\mathrm{i,c}}\right) \quad = P_{\mathrm{PRED}} P\left(S_{\mathrm{i,c}}|\mathrm{PRED}\right) \quad + \quad \left(1 \;\; P_{\mathrm{PRED}}\right) P\left(S_{\mathrm{i,c}}|\mathrm{NONE}\right)$$

Therefore, on specifying B_{PRED}, B_{NONE}, μ_{PRED}, and μ_{NONE}, the value of $S_{i,c}$ is known (see Supplementary Material for the explicit equation for $S_{i,c}$).

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

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

and

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

where erf(x) is the error function of x.

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

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

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

where $P(S_1 \mid \mathrm{PRED})$ is the probability of receiving a stimulus with magnitude S_1 when a predator is present. Because we have assumed that the probability of receiving S_1 in each state is a normal distribution with unit SD,

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

$P(S_1)$ 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:

$$P\left(S_1\right) \quad = P_{\mathrm{PRED}} P\left(S_1|\mathrm{PRED}\right) \quad + \quad \left(1 \;\; P_{\mathrm{PRED}}\right) P\left(S_1|\mathrm{NONE}\right).$$

The animal then receives a second stimulus having properties $\mu_{2,\mathrm{NONE}}$ and $\mu_{2,\mathrm{PRED}}$. Because processing costs are likely to be greater with increasing number of stimuli, we assumed that $K_1 \leq K_2$. Setting $P_{\mathrm{PRED}} = P_{\mathrm{PRED}}{'}$, 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 by the fact that 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 stimulus to inform its perception regarding the presence/absence of a predator.

When discussing uncertainty, we are referring to a unitless parameter U_i, which is the proportion of overlap between the NONE and PRED distributions of the ith stimulus. By doing so, uncertainty, which is the difference in means of PRED and NONE distributions, is on a unitless scale.

Sensitivity analysis

We assessed the sensitivity of V_2 to P_{PRED}, B_{NONE}, B_{PRED}, U_1, U_2, K_2, and S_1 by calculating Spearman partial rank correlation coefficients (PRCC) between input parameters and V_2. We ran 500 simulations with parameters sampled using Latin Hypercube Sampling (LHS). LHS is commonly used to explore the behavior of models by, effectively, simultaneously varying all the values of all input parameters (McKay et al. 1979; see Blower and Dowlatabadi 1994 for an example). Because we were interested in an exploratory LHS analysis, we assigned uniform Supplementary Material (Helton 1993) to all parameters. We varied U_1 and U_2 from 0 to 1; S_1 from −1 to 1; P_{PRED} from 0 to 1; B_{NONE} and B_{PRED} from 0 to 5; and K_2 from 0 to 5 (because V_2 is only calculated when $V_1 \geq 0$, we assumed $K_1 = 0$ as a simplification. By doing so, $V_1 \geq 0$ for all parameter combinations).

Graphical methods

We examined different situations where information use switches from unimodal to bimodal. In presenting our results graphically we frame our results in terms of the "favorability of integration" A, which we define as the proportion of a 2D parameter area in which V_2 is positive while the other parameters are held constant (see Supplementary Figure S1). Each area consisted of 40 × 40 simulations and each plot consists of 20 values of A. All simulations and analyses were done using R, version 3.0.2 (R Core Team 2016).

Model 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 deciding to engage in one of two behaviors. Two different modalities were modeled by specifying different U_1 and U_2. When integrating additional stimuli, an animal increases the accuracy of its perception of the world, thereby increasing the likelihood that the animal makes a correct decision. However, our model demonstrates that, in some situations, due to the costs of mistakes and the costs of attending to stimuli, the benefit from making more accurate decisions is not sufficient to warrant integration.

Spearman PRCC between model parameters and V_2 sampled using LHS are given in Table 4. Because K_2 is a cost of attending to the second stimulus, a greater K_2 decreases V_2 (PRCC = −0.80, $P = 9.87 \times 10^{-141}$, Est. = −25.26).

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Table 4

Results of PRCC sensitivity analysis of V_2

	PRCC	*P* value	Est.
P_{PRED}	0.74	4.87×10^{-94}	20.57
U_1	0.004	0.93	0.09
U_2	−0.25	1.41×10^{-6}	−4.82
B_{NONE}	−0.25	9.79×10^{-7}	−4.90
B_{PRED}	0.70	1.31×10^{77}	18.65
K_2	−0.80	9.87×10^{-141}	−25.26
S_1	0.65	5.18×10^{-60}	16.34

Parameters were sampled 500 times using LHS.

A larger P_{PRED} increases the favorability of integration (PRCC = 0.74, $P = 4.87 \times 10^{-94}$, Est. = 20.57; Figure 2). Larger U_2 decreases the favorability of integration (PRCC = −0.25, $P = 1.41 \times 10^{-6}$, Est. = −4.82). The magnitude of the first stimulus S_1 influences integration through its action in the prey's updated prior after receiving the first stimulus P_{PRED}'. An S_1 that is more like a predator (i.e., $S_1 > 0$) generates $P_{\mathrm{PRED}}' > P_{\mathrm{PRED}}$, indicating an increased likelihood of encountering a predator. An S_1 that is more like a nonthreat (i.e., $S_1 < 0$) indicates a decreased likelihood of encountering a predator ($P_{\mathrm{PRED}}' < P_{\mathrm{PRED}}$). Therefore, greater S_1 increases the importance of distinguishing predators from nonpredators (PRCC = 0.65, $P = 5.18 \times 10^{60}$, Est. = 16.34). This effect is also seen by, for a given U_1 and P_{PRED}, a smaller A when S_1 is more likely to have originated from a nonthreat (Figure 2a) than predator (Figure 2b).

The relationship between U_1 and favorability of integration is nuanced. Sensitivity analysis shows a negligible correlation between U_1 and V_2 (PRCC = 0.004, $P = 0.93$, Est. = 0.09). This result emerges because the directional effect of U_1 on V_2 depends on S_1; thus, on average, the effect of U_1 is negligible. For S_1, highly indicative of a nonthreat (i.e., $S_1 < 0$), greater U_1 increases the favorability of integration (Figure 2a). For S_1, highly indicative of a predator (i.e., $S_1 > 0$), smaller U_1 increases the favorability of integration (Figure 2b). When S_1 is equally likely to have originated from a predator and nonthreat (i.e., $S_1 = 0$), U_1 has no effect on integration and the effect of U_2 is most strongly observed for smaller P_{PRED} (Figure 2c top vs. bottom).

B_{PRED} is the benefit for correctly hiding (i.e., hiding when a predator is present). As B_{PRED} increases, the prey's perception should tend toward integration (PRCC = 0.70, $P = 1.31 \times 10^{-77}$, Est. = 18.65). A larger B_{NONE} means that the prey receives a greater benefit for correctly foraging (i.e., foraging when a nonthreat is present). As the need for accuracy in detecting a predator decreases, as might arise when the prey's energy reserves run low and a missed foraging opportunity could compromise the prey's health, the prey does better to ignore the second stimulus and always forages even if it means increasing the rate at which the prey misses detecting a predator. Consequently, higher B_{NONE} tends to decrease the favorability of integration (PRCC = −0.25, $P = 9.79 \times 10^{-7}$, Est. = 20.57). However, B_{PRED} has more than three times the effect on integration compared with B_{NONE} (Est = 18.65 compared with −4.90).

PART II: EMPIRICAL TESTS

Methods

Through three separate field studies, we illustrate how three predictions of our model can be empirically tested. We examined the effects of B_{PRED}, U_2, and B_{NONE} on integration in free-living yellow-bellied marmots. We measured marmot responses to coyote olfactory and/or acoustic stimuli while foraging at a feed station (we refer readers to Supplementary Material for details of the feed station and playback setup). Individuals received four 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 model parameter we were testing in the given experiment (i.e., B_{PRED}, U_2, or B_{NONE}). We assigned treatments according to a predefined Latin square.

The study testing the model prediction that higher B_{PRED} favors integration was conducted in 2011. Within the framework of our model, B_{PRED} is the benefit to marmots of correctly increasing alert behavior when a predator is present. We manipulated B_{PRED} based on the distance of the feed station to the burrow. Assuming a greater severity of injury when failing to appropriately respond to a predator when farther from the burrow, the higher-B_{PRED} condition is associated with marmots foraging further 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.

The study testing the model prediction that higher U_2 decreases the favorability of integration was conducted in 2012. U_2 is the uncertainty of the second stimulus, which in our setup is vocalizations. We established two levels of U_2 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 (see Supplementary Material for spectrograms and waveforms). The overall amplitude of the playback was not adjusted after embedding in noise. The feed station was set up 3.5 m from burrow.

The study testing the model prediction that greater B_{NONE} decreases the favorability of integration was conducted in 2013. Within the framework of our model, B_{NONE} is the benefit to marmots of foraging in the absence of a predator. We manipulated B_{NONE} through handling time of the bait by mixing the bait with pebbles approximately 7 mm in diameter ("Pea Pebbles," Pavestone, Tyrone, GA). The ratio of bait to pebbles was either 6:1 or 4:3. A lower ratio of bait to pebbles (4:3) establishes a longer handling time such 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 low- and high-B_{NONE} conditions are associated with the 4:3 mixture and 6:1 mixtures, respectively. The feed station was set up 3.5 m from burrow.

All analyses were done using R (V. 3.3.2) (R Core Team 2016). 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 arcsine square root transformation of proportion of time spent foraging as the dependent variable. Fixed factors were odor:acoustic stimulus [water:none, water:vocalizations, urine:none, and urine:vocalizations], age (yearling, adult), sex, audio exemplar (1–3), trial number (1–4), model parameter (X_1, X_2), and the interaction between stimulus and model parameter. We tested the significance of fixed effects through Wald tests using the function *anova.lme* in the package *nlme* (Pinheiro et al. 2013). If a significant stimulus × parameter interaction was found, we ran separate models for each parameter level and conducted post hoc pairwise comparisons with Tukey contrasts using the function *ghlt* in the package *multcomp* (Hothorn et al. 2008).

Marmots were studied under protocols approved by the Animal Use and Care Committees of the University of California Los

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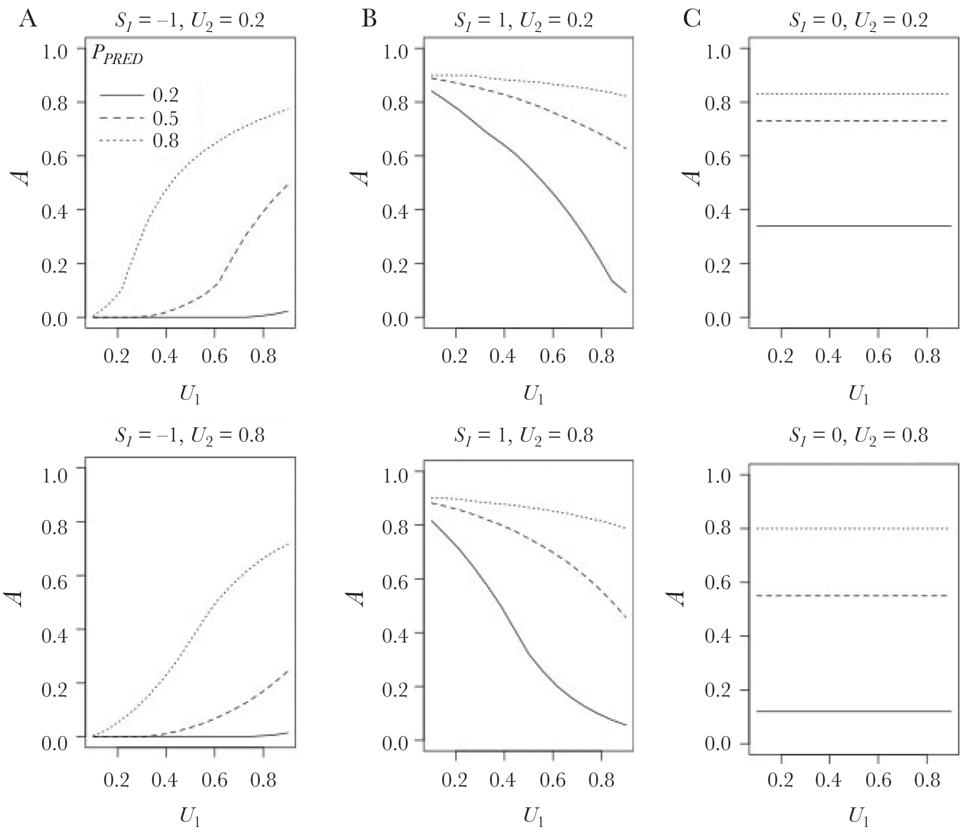

Figure 2
The effects of P_{PRED}, U_2, S_1, and U_1 on the favorability of integration (A) over parameter area $B_{\text{PRED}} \times B_{\text{NONE}}$. In all graphs, B_{NONE} and B_{PRED} were varied between 0 and 5; $K_1 = 0$ and $K_2 = 1$; each line represents a different P_{PRED}; the legend in the first graph applies to all graphs. A larger P_{PRED} increases A. $U_2 = 0.2$ (top) and 0.8 (bottom). Larger U_2 decreases A. In (a)–(c), $S_1 = -1$, 1, 0, respectively. These S_1 correspond to magnitudes of the first stimulus more likely from a nonthreat, more likely from a predator, or equally likely from a nonthreat and predator, respectively. When S_1 is more like a nonthreat, increasing U_1 increases A. When S_1 is more like a predator, increasing U_1 decreases A. When S_1 is equally likely to have come from a nonthreat and a predator, U_1 does not affect A.

Angeles and the RMBL (UCLA Protocol No. 2001-191-01, RMBL protocol No. 1, both renewed annually) and under permits from the Colorado Division of Wildlife (TR917 issued annually). By design, animals were not harmed by routine live trapping or by these brief experiments.

Results

We found that marmots' ($N = 21$) pattern of responses to predator stimuli was influenced by noise level of vocalizations U_2, shown by a significant noise × stimulus interaction ($F = 3.887$, $P = 0.011$; Table 5). Post hoc comparisons (Figure 3) of responses to stimuli show a different pattern of responses to low-noise (Table 6) and high-noise (Table 7) situations. In the low-noise condition, the multimodal response was different from urine (Est. = −0.355, SE = 0.69, $Z = -5.142$, $P < 0.001$) and vocals (Est. = −0.207, SE = 0.066, $Z = -3.130$, $P = 0.009$). In the high-noise condition, the multimodal response was different from urine (Est. = −0.399, SE = 0.049, $Z = -8.142$, $P < 0.001$) but not different from vocals.

We did not find a significant parameter × stimulus interaction in the studies testing B_{PRED} ($N = 24$) or B_{NONE} ($N = 21$) on marmots' pattern of responses to predator stimuli. We refer readers to Supplementary Material for tables summarizing these results.

Table 5
Results from linear mixed-effects model of the proportion of time allocated to foraging in the study testing the influence of U_2 (vocalization noise) on integration

Fixed factor	df	*F*	*P*
Age	1, 18	0.558	0.465
Sex	1, 18	0.003	0.958
Audio exemplar	2, 137	0.181	0.835
Treatment number	1, 137	9.479	**0.003**
Stimulus	3, 137	35.050	**<0.001**
Noise	1, 137	3.027	0.084
Stimulus × noise	3, 137	3.887	**0.011**

Significant *P*-values are highlighted in bold. $N = 21$. Individual ID was the random effect.

DISCUSSION

Understanding the factors responsible for the diverse types of multimodal integration responses and the evolution or loss of integration abilities is challenging. Through a mathematical model, we suggested that multimodal integration may be situation dependent as has been reported in previous studies (e.g., population-specific differences in multimodal integration in squirrels: Partan et al. [2010]; reproductive state influenced multimodal integration in

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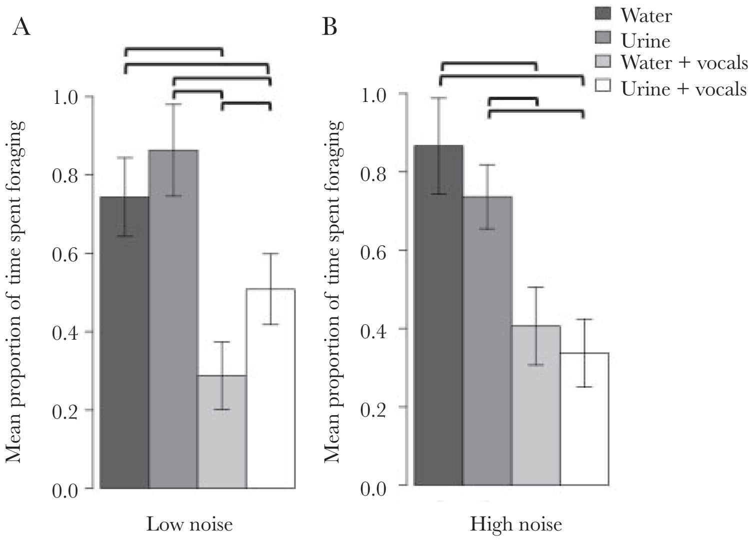

Figure 3

Mean proportion of time marmots spent foraging when coyote vocalizations were (a) less noisy or (b) more noisy. Brackets indicate significantly different pairwise comparisons. Error bars show 95% confidence intervals. $N = 21$.

Table 6

Pairwise comparisons of stimulus types for low-noise vocalizations

Stimulus comparison		Est.	SE	Z	P
Urine + vocals	Urine	−0.355	0.069	−5.142	**<0.001**
Water	Urine	−0.105	0.066	−1.591	0.383
Water + vocals	Urine	−0.561	0.066	−8.500	**<0.001**
Water	Urine + vocals	0.250	0.066	3.779	**<0.001**
Water + vocals	Urine + vocals	−0.207	0.066	−3.130	**0.009**
Water + vocals	Water	−0.456	0.060	−7.639	**<0.001**

Proportion of time spent foraging is the dependent variable ($N = 21$). Significant P-values are in bold.

Table 7

Pairwise comparisons of stimulus types for low-noise vocalizations

Stimulus comparison		Est.	SE	Z	P
Urine + vocals	Urine	−0.399	0.049	−8.142	**<0.001**
Water	Urine	0.117	0.056	2.089	0.156
Water + vocals	Urine	−0.343	0.056	−6.106	**<0.001**
Water	Urine + vocals	0.516	0.056	9.202	**<0.001**
Water + vocals	Urine + vocals	0.057	0.056	1.007	0.744
Water + vocals	Water	−0.460	0.057	−8.124	**<0.001**

Proportion of time spent foraging is the dependent variable ($N = 21$). Significant P-values are in bold.

gobies: Kasurak et al. [2012]). We demonstrated in three field experiments how an animal's environment may be parameterized in our model and by doing so hope to stimulate future empirical tests.

Our model defines “multimodal integration” as occurring when the values of information for sequential stimuli are >0. We modeled different sensory modalities by defining differing uncertainties for each stimulus. The following parameters were found to increase the favorability of integration: greater prior probability of a predator present, greater probability that the first stimulus came from a predator, lower uncertainty of the second stimulus, lower benefit of foraging in the absence of a predator (B_{NONE}), greater benefit of increased antipredator behavior in the presence of a predator (B_{PRED}), and lower cost of attending to a stimulus. The directional effect of uncertainty of the first stimulus on the favorability of integration depends on whether S_1 is more indicative of a nonthreat or a predator. For S_1 more like a nonthreat, the favorability of integration increases with increasing U_1. For S_1 more like a predator, the favorability of integration decreases with increasing U_1. For S_1 equally likely to have been produced by a predator or nonthreat, U_1 has no effect on integration.

In the field, we tested the effect of uncertainty of the second stimulus (U_2) on olfactory-acoustic integration by playing back coyote vocalizations embedded in one of two different noise levels. We found that noise influences multimodal integration in marmots. Under low noise, marmots' multimodal response was different from the unimodal responses, consistent with the formation of a

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multimodal percept (sensu Partan and Marler 1999; Stein et al. 2009; Halfwerk et al. 2019). The multimodal foraging response was less compared with urine alone but greater compared with vocals alone. For an interpretation of foraging levels on marmots' perception of risk, we refer readers to Supplementary Materials. Under high-noise marmots, we did not find evidence of multimodal integration. The result dovetails with predictions from our model that integration is favored under lower U_2. Furthermore, this result is an example of how noise can cause a shift in multimodal perception at the level of the individual and demonstrates how changes in perception could ultimately impact changes in signaling (Partan 2017).

In the field, we manipulated B_{PRED} and B_{NONE} through distance at which marmots foraged from the burrow and bait handling time, respectively. We did not find an effect of B_{PRED} or B_{NONE} on olfactory-acoustic integration in marmots. This result could be because 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 favorability of integration does not strongly respond to B_{PRED} or B_{NONE}. It is possible that, if we had chosen more disparate levels of these parameters, we could have detected a change in integration response.

Although we have developed and tested our model within the context of a prey making antipredator decisions, our model can predict integration in a variety of ecological contexts (see Supplementary Materials for an example of mate recognition). Furthermore, our model can be modified to capture more complex situations. In nature, objects often have several attributes (e.g., size, color, and 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 nonthreat is present (e.g., Brilot et al. 2012). Furthermore, behavior decisions may not be bimodal as 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.

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) provide a thorough review of how animals might have this knowledge in order to adaptively respond to changing environments. Given the premise that multimodal integration is an adaptive response to an individual's environment (Partan 2017), knowledge of a changing environment assumed by our model may be obtained by animals through mechanisms identified by Sih et al. (2011).

In conclusion, we have developed and tested a model that predicts the extent to which animals should integrate multisensory stimuli given a set of environmental conditions. Uncertainty and the value of information (Stephens 1989; Koops 2004) have previously been applied to several problems involving a single stimulus. Our model is relevant to multimodal situations because of differing degrees of uncertainty specified for each stimulus. We hope the model will inspire future empirical tests of the model, which 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.

SUPPLEMENTARY MATERIAL

Supplementary data will be available online after publication.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Munoz and Blumstein (2019).

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