

Short communication

Measures of individual uncertainty for ecological models: Variance and entropy

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ABSTRACT

Organisms on the move face uncertainty regarding the state of their environments, and characterizing the magnitude of this uncertainty is important because of its influence on organismal decision making. Two common measures of the uncertainty inherent in a distribution of possible outcomes are variance and entropy, yet there is currently no standard for when one measure should be used over the other. This paper explores this question using two models of resource uncertainty. For small numbers of discrete possible outcomes, variance is the better measure because it captures the spread between outcomes as well as their differential possibilities. However, variance can categorically fail as a measure of uncertainty when distributions are multimodal or discontinuous, in which case entropy should be used to characterize uncertainty.

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1. Introduction

Organisms make decisions in uncertain environments. Uncertainty represents a significant evolutionary force, and coping with this force is one of the key adaptations of motile organisms (Glimcher, 2003). A major source of uncertainty stems from the fact that environments vary in time and space (Frank and Slatkin, 1990). This variation means that an individual organism cannot reliably adapt to any specific condition, but rather must be capable of adjusting to a range of possibilities. Understanding the sources of an organism's uncertainty and how to measure it are important, because uncertainty plays a large role in the decision processes of animals, as decades of literature on decision making under uncertainty can attest. For example, many animals must balance their behavior to serve competing needs, such as feeding vs. antipredator defense. Uncertainty about the estimated returns of either of these activities will therefore influence decision making (Sih, 1992). Moreover, a small amount of uncertainty ("it will take between two and three hours to find sufficient food") influences decision making differently than a large degree of uncertainty ("it will take between one and ten hours to find sufficient food"), as has been demonstrated in humans (Rakow and Newell, 2010) and is likely true for many species. The degree to which an outcome is uncertain is therefore a relevant factor in models in which organisms must respond to uncertainty.

This paper concerns the way environmental uncertainty should be measured in mathematical and computational models. As a

simplification, a model may assume that some aspect of the state of the environment (e.g., resource availability, climate, predation risk, nest sites, mating options) can be represented by a single value indicating either quality or quantity. The likelihood of any given value occurring at any given time is then given by a probability density function. In ecology, evolutionary biology, and economics, an individual's uncertainty about the state of the environment is often modeled as the variance of this density function (Hoffman, 1978; Real, 1980; Heino et al., 2000; Andras et al., 2003, 2007; Wilbur and Rudolf, 2006). This makes intuitive sense when dealing with unimodal sampling distributions, because increased variance implies more frequent deviations from the mean and a wider range of possible outcomes. In many circumstances, however, the probability density distribution of outcomes will be multimodal. Climatic variation, for example, is often multimodal both year-to-year (Corti et al., 1999; Viau et al., 2002) and day-to-day (Goldreich, 1995). These climatic changes may also correlate with resource variability (Péron et al., 2007), though multimodal distributions of resource availability can exist independent of climate (Araújo et al., 2009). An individual's uncertainty may also concern physical or behavioral properties of prey species or conspecifics. Multimodal distributions of body size are well-documented in many species (Brown, 1984; Cumming and Havlicek, 2002; Allen et al., 2006), and theoretical investigations have shown that multimodal distributions of phenotypes should be expected for a wide range of conditions (Doebeli et al., 2007; Wolf and McNamara, 2012).

When the distribution of possible outcomes is spread around two or more peaks, the overall spread is not captured by the variance of the distribution. Variance is thus a poor measure of uncertainty for multimodal distributions. In the following section, I will discuss an alternative measure of uncertainty, Shannon

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entropy. I will then present two models in which an organism faces uncertainty about either two discrete possibilities or a bimodal range of continuous possibilities. I will show, in the first case, that variance captures an important feature of the environment missed by entropy. In the second case, however, I will show that entropy can give contrasting results to variance when resource distributions are multimodal. Specifically, that it is possible for the variance of a multimodal resource distribution to increase even as the entropy decreases. I will conclude with a discussion of how to take care in employing measures of organismal uncertainty in ecological models.

2. Entropy

Shannon entropy was first introduced in the late 1940s as a mechanism for ensuring adequate signal in digital communication (Shannon, 1948), and is often employed as a measure of information by ecologists interested in animal communication (McCowan et al., 2002). Entropy is also sometimes used as a measure of the uncertainty inherent in a distribution of possible outcomes. A key property is that entropy is maximal when all outcomes are equally likely and minimal when there is only one possible outcome. For a discrete variable X , which can take on values $\{x_1, x_2, \dots, x_n\}$, the Shannon entropy is

$$H(X) = -\sum_{i=1}^n p_i \log p_i \quad (1)$$

where p_i is the probability that $X=x_i$. For continuous variables, the analogous measure is the *differential entropy*. For a probability density function $f(x)$ this is defined as

$$h(x) = -\int_S f(x) \log f(x) dx \quad (2)$$

where S is the support set of the variable x , i.e., all the possible values of x for which $f(x) > 0$. The logarithms are often taken with base 2, in which case the resulting uncertainty measure is given in bits.

For a unimodal distribution of resources, entropy and variance will enjoy a monotonic relationship. Nevertheless, entropy may capture simple intuitions about uncertainty better than variance. For example, if the probability density function of a random variable is a normal distribution, the differential entropy scales with the *logarithm* of the variance (Cover and Thomas, 2006). This means that changes to variance for very narrow distributions will have more of an effect on uncertainty than equivalent changes for very wide distributions. In the following sections, I will examine in more detail two models of organismal uncertainty and compare the measures of variance and entropy.

3. Model 1: Two discrete possibilities

Consider an aquatic predator that feeds exclusively on a particular species of fish. When not hunting, the predator conserves energy by spending time in a cave. Factors such as weather and migration will change the day-to-day availability of prey fish, but predictive measures of these factors are difficult to detect from the safety of the predator's cave. However, let us assume that the predator has, over time, gathered a large sample of the availability of its prey. Some days fish are plentiful and the predator can consume its fill, while on other days fish are scarce and the predator eats little. If the predator knew what quantity of fish to expect, it could allocate its resources so that it hunted on days when fish were plentiful and rested on days when they were scarce. Unfortunately, the predator does not know how much fish it can expect – it is uncertain.

Suppose that the quantity of prey fish can only take on one of two values, few and many, denoted x_f and x_m , respectively, and that with probability p the predator finds many fish, and thus finds few fish with probability $1-p$. The predator's uncertainty should be reflected in how well it can predict which prey quantity will be available. The variance of the prey distribution is given by

$$\text{Var}(x) = p(1-p)(x_m - x_f)^2, \quad (3)$$

while the entropy is given by

$$H(x) = -[p \log p + (1-p) \log(1-p)]. \quad (4)$$

In both cases, the predator's uncertainty is predicted to be maximal when the two outcomes, few or many fish, are equally likely, and minimal when either outcome is certain. Moreover, both measures predict a monotonic decrease in uncertainty as one outcome becomes increasingly more likely. However, variance in this case captures something that entropy does not: the variance increases with the difference in magnitude between outcomes, whereas entropy is not affected by this difference. In other words, variance captures the fact that a coin toss between two fish and ten fish embodies more uncertainty than one between three fish and four, while entropy treats these cases as equivalent.

When options are discrete, entropy has nothing to say about the positional relationships between options, and only captures their relative probabilities of occurrence. Nevertheless, if there are many possible options with probabilities that cluster around two or more values, entropy may be an important tool in calibrating the uncertainty, since variance will not be sensitive to multiple modes.

4. Model 2: A continuous bimodal distribution

Here I adapt the model of Andras et al. (2007), which concerns an organism's perception of resource availability in a temporally varying environment. The model is similar to Model 1, with the primary difference being that resource quantities can take on continuous values. Let the amount of resources, r , available to the organism vary across sampling intervals. As in Model 1, we will assume that resource availability at any given time is independent of the resources available at any previous time (i.e., resource sampling is a Markov process). Let $D(r)$ be the probability density function of the available resources at any given time. We will assume that the fitness payoff from resource accumulation increases monotonically with the quantity of resources collected, and therefore that information about the specific amount of resources is desirable. At each time interval, however, the organism requires a minimum acceptable level of resources, m , which can act as a measure of the environmental adversity. Any resource amount below this threshold is treated by the organism as equivalent to no resources whatsoever. Andras et al. (2007) modeled the organism's *perceived* resource distribution as equivalent to $D(r)$ for $r \geq m$, plus a Dirac delta function δ_0 centered at zero with an integral equal to the probability density for $r < m$. That is,

$$\int_0^m \delta_0 dr = \int_0^m D(r) dr. \quad (5)$$

Let $D(r)$ be a uniform distribution in the interval $[0, a]$, $a > 1$. One downside of the differential entropy metric is that it is equal to negative infinity for a Dirac delta function. I will sidestep this issue by introducing a small degree of additional uncertainty, assuming that resource values less than m are treated by the organism as very small but possibly nonzero. Specifically, they will be viewed as being drawn from a uniform distribution in the interval $[0, \epsilon]$, $\epsilon \ll m$. The organism's subjective resource probability density is depicted in Fig. 1. (It is important to note that the following discussion would

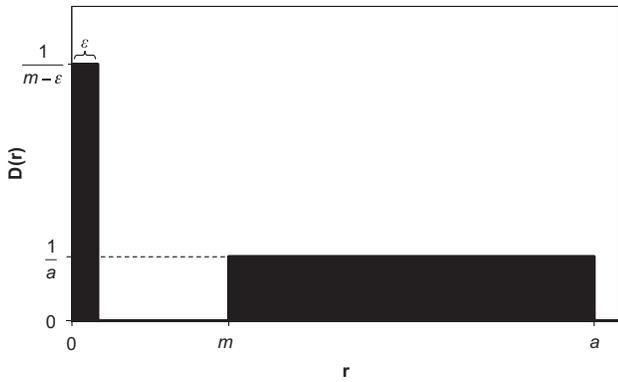


Fig. 1. Subjective resource probability density function assuming a uniform objective density function in the range $[0, a]$ with a subjective minimum threshold of m . The original model of Andras et al. (2007) is recovered as $\epsilon \rightarrow 0$.

also apply if we were to assume that this is the *actual* resource distribution – i.e., resources are always either above m or below ϵ .)

The differential entropy of the subjective resource availability is

$$h(r) = \int_0^\epsilon \frac{m}{a\epsilon} \log\left(\frac{a\epsilon}{m}\right) dr + \int_m^a \frac{1}{a} \log a dr = \log a - \frac{m}{a} \log\left(\frac{m}{\epsilon}\right). \tag{6}$$

The entropy of the true resource distribution, $D(r)$, is recovered if $m=0$ or $\epsilon=m$. More importantly, it is always true that $m \geq \epsilon$, which means that $\log(m/\epsilon) \geq 0$. If the organism’s uncertainty is construed as the differential entropy of the subjective probability density function, then it is clear from Eq. (6) that for any ϵ such that $0 < \epsilon < m$, uncertainty will decrease monotonically as m increases toward a . There is something intuitive in this result. If there is a larger probability of a zero (or near-zero) result, then there are fewer possible outcomes with which the organism must concern itself, and the organism’s uncertainty about its resources will decrease as the environment becomes more adverse (i.e., as m increases).

We can contrast this with the variance of the subjective resource availability as a measure of the organism’s uncertainty. The variance is equal to

$$\text{Var}(r) = E(r^2) - \mu^2 \tag{7}$$

where

$$E(r^2) = \frac{1}{3a}(a^3 - m^3 + m\epsilon^2) \tag{8}$$

and

$$\mu = \frac{a}{2} - \frac{1}{2a}(m^2 - m\epsilon). \tag{9}$$

The variance and differential entropy of the organism’s subjective resource availability are plotted against the environmental adversity in Fig. 2. Although the entropy decreases monotonically as the number of possible outcomes grows fewer, variance increases and then decreases. The reason is that variance is based on how the probability density clumps around the arithmetic mean, and so is not sensitive to multimodal distributions in which the mean is an inappropriate measure of centrality.

Using variance as their measure of uncertainty, Andras et al. (2007) claimed that their model demonstrates that an organism’s uncertainty should increase as environmental adversity increases, operationalized as an increase in m . There are many ways in which environments may be adverse and many things about which an organism may be uncertain, and it is certainly possible that their general claim is true in some cases. Nevertheless, the analysis presented here shows that a decrease in the number of possible environmental outcomes should not, *contra* Andras et al., increase an organism’s uncertainty about the state of the environment.

5. Discussion

Neither variance nor entropy is an ironclad measure of the uncertainty inherent in a distribution of possible outcomes. Each measure has its strengths and weaknesses. Entropy, especially for discrete or discontinuous distributions, may fail to capture the fact that outcomes close in value present less uncertainty than highly different values, whereas this facet is captured by variance. Nevertheless, entropy may be an important tool in calibrating the accuracy of other measures such as variance, particularly if there exist many possible outcomes that cluster around two or more disparate values, since variance will not be sensitive to multiple modes. Moreover, when the distribution of outcomes is given by a continuous probability density function, the spread of that distribution is captured by entropy. As discussed, for a normal distribution the entropy scales with the logarithm of the variance. As such, entropy may be the better measure of uncertainty whenever the distribution of possible outcomes is a continuous probability density function.

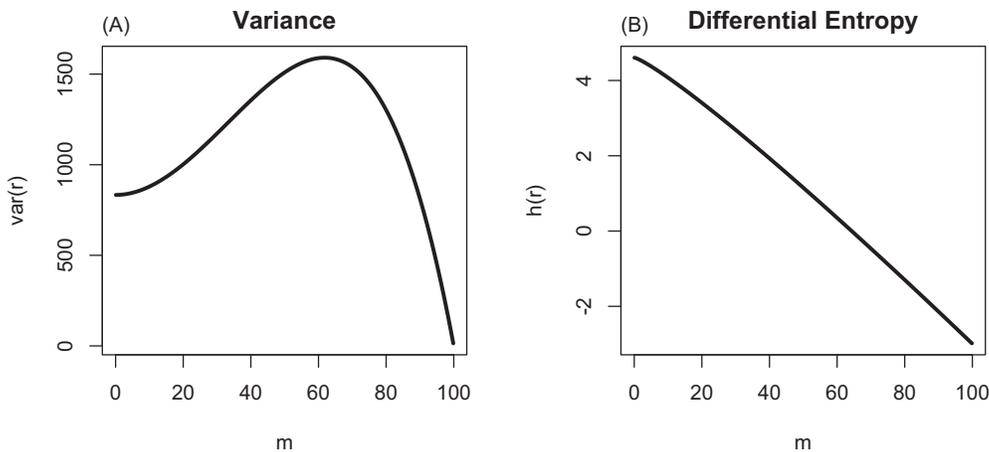


Fig. 2. Subjective variance and differential entropy (in nats) for the resource probability density depicted in Fig. 1 as a function of the organism’s minimum acceptable resource level, m . $a = 100$, $\epsilon = 0.5$.

Crucially, variance is a poor measure of uncertainty for multimodal or discontinuous probability densities, because variance measures the average squared distance from the mean, which obfuscates important structural features of more complex densities and can lead to counterintuitive estimations of an organism's uncertainty. Information theoretic measures such as entropy are better suited for models which incorporate measures of an organism's uncertainty about the state of the environment.

Differential entropy is not necessarily the ideal measure for uncertainty. While Shannon entropy for discrete variables is always non-negative and can be quantified in bits which have a relatively clear interpretation, the same is not true of differential entropy. Moreover, discrete and continuous entropy measures are non-commensurable, although the entropy of an n -bit quantization of a continuous random variable X can be approximated as $h(X) + n$ (Cover and Thomas, 2006). Nevertheless, the first derivative of the differential entropy can reliably show whether uncertainty is increasing or decreasing with respect to some other variable, whereas variance is not equivalently sensitive for multimodal and discontinuous distributions. An important goal for future research will be an extensive study of metrics of uncertainty that assesses each measure's performance across a wide spectrum of outcome distributions. In addition, if learning occurs and events are correlated in time, then metrics that can capture predictive information will be appropriate (e.g., Bialek et al., 2001).

Finally, the type of models presented in this paper assume that precise information about different environmental states is valuable to an organism. This is an assumption about organismal utility and psychology that should be applied with caution. Many animals, including humans, may break a problem down much more simply (Reyna, 2012; Todd et al., 2012). For example, perceived choices may only concern whether or not the available resources are above a critical threshold – “either I get enough to eat or I don't.” In this case, for a uniform probability density, uncertainty is maximal when the critical threshold is closest to the mean of the density function.

6. Conclusion

Uncertainty is a crucial factor in the behavior and cognition of humans and non-human animals, and coping with uncertainty has played a key role in the evolution of mobile organisms (Caraco, 1980; Rubenstein, 1982; Winterhalder, 1986; Rubenstein and Lovette, 2007; Whitehead and Richerson, 2009). As such, ecological and evolutionary models must often include environmental variability and clearly translate that variability into quantifiable uncertainty from the perspective of individual organisms. Entropic measures, which directly capture that uncertainty, are often more appropriate than variance and related measures of spread when distributions are multimodal. Care should be taken in applying appropriate measures of uncertainty, dependent on both the distribution of possible outcomes as well as the organism's individual psychology, in ecological models.

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References

- Allen, C.R., Garmestani, A.S., Havlicek, T.D., Marquet, P.A., Peterson, G.D., Restrepo, C., Stow, C.A., Weeks, B.E., 2006. Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters* 9, 630–643.
- Andras, P., Lazarus, J., Roberts, G., 2007. Environmental adversity and uncertainty favour cooperation. *BMC Evolutionary Biology* 7, 240.
- Andras, P., Roberts, G., Lazarus, J., 2003. Environmental risk, cooperation, and communication complexity. In: *Adaptive Agents and Multi-Agent Systems*. Vol. 2636 of Lecture Notes in Computer Science. Springer, Berlin, Heidelberg, pp. 49–65.
- Araújo, M.S., Bolnick, D.I., Martinelli, L.A., Giaretta, A.A., dos Reis, S.F., 2009. Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology* 78, 848–856.
- Bialek, W., Nemenman, I., Tishby, N., 2001. Predictability, complexity, and learning. *Neural Computation* 13, 2409–2463.
- Brown, J.H., 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124, 255–279.
- Caraco, T., 1980. On foraging time allocation in a stochastic environment. *Ecology* 61, 119–128.
- Corti, S., Molteni, F., Palmer, T.N., 1999. Signature of recent climate change in frequencies of natural atmospheric circulation regimes. *Nature* 398, 799–802.
- Cover, T.M., Thomas, J.A., 2006. *Elements of Information Theory*, 2nd ed. Wiley, Hoboken, NJ.
- Cumming, G.S., Havlicek, T.D., 2002. Evolution, ecology, and multimodal distributions of body size. *Ecosystems* 5, 705–711.
- Doebeli, M., Blok, H.J., Leimar, O., Dieckmann, U., 2007. Multimodal pattern formation in phenotype distributions of sexual populations. *Proceedings of the Royal Society B* 274, 347–357.
- Frank, S.A., Slatkin, M., 1990. Evolution in a variable environment. *American Naturalist* 136, 244–260.
- Glimcher, P.W., 2003. *Decisions, uncertainty, and the brain: the science of neuroeconomics*. MIT Press, Cambridge, MA.
- Goldreich, Y., 1995. Temporal variations of rainfall in Israel. *Climate Research* 5, 167–179.
- Heino, M., Ripa, J., Kaitala, V., 2000. Extinction risk under coloured environmental noise. *Ecography* 23, 177–184.
- Hoffman, R.J., 1978. Environmental uncertainty and evolution of physiological adaptation in *Colias* butterflies. *American Naturalist* 112, 999–1015.
- McCowan, B., Doyle, L.R., Hanser, S.F., 2002. Using information theory to assess the diversity, complexity, and development of communication repertoires. *Journal of Comparative Psychology* 116, 166–172.
- Péron, G., Henry, P., Provost, P., Dehorter, O., Julliard, R., 2007. Climate changes and post-nuptial migration strategy by two reedbed passerines. *Climate Research* 35, 147–157.
- Rakow, T., Newell, B.R., 2010. Degrees of uncertainty: an overview and framework for future research on experience-based choice. *Journal of Behavioral Decision Making* 23, 1–14.
- Real, L.A., 1980. Fitness, uncertainty, and the role of diversification in evolution and behavior. *American Naturalist* 115, 623–638.
- Reyna, V.F., 2012. A new intuitionism: meaning, memory, and development in fuzzy-trace theory. *Judgment and Decision Making* 7, 332–359.
- Rubenstein, D.I., 1982. Risk, uncertainty, and evolutionary strategies. In: Bertram, B.C.R., Clutton-Brock, T.H., Dunbar, R., Rubenstein, D.I., Wrangham, R.W. (Eds.), *Current Problems in Sociobiology*. Cambridge University Press, Cambridge, UK, pp. 91–111.
- Rubenstein, D.R., Lovette, I.J., 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology* 17, 1414–1419.
- Shannon, C.E., 1948. A mathematical theory of communication. *The Bell System Technical Journal* 27, 379–423.
- Sih, A., 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist* 139, 1052–1069.
- Todd, P.M., Gigerenzer, G., The ABC Research Group, 2012. *Ecological rationality: intelligence in the world*. Oxford University Press, New York.
- Viat, A.E., Gajewski, K., Fines, P., Atkinson, D.E., Sawada, M.C., 2002. Widespread evidence of 1500 yr climate variability in North America during the past 14,000 yr. *Geology* 30, 455–458.
- Whitehead, H., Richerson, P.J., 2009. The evolution of conformist social learning can cause population collapse in realistically variable environments. *Evolution and Human Behavior* 30, 261–273.
- Wilbur, H.M., Rudolf, V.H.W., 2006. Life-history evolution in uncertain environments: bet hedging in time. *American Naturalist* 168, 398–411.
- Winterhalder, B., 1986. Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology* 5, 169–392.
- Wolf, M., McNamara, J.M., 2012. On the evolution of personalities via frequency-dependent selection. *American Naturalist* 179, 679–692.