

**RISK-SENSITIVE FORAGING IN RUFOUS HUMMINGBIRDS (*SELASPHORUS
RUFUS*): A TEST OF THE TWIN-THRESHOLD MODEL**

MARK E. KLASSEN
B.Sc. University of Lethbridge, 2002

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

MASTER OF SCIENCE

Department of Biological Sciences
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

© Mark E. Klassen, 2005

General Abstract

I tested the twin-threshold model, a risk-sensitive foraging model incorporating both a starvation threshold and a higher reproductive threshold. The model predicts risk-averse foraging when an animal's energy state is close to the starvation threshold and risk-prone foraging when the animal's energy state is close to the reproductive threshold. Wild rufous hummingbirds (*Selasphorus rufus*) were presented with a choice of three artificial flower types that had either no, moderate or high variability around a common mean. I manipulated energy state by changing either the mean nectar volume or altering the cost of foraging (long versus short corollas). When the energy state of hummingbirds was close to the reproductive threshold they preferred the variable options. When the energy state of hummingbirds was close to the starvation threshold they preferred the nil option. Hummingbirds responded in a manner consistent with the twin-threshold model.

Acknowledgements

First and foremost I would like to thank my supervisor, Dr. T. A. Hurly. He introduced me to the topic of risk-sensitive foraging in 2000 and has guided me in the design of several experiments investigating the topic. His knowledge and expertise has been invaluable over the past several years. Also, I would like to thank him for the successful duck hunting trips, which have resulted in some great meals.

I would also like to thank my thesis committee, Dr. R.V Cartar, Dr. D. Rendall, and Dr. J.N. Davis for their advice on experimental design and general comments on my thesis work. I especially thank Dr. Cartar for advice on the appropriate statistics to use in my data analyses.

Without the help of three great field assistants, the sample size for my experiments would have been considerably lower. Chelsea Matisz helped collect data during the summer of 2003, and Erika Droessler and Kim Urbaniak helped collect data during the 2004 field season. All three put in tremendously long hours each day in the field collecting data and late hours in the evening entering it. Also, thank you to Melissa Groeneweg for all the data she entered. As well, the whole crew at the Westcastle field station created a great atmosphere to discuss foraging behaviour and hummingbird research. I especially thank them all for the great meals and late night festivities. A special thanks to Dr. S.D. Healy and Dr. M. Bateson for helpful comments on experimental design. As well, thanks to Jono Henderson for the comic relief out at the cabin.

I am grateful to both Katheryn Taylor and Simone Franz for their encouragement, sense of humour and friendship. They were always there to bounce ideas off of and to provide helpful comments and suggestions during the development of my thesis. As well, their assistance in the aviary was greatly appreciated.

Lastly, I would like to thank my family. Andrea has provided an endless amount of encouragement, support, and love throughout my thesis. Thank you so much Andrea. Also, thank you to my Mother for all her love and advice over the years.

Much of this thesis work would not have been possible without the financial support of NSERC. As well, I gratefully acknowledge the *ACA Grants in Biodiversity* (supported by the Alberta Conservation Association).

CHAPTER 1.....	1
<u>Introduction to risk sensitivity and the twin-threshold model.....</u>	1
Introduction	1
Effects of energy budget manipulations	2
Variance in amount or delay to food	3
Coefficient of variation as a predictor of risk	5
Number of options in the choice set	6
Twin-threshold Model of risk sensitivity	7
Field experiments with rufous hummingbirds	9
References	12
CHAPTER 2.....	16
<u>The effect of altering reward means and standard deviations on foraging preferences of rufous hummingbirds (<i>Selasphorus rufus</i>).....</u>	16
Abstract.....	16
Introduction	17
Predictions of the Twin-threshold model	21
Methods	22
Subjects and Study Site.....	22
Initial training.....	23
Trinary comparisons.....	23
Analysis	25
Results	25
Nectar volumes experienced by birds.....	26
Test of the twin-threshold model	27
Discussion.....	29
Why are thresholds important?.....	29
Individual variation	31
Test of the twin-threshold model.....	32
Summary.....	36
References	38
CHAPTER 3.....	48
<u>Risk-sensitive inflorescence departure: a test of the twin-threshold model.....</u>	48
Abstract.....	48
Introduction	49
Methods	53
Study Site and Study Animals	53
Training	54
Trinary choice.....	54
Analysis	56
Results	57
Nectar volumes experienced by birds.....	57
Individual preferences.....	57
Number of flowers visited before departure	58
Inflorescence choice.....	58

Discussion.....	59
Inflorescence choice.....	67
Summary.....	68
References	69
CHAPTER 4.....	80
<u>Conclusions and General Discussion</u>	80
Introduction	80
Discussion.....	83
References	89

List of Tables

Table 2.1. Volume reward regimes used in the trinary comparisons. Quantity refers to the total number of each flower type presented on one plate. Each plate consisted of a total of 18 flowers.....	40
Table 2.2. Mean (\pm SE) number of flowers visited per bout for both baseline and shift treatment according to mean volume (low or high).....	41
Table 2.3. Mean (\pm SE) volume of sugar solution consumed per bout from each flower type for both the low and high mean volume treatments. The mean volume should be close to that of the nil flower type.....	42
Table 2.4. Individual flower rankings for both mean volume treatments and foraging environments (Baseline, Shift Down, and Shift Up).....	43
Table 3.1. Mean number of inflorescences visited and number of flowers visited by each subject per bout.....	72
Table 3.2. Inflorescence rankings and chi square results of subjects for both long and short corolla treatments. $df = 2$ for all chi square tests.....	73

List of Figures

Figure 1. 1. Graphical presentation of the energy budget rule. C represents the frequency distribution of the possible energy state of an animal foraging from a constant volume option. V represents the frequency distribution of the possible energy state of an animal foraging from a variable volume option. a. When the mean energy acquired is above the starvation threshold risk-aversion is predicted. b. When the energy acquired is below the starvation threshold risk-prone foraging is predicted.	14
Figure 1. 2. Graphical presentation of the twin-threshold model. Distributions are the possible energy states of a forager feeding from a particular distribution. When the mean energy state of the forager is close to the reproduction threshold (as in a. low cost of foraging) the optimal choice is a variable option (Moderate or High). When a forager's energy state is closer to the starvation threshold (as in b. high cost of foraging) the optimal choice is the constant option (Nil). ↑ represents the mean energy state of the animal foraging from the reward distributions.	15
Table 2.1. Volume reward regimes used in the trinary comparisons. Quantity refers to the total number of each flower type presented on one plate. Each plate consisted of a total of 18 flowers.	40
Table 2.2. Mean (±SE) number of flowers visited per bout for both baseline and shift treatment according to mean volume (low or high).	41
Table 2.3. Mean (±SE) volume of sugar solution consumed per bout from each flower type for both the low and high mean volume treatments. The mean volume should be close to that of the nil flower type.	42
Table 2.4. Individual flower rankings for both mean volume treatments and foraging environments (Baseline, Shift Down, and Shift Up).	43
Figure 2. 1. Graphical presentation of the twin-threshold model. Distributions are the possible energy states of a forager feeding from a particular distribution. When the mean energy state of the forager is close to the starvation threshold (as in a. low mean volume) the optimal choice is the constant option (Nil). When a forager's energy state is closer to the reproduction threshold (as in b. high mean volume) the optimal choice is a variable option (Moderate or High). ↑ represents the mean energy state of the animal foraging from the reward distributions.	44
Figure 2. 2. Proportion of visits to a variable flower when the variable flower was the last flower visited. A strong association exists between departure and the volume of the variable flower (bust (lower volume) or bonanza (higher volume)). Subjects ended more bouts after visiting a bonanza flower versus a bust flower (n = 20).	45
Figure 2. 3. Mean (±SE) volume of sucrose consumed from each flower type per bout. The nil flower type must be 20 µl (low volume treatment) and 30 µl (high volume treatment), averages for the variable flowers should equal that of the nil flower type of the same volume treatment (Nil: n = 20; Low: n = 10; Moderate: n = 20; High: n = 20; Extreme: n = 10).	46
Figure 2. 4. Least square mean (±SE) proportion of visits to each flower type according to mean volume (high or low) and environment (baseline or shift). * indicates different from random (0.33). Letters represent least square means that are significantly different (Tukey-Kramer hsd (P = 0.05)) (n = 10).	47

Table 3.1. Mean number of inflorescences visited and number of flowers visited by each subject per bout.	72
Table 3.2. Inflorescence rankings and chi square results of subjects for both long and short corolla treatments. $df = 2$ for all chi square tests.....	73
Figure 3. 1. Graphical presentation of the twin-threshold model. Distributions are the possible energy states of a forager feeding from a particular distribution. When the mean energy state of the forager is close to the starvation threshold (as in a. high cost of foraging) the optimal choice is the constant option (Nil). When a forager's energy state is closer to the reproduction threshold (as in b. low cost of foraging) the optimal choice is a variable option (Moderate or High). \uparrow represents the mean energy state of the animal foraging from the reward distributions.....	74
Figure 3. 2. Mean (\pm SE) volume of sucrose consumed per flower from each inflorescence type per bout. Mean volume for the nil inflorescence must be 10 μ l, and the average for both the moderate and high inflorescences should be 10 μ l.	75
Figure 3. 3. Least square mean (\pm SE) number of flowers visited per inflorescence according to corolla length (Short and Long). Letters represent means that are different from each other (Tukey-Kramer hsd ($P = 0.05$)) ($N = 9$).	76
Figure 3. 4. Mean (\pm SE) number of flowers visited across inflorescences according to corolla length (short or long) and treatment order (Order 1: Long corolla followed by Short corolla and Order 2: Short corolla followed by Long corolla). Letters represent means that are different from each other (Tukey-Kramer hsd ($P = 0.05$)).	77
Figure 3. 5. Least square mean (\pm SE) proportion of visits to inflorescence type according to corolla length (Short and Long). * indicate means that are significantly different from random expectation (0.33). Letters represent means that are different from each other (Tukey-Kramer hsd ($P = 0.05$)) ($N = 9$).	78
Figure 3. 6. Specific configuration of the twin-threshold model accounting for the change in the number of flowers visited on moderate inflorescence between corolla treatments (see text for details). Distributions are the possible energy states of a forager feeding from a particular distribution (Nil, Moderate or High). When the mean energy state of the forager is close to the reproduction (as in a. low cost of foraging (Short corolla) the optimal choice is a variable option (Moderate or High). When a foragers' energy state is closer to the starvation threshold (as in b. high cost of foraging (Long corolla) the High option may be of more value than the moderate option. \uparrow represents the mean energy state of the animal foraging from the reward distributions.	79

Chapter 1

Introduction to risk sensitivity and the twin-threshold model

Introduction

Risk-sensitive animals respond to foraging rewards that differ in the amount of variability about the mean value of the reward. Risk-sensitive foraging is evident across several taxonomic groups (e.g., fish, birds, mammals, insects), suggesting that risk-sensitivity is common and widespread phenomenon (reviewed by Kacelnik and Bateson 1996). Experiments investigating risk-sensitivity usually present a subject with a simultaneous choice between a constant and a variable option. Four patterns have emerged from the risk-sensitive literature (Kacelnik and Bateson 1996; Shafir, 2000): (1) The direction of risk-sensitive preferences is influenced by the forager's energy budget as summarized by the 'energy-budget rule' summarizes this pattern (Stephens 1981). The energy budget rule states that a forager on a positive energy budget should choose a less variable option (risk-averse) than a forager on a negative energy budget (risk-prone). (2) The direction of risk-sensitive preferences is dependent on whether variability is in delay to the reward or in amount of reward. Risk proneness is usually associated with variance in delay to reward, whereas risk aversion is usually associated with variance in amount of reward (Kacelnik and Bateson 1996). (3) The magnitude of risk-sensitive preferences is influenced by the coefficient of variation (CV) of the variable options. Risk-averse foragers tend to increase their preference for the constant reward as the coefficient of variation of the variable reward increases. Risk-prone animals tend to become more risk preferring as the CV of the variable reward increases (Shafir 2000). (4) The direction and

magnitude of risk-sensitive preferences are influenced by the number of foraging options that are available simultaneously. The inclusion of a third option in the foraging set has resulted in some foragers preferring intermediate risk even when they were risk averse in a traditional binary risk experiment (Hurly and Oseen 1999; Bateson 2002; Hurly 2003). Hurly (2003) describes a new risk-sensitive model, the twin-threshold model, which incorporates two thresholds to explain preference for variability. The addition of a second threshold also reverses some of the predictions of the traditional energy-budget model, which is a single threshold model. I now review these four patterns evident in the literature.

Effects of energy budget manipulations

The direction of risk-sensitive preferences is influenced by the energy budget of the forager when variability is in the amount of reward. The effect of reward variance and energy budget manipulations on foraging preferences was first demonstrated by Caraco et al. (1980), who offered yellow-eyed juncos (*Juncos phaenotus*) a choice between two feeding stations. One station provided a constant number of seeds, whereas the other station provided a variable number of seeds. The mean number of seeds provided by the variable station equaled the number of seeds provided by the constant station. Therefore, the long-term rate of energy intake of the juncos would be the same from each station provided that the cost of foraging was equal at both low- and high-rewarding stations. Caraco et al. (1980) demonstrated that when expected daily energy intake exceeded expected energy expenditures, juncos were risk-averse. However, when the juncos' expected daily energy intake was below expected energy expenditures, they switched to risk-prone behaviour. This switch in preference was explained as a strategy to minimize

the probability of an energy short-fall. Caraco et al. (1980) proposed a simple rule for foragers: be risk-averse if your expected energy budget is positive, and be risk-prone if your expected energy budget is negative. Stephens (1981) formalized this rule with a descriptive model, and concluded that a forager should be risk-averse when the mean food reward is greater than its energy requirement, and should be risk-prone when the mean food reward is lower than its energy requirement (see Figure 1.1). This is known as the energy budget rule. This model assumes that there is a nonlinear relationship between fitness and energy intake.

Many studies support the energy-budget rule, as 77% of studies that tested the energy budget rule showed evidence of a switch in preference when energy budgets were manipulated (Kacelnik and Bateson 1996). As well, Kacelnik and Bateson suggest that preference shifts caused by energy budget manipulations were most prevalent in species of low body mass. The small size of these species may result in greater selection for shortfall minimization. The limited reserves of small animals make starvation a lethal threat each night. However, body size is confounded by whether the amount of reward or delay to reward is variable. Studies in which the amount of food varied were conducted with small animals, whereas experiments where variability was involved delay in food availability were conducted with larger mammals or birds.

Variance in amount or delay to food

Risk proneness is usually associated with variance in delay of food availability, whereas risk aversion is usually associated with variance in food quantity (Kacelnik and Bateson 1996). No one model of risk sensitivity has accounted for this difference.

Functional models of risk (e.g., energy-budget model; Stephens 1981) explain risk sensitivity to variability in amount; however, no energy budget manipulation studies have successfully demonstrated a switch in preference when variability occurs in delay (Ha et al. 1990; Batson and Kacelnik 1997). Kacelnik and Bateson (1996) pointed out that studies that have manipulated energy budgets and tested for variability in delay have been conducted exclusively with larger animals (e.g., gray jays, (*Perisoreus canadensis*) and European starlings (*Sturnus vulgaris*)). Smaller species may be more subject to short-fall minimization and therefore more sensitive to energy-budget manipulations. No studies have investigated the affect of variability in delay to reward with small animals.

Several mechanistic models have been derived to explain why animals are always risk-prone when they experience variability in delay to a food reward. Mechanistic models of risk sensitivity consider the cognitive processes animals use to perceive and learn about their environment. Scalar expectancy theory (SET), predicts that foragers should be risk-prone when variability is in delay and risk-averse when variability is in amount (Reboreda and Kacelnik 1991), but this model fails to explain the effect of energy budget. SET predicts universal risk-aversion and risk-proneness towards variability in amount and delay respectively. Another hypothesis proposes that animals maximize their short-term rate of intake (expected ratio of amount over time) instead of long-term intake (ratio of expected amount over expected time) (Bateson and Kacelnik 1996). Again, this hypothesis does not explain risk-aversion when food quantity varies, unless there is a strong positive correlation between quantity and handling time and handling time is a large part of the foraging cycle.

Animals may maximize short-term rate of intake. Harder and Real (1987) demonstrated that Bumblebees (*Bombus spp.*) maximize short-term rate of intake. Rate of energy intake is a decelerating function of nectar volume for bumblebees (Harder and Real 1987; Cartar and Dill 1990). Foraging from flowers with differing nectar volumes provides a lower expected rate of net energy intake than from flowers with a fixed volume and equivalent mean, and bees prefer the latter option, because it provides the highest expected rate of energy intake. However, bumblebees still responded in a risk-sensitive manner consistent with the energy-budget model when foraging from floral rewards that provide the same expected rate of net energy intake, switching from risk-averse to risk-prone behaviour when colony energy stores were experimentally depleted (Cartar and Dill 1990). Short-term rate of intake does not account for the change in preference between risk-averse and risk-prone foraging when energy states are manipulated. In the future an integrated model that includes both mechanistic and functional explanations may explain the difference in preference for variability in amount or delay to a foraging reward.

Coefficient of variation as a predictor of risk

Shafir (2000) proposed that the magnitude of risk-sensitive preferences depend on the coefficient of variation of the variable reward. The coefficient of variation (CV) is the standard deviation divided by the mean. In the context of foraging, CV measures risk per unit of expected return (Weber et al. 2004). The CV is a better predictor of risk sensitivity than are the more traditional predictors, namely standard deviation and variance, which have been employed in studies of risk sensitivity. In an analysis of several experiments conducted with bees and wasps, Shafir (2000) demonstrated that the

CV accounted for the greatest proportion of the variation in risk sensitivity ($R^2 = 0.71$). Neither the standard deviation nor the variance accounted for any of the variation in risk-sensitivity (standard deviation: $R^2 = 0.0$; Variance: $R^2 = 0.01$). The CV model does not predict the direction of risk sensitivity (e.g., risk-prone or risk averse), but only the magnitude of the preference. Risk-averse foragers tend to increase their preference for the constant option as the CV of the variable option increases, whereas risk-prone animals tend to accept more risk as the CV of the variable reward increases. However, few studies have been conducted under conditions that predict risk-prone foraging, so that this relationship between increasing risk-proneness and CV is not as well established. The relationship between CV and risk sensitive preferences accounts for most of the variation in the magnitude of risk-sensitivity studies on nectarivores, but not for studies on non-nectarivores. The strength of the preference for or against risk is based on perceptual considerations, and preference direction is based on functional considerations (energy budget rule) (Shafir 2000). Shafir (2000) concluded that there is a “gradient of responses to variability, which is more informative of choice behaviour in animals, than merely whether or not the choice behaviour is statistically significant”. This gradient of response is evident between species (Shafir 2000); however, no data have been collected to support the gradient of response within a single species.

Number of options in the choice set

Most studies of risk-sensitivity have focused on binary choice experiments between a constant and a variable option. However, recent research has demonstrated that an additional option in the choice set influences a forager’s reward preference (Hurly and Oseen 1999; Bateson 2002). Rufous hummingbirds were risk-averse when presented

with the binary choice between flowers with constant nectar volumes versus flowers with variable nectar volumes. Binary comparisons were conducted both between a constant flower type and a moderately variable flower type, and one between a constant flower and highly variable flower type. When all three options were presented simultaneously, hummingbirds preferred the moderately variable flower to both the constant and highly variable flower options. Bateson (2002) conducted a similar experiment with starlings (*Sturnus vulgaris*) and found that individuals increased for their own preferred option between the binary and trinary sets; however, there was little concordance between subjects' preferences. Nearly half of the subjects preferred the constant option and the remaining subjects preferred the low variance option in the trinary set.

Twin-threshold Model of risk sensitivity

The energy budget rule described earlier cannot explain the behaviour exhibited by both rufous hummingbirds and European starlings. The twin-threshold model described by Hurly (2003) considers the consequence of including a second energetic threshold in the energy-budget model of risk sensitivity. In addition to a starvation threshold this model considers a higher threshold that could represent the energy needed to participate in reproductive activities. The twin-threshold model also considers a foraging set of three options, rather than two as considered in most risk-sensitive experiments. The three foraging options all share a common mean, but differ in variability about this mean. Hurly and Oseen (1999) considered options of nil, moderate and high variance in their initial experiment (foraging options will be referred throughout by their variability). Foraging preferences result from the proximity of a foragers' energy state to the starvation and reproductive thresholds. As in the original energy-budget

model, the twin-threshold model predicts that a forager that fails to acquire an energy state above the starvation threshold dies. Additionally, this model predicts that a forager whose energy state does not surpass the reproductive threshold will survive, but does not reproduce.

The resulting energy states for an animal foraging from the nil, moderate and high variability options with different foraging costs are represented in Figure 1.3. The location of the common mean of the foraging options in Figure 1.3a creates a situation in which there is a tradeoff between foraging from specific options. The nil variability avoids starvation, but does not allow reproduction. Both the moderate and high variability options offer the possibility of reproduction (area beneath the curves to the right of the reproduction threshold), but there is also a chance of starvation (area beneath the curves to the left of the starvation threshold). For the situation illustrated in Figure 1.3a the moderate variability option may offer the greatest fitness, because there is a reasonable possibility of reproduction and the threat of starvation is very low. The situation in Figure 1.3b is an example of a foraging environment where the cost of foraging is high, resulting in a lower mean energy state for the forager. In this situation, both variable options provide a low probability of reproduction and a high threat of starvation. The nil variability option provides a low threat of starvation, but also no chance of reproduction. In this situation, the nil option is preferred because there is no threat of starvation.

The twin-threshold model accounts for preference for the moderately variable reward exhibited by rufous hummingbirds and European starlings. When starvation is more important than reproduction, the twin-threshold model predicts preference for

variability when the mean energy state of the forager is closer to the reproductive threshold. The rufous hummingbirds studied by Hurly and Oseen (1999) behaved as if their energy state was closer to the reproductive threshold. The twin-threshold model also predicts the increased risk-aversion, exhibited by European starlings, when the ambient temperature was decreased, which should affect energy state as would an increase in foraging costs (Figure 1.3b) favouring, risk-aversion. This prediction is opposite to that of the original energy-budget model.

Field experiments with rufous hummingbirds

The work presented in this thesis concentrates mainly on two of the four patterns evident in the risk-sensitive literature: energy budget manipulations and number of options in the choice set. Both of the field experiments described in this thesis test the twin-threshold model. Predictions from the twin-threshold model depend on the energy state of the forager. In my tests of the model I knew the relative position of the energy state with respect to the two thresholds, but not the absolute energy state. I assume that an increase in average nectar availability or decrease in the cost of foraging will shift a bird's energy state closer to the higher reproductive threshold compared to a lower nectar volume or a higher foraging cost. Nectar volumes are based on values used in past studies (Hurly and Oseen 1999; Hurly 2003, which have stimulated risk-sensitive foraging by hummingbirds.

The first field experiment investigated the effect of shifting the standard deviation of either the moderate or high variability option after the hummingbirds had foraged from a baseline treatment of nil, moderate, and high variability. The experiment was carried out at both a low-and a high-volume treatment to manipulate the energy

budgets of the subjects. The twin-threshold model predicts that when the mean nectar volume is low and therefore closer to the starvation threshold, hummingbirds should prefer the nil variability option. When the mean volume is high and therefore closer to the reproductive threshold, hummingbirds should prefer the variable options. When the mean volume is low, preference for nil variability should be greater when presented with rewards with high and extreme standard deviations than when presented with rewards of low and moderate standard deviations. Also, preference for nil variability in the high mean treatment when presented with rewards with high and extreme standard deviations should be lower when presented with the same options but at a low mean volume.

The second field experiment tested the twin-threshold model, by altering the cost of foraging. Subjects foraged from flowers with long and short corollas. An increased cost of foraging should reduce the net energy budget and cause the subjects to be risk-averse. Inflorescence departure was used as a measure of risk, as Biernaskie et al. (2002) suggested that it is a sensitive measure of risk sensitivity. A risk-prone forager should visit more flowers on the variable inflorescence than on the nil variable inflorescence. A risk-averse forager should visit more flowers on the nil variable inflorescence before departing. Therefore, when the cost of foraging is high a risk-sensitive forager should depart sooner from the variable inflorescence, whereas when the cost of foraging is low, it should depart sooner from the nil variability inflorescence.

The experiments described in this thesis involved wild male rufous hummingbirds during mating season, and therefore, may offer new insight into the effect reproduction may have on risk-sensitive foraging. The inclusion of a second threshold (a reproductive threshold) reverses some of the predictions of the traditional single threshold models of

risk-sensitive foraging. My results are consistent with one previous test of the twin-threshold model (Hurly 2003) and also extend the generality of the model through novel tests of the model. Finally, the data provide preliminary information on how hummingbirds respond in a risk-sensitive manner to a novel foraging reward. Both energetic reserves and reward variability may interact to influence sampling behaviour toward novel flowers.

References

- Barnard, C.J. and Brown, C.A.J.** 1985. Risk sensitive foraging in common shrews (*Sorex araneus* L.). Behavioral ecological and Sociobiology, **16**, 161-164.
- Bateson, M.** 2002. Context-dependent foraging choices in risk-sensitive starlings. Animal Behaviour, **64**,251-260.
- Bateson, M. and Kacelnik, A.** 1997. Rate currencies and the foraging starling: the fallacy of the average revisited. Behavioral Ecology, **7**, 341-352.
- Biernaskie, J.M., Cartar, R.V., and Hurly, T.A.** 2002. Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar volumes? Oikos, **98**, 98-104.
- Caraco, T., Martindale, S., and Whittam, T.S.** 1980. An empirical demonstration of risk-sensitive foraging preferences. Animal Behaviour, **28**, 820-830.
- Caraco, T.** 1981. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). Behavioral Ecological and Sociobiology, **8**, 213-217.
- Caraco, T.** 1983. White crowned sparrows (*Zonotrichia leucophrts*) foraging preferences in a risky environment. Animal Behaviour, **30**, 719-727.
- Cartar, R.V., and Dill, L.M.** 1990. Why are bumble bees risk-sensitive foragers? Behavioral Ecology and Sociobiology, **26**, 121-127.
- Ha, J.C., Lehner, P.N., and Farley, S.D.** 1990. Risk-prone foraging behaviour in captive gray jays, *Perisoreus canadensis*. Animal Behaviour, **39**, 91-96.
- Harder, L.D., and Real, L.A.** 1987. Why are bumble bees risk averse? Ecology, **68**, 1104-1108.
- Hurly, T.A.** 2003. The twin-threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. Animal Behaviour, **66**, 751-761.
- Hurly, T.A., and Oseen, M.** 1999. Context dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. Animal Behaviour, **58**, 59-66.
- Kacelnik, A., and Bateson, M.** 1996. Risky theories – The effects of variance on foraging decisions. American Zoologist, **36**, 402-434.
- Reboreda, J.C., and Kacelnik, A.** 1991. Risk sensitivity in starlings: Variability in food amount and food delay. Behavioral Ecology, **2**, 301-308.

Shafir, S. 2000. Risk-sensitive foraging: the effect of relative variability. *Oikos*, **88**, 663-669.

Stephens, D.W. 1981. The logic of risk-sensitive foraging preferences. *Animal Behaviour*, **29**, 628-629.

Weber, E.U., Shafir, S. and Blais, A. 2004. Predicting risk sensitivity in humans and lower animals: Risk as variance or coefficient of variation. *Psychological Review*, **111**, 430-445.

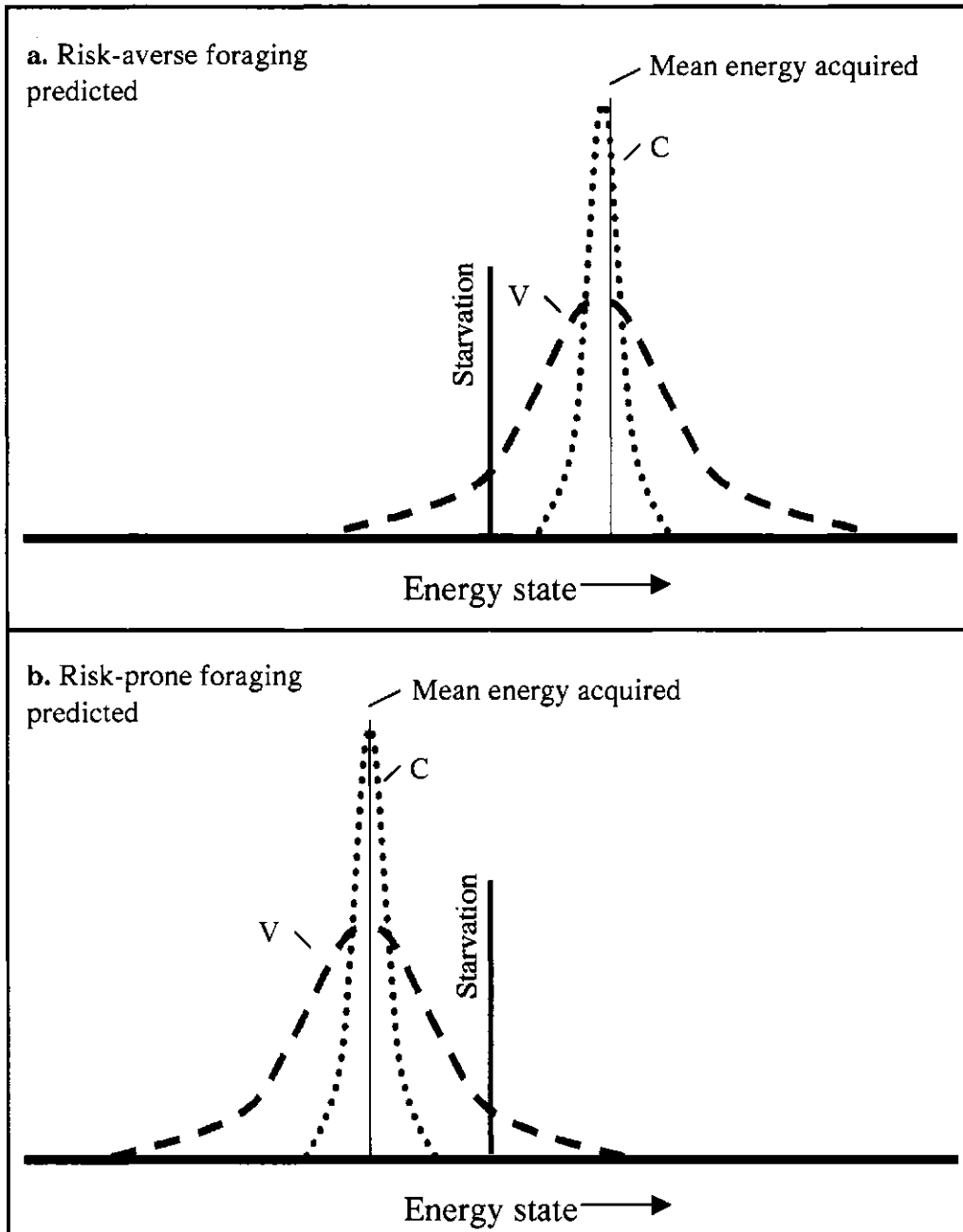


Figure 1. 1. Graphical presentation of the energy budget rule. C represents the frequency distribution of the possible energy state of an animal foraging from a constant volume option. V represents the frequency distribution of the possible energy state of an animal foraging from a variable volume option. a. When the mean energy acquired is above the starvation threshold risk-aversion is predicted. b. When the energy acquired is below the starvation threshold risk-prone foraging is predicted.

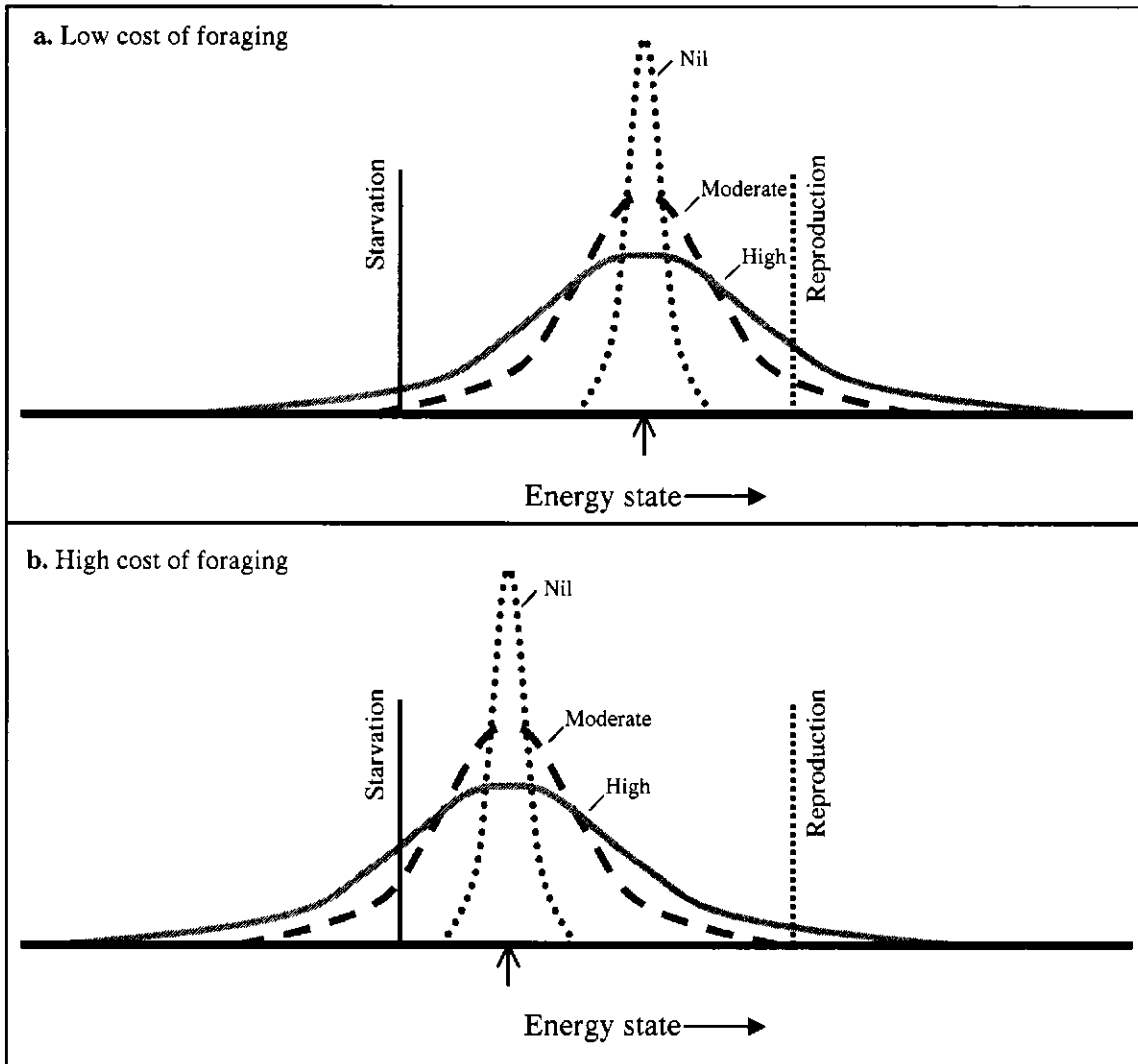


Figure 1. 2. Graphical presentation of the twin-threshold model. Distributions are the possible energy states of a forager feeding from a particular distribution. When the mean energy state of the forager is close to the reproduction threshold (as in a. low cost of foraging) the optimal choice is a variable option (Moderate or High). When a forager's energy state is closer to the starvation threshold (as in b. high cost of foraging) the optimal choice is the constant option (Nil). \uparrow represents the mean energy state of the animal foraging from the reward distributions.

Chapter 2

The effect of altering reward means and standard deviations on foraging preferences of rufous hummingbirds (*Selasphorus rufus*)

Abstract

The twin-threshold model proposes that a forager's risk sensitivity depends on the relation of expected foraging returns to energy thresholds that determine starvation and reproduction. This model makes two predictions. First, it predicts that foragers should be sensitive to reward mean, tending to be risk-averse when expected rewards are low and risk-prone when expected rewards are high. Second, foragers should be sensitive to reward variation and their response to variation manipulations should depend on reward means. I tested these predictions with wild rufous hummingbirds (*Selasphorus rufus*) foraging from artificial flowers in southwest Alberta, Canada by manipulating reward means and variances. All subjects first received a baseline trinary comparison of foraging rewards with nil, moderate and high variance all with a common mean. Half of the subjects received the comparisons with a mean volume of 20 μ l and the remaining subjects with a mean volume of 30 μ l. After the baseline comparison, either the standard deviation of the high-variable flower type was decreased (shift down) or the standard deviation of the moderate variable flower type was increased (shift up). Half of the subjects from each mean volume treatment received the shift down treatment and the other half received the shift up treatment. In the baseline trials hummingbirds subjected to the low-volume treatment preferred the nil variance, whereas those exposed to the high-volume treatment preferred the moderate variance option. These results are consistent with the twin-threshold model. For all four shift-treatments hummingbirds

preferred the nil variance. Therefore, hummingbirds that experienced the treatments with a high mean volume preferred the moderate variance in the baseline, but the nil variance flower type in the shift treatment. This change in preference between the baseline and the shift is not predicted by the twin-threshold model, but may be an adaptive response to a new uncertain environment. In all four-shift treatments, the new variable flower in the trinary comparison (i.e., low or extreme) was the least preferred flower, suggesting that when hummingbirds encounter a new foraging environment they respond in a risk-averse manner to ensure energy requirements are met.

Introduction

Animals foraging in a stochastic environment often base their foraging decisions on both the mean and variance of the distribution of their food resources. Foragers that respond to both mean and variation in their energy intake are termed risk-sensitive foragers, where 'risk' refers to the uncertainty in foraging outcome, rather than the 'risk' of predation. Most studies of risk sensitivity compare preference for a constant option with zero variance and a variable option with an equal mean volume to that of the constant option, but a non-zero variance. One model of risk-sensitivity, the energy-budget model, predicts that animals on a positive energy budget will be risk-averse (prefer the constant option), whereas animals on a negative energy budget should be risk-prone (prefer the variable option) when the mean value of the constant and variable options is equal (Caraco et al. 1980; Stephens 1981, Stephens and Krebs 1986).

Most studies of risk sensitivity have been carried out in a laboratory setting (Caraco et al.1980; Caraco 1983; Stephens and Paton 1986; Bateson 2002; Schuck-Paim and Kacelnik 2002), where animals may be restricted by the experimental set-up, and

therefore, forced to respond in a risk-sensitive manner. On the other hand, animals in the wild may alter their time budgets (e.g., decrease reproductive activities, spend more time foraging) to minimize the probability of an energy shortfall and therefore not exhibit risk sensitive behaviour. However, increasing evidence indicates that wild animals are also sensitive to variance in resource distributions (Barkan 1990; Cartar 1991; Waser and McRobert 1998; Hurly and Oseen 1999; Hurly 2003). These studies have extended the generality of risk sensitive foraging from captive lab situations to natural foraging conditions. Studies with wild animals provide convincing evidence that animals are responding to risk in their natural environments.

Most tests of risk-sensitive models have presented foragers with two foraging options (constant and variable) (Caraco 1980; Caraco 1983; Stephens and Paton 1986; Barkan 1990, Cartar 1991; Waser and McRoberts 1998; Biernaskie et al. 2002; for a review see Kacelnik and Bateson 1996). Recent research has shown that animals prefer intermediate variance when presented with more than two foraging options with the same mean. When rufous hummingbirds were presented with nil variance, moderate variance, and high variance options all with a common mean, they preferred the moderate variance option (Hurly and Oseen 1999). Since then, these results have been replicated again with rufous hummingbirds (Hurly 2003) and with European starlings (*Sturnus vulgaris*), but to a lesser extent (Bateson 2002; but see Schuck-Paim and Kacelnik 2002). The energy-budget model predicts risk-averse behaviour when a forager's expected energy budget is positive. Both rufous hummingbirds and European starlings were on positive energy budgets, so according to the energy-budget model, they should have been risk-averse. However, preference for a moderate level of variance may have added fitness

benefits for animals in particular situations, even when experiencing a positive energy budget.

Several models of risk-sensitivity consider how a forager should respond to resource variability when reproduction is possible, and predict risk-prone foraging (Caraco and Gillespie 1986; McNamara et al. 1991; Schmitz and Ritchie 1991; Bednekoff 1996). These models assume that a certain resource intake must be attained before reproduction can occur. MacNamara et al. (1991) considered a reproductive threshold instead of a starvation threshold and predicted added benefits from risk-prone behaviour when an animal's energetic reserves are high. Bednekoff's (1996) model predicted that animals should be more willing to accept risk when reproduction is imminent, because the extra resources that could be gained from the riskier option will increase reproductive success. Hurly and Oseen (1999) considered starvation reproductive thresholds simultaneously to explain the preference for a moderate variance demonstrated by rufous hummingbirds, whereas past models considered only a starvation or a reproduction threshold (e.g., Stephens 1981; Bednekoff 1996: see also McNamara et al. 1991 for a model that considers two thresholds). The fitness consequences resulting from the three foraging options may have differed relative to both a starvation threshold and a higher reproductive threshold.

Hurly (2003) formalized the hypothesis of a second threshold with the twin-threshold model of risk sensitivity. The twin-threshold model incorporates both a starvation and a higher reproductive threshold and makes foraging predictions for an animal that has a choice of three foraging options that differ in variability. In general when the mean of the rewards is between the starvation and reproductive thresholds, and

the mean is closer to the starvation threshold, the model predicts that a forager should prefer the option that provides a nil variance. When the mean of the rewards is closer to the reproductive threshold a forager should prefer the option that provides a high variance. However, an energetic region exists between these two thresholds for which a forager should prefer the option that provides a moderate level of variance. Hurly (2003) tested this model by shifting the mean volume of the rewards towards either the starvation threshold or the reproductive threshold. Hummingbirds responded in a manner consistent with the model. Aside from this single test there is no published empirical evidence testing risk-sensitive models that consider a reproductive threshold, and the connection between risk-sensitive foraging and reproduction remains largely unexplored (Bednekoff 1996).

The purpose of this study is to test the twin-threshold model of risk-sensitivity with wild rufous hummingbirds (*Selasphorus rufus*). All hummingbirds were first presented with a baseline trinary comparison between artificial flowers with nil, moderate and high variance. Half of the hummingbirds experienced a baseline treatment at a low mean volume, whereas the other half experienced a high mean volume. The comparison between flower preferences for hummingbirds on the low volume baseline treatment and the high volume baseline treatment replicates Hurly (2003), but uses a between-subjects design. After the baseline treatment either the standard deviation of the moderate flower type was increased to extreme variability or, the standard deviation of the high flower type was decreased to low variability. Shifting the standard deviation of reward options is a novel test of the twin-threshold model.

Predictions of the Twin-threshold model

Predictions of the twin-threshold model are based on the relative position of an animal's energy state to both starvation and reproductive thresholds. Good knowledge is needed on the energy state of the forager and of the energetic thresholds considered in the model to make precise predictions of which options will be preferred. However, no data exist for either the energy state of the hummingbirds used in this experiment or for the energy thresholds. Predictions were based on the position of the reward distribution in relation to both a lower and higher threshold simultaneously. I made the assumption that the reward distributions were between the two energetic thresholds.

Risk-prone behaviour is always predicted when the common means of the distributions, or more specifically the energy state acquired from foraging from these distributions, is below the starvation threshold. On the other hand, when the common mean exceeds the reproduction threshold risk-averse foraging is always predicted. In contrast, this study considers reward means, and therefore energy states, that are between the lower starvation and the higher reproduction thresholds. The model predicts that when the common mean is closer to the lower starvation threshold, foragers should prefer the nil variance option, whereas when the common mean is closer to the higher reproductive threshold the model predicts that foragers should prefer the moderate or high variance options. Hummingbirds foraging in the low-volume baseline environment should therefore prefer the nil variance option (see Figure 2.1a) and hummingbirds foraging in the high-volume baseline environment should prefer the moderate or high variance options (see Figure 2.1b). Because neither the energy values of the thresholds, nor the energy state of individual hummingbirds are known, I cannot definitively predict

whether hummingbirds will prefer the moderate or high variance option in the high-volume baseline environment. Differences in preferences between the low- and high-volume treatments will not be perfect, but will be expressed in terms of changes in ordering of the frequency of visits to different flower types.

In the variance modification treatment, a nil variance option was always present but the standard deviation of one of the variable options was either increased or decreased. Two clear predictions emerge from the twin-threshold model. First, when the mean volume is low, subjects should greatly increase preference for nil variable option in the shift-up treatment and may decrease preference for this option in the shift-down treatment. Second, comparing the preference for the nil variance option in the shift-up environments between low and high mean volume treatments, preference for nil variability should be greater in the low mean volume treatment than in the high mean volume treatment.

Methods

Subjects and Study Site

The subjects were 20 wild, male rufous hummingbirds that established territories in the Westcastle River Valley (49°3'N, 114°3'W) west of Pincher Creek, AB, Canada. During early May 2003 and 2004, 30 commercial hummingbirds feeders were placed throughout the valley, with a minimum distance of 100 m between feeders. Feeders contained 14% sucrose solution, which was changed weekly. By early June, male hummingbirds were defending territories around the feeders and a small mark was sprayed onto the breast of the subjects with non-toxic, waterproof ink. Marking subjects allowed us to identify individual birds. Data were collected between 0630 and 2030 from

early June to mid-July. Data from 16 subjects were collected in 2003 and from four subjects in 2004.

Initial training

Birds were trained to drink 20% sucrose solution from two wells (3.5 mm diameter \times 10 mm deep) drilled into a small Plexiglas plate (5.5 \times 4.8 \times 1.2 cm) mounted on the hummingbird feeder. Wells were marked with a yellow reinforcement ring and were filled with 120 μ l of sucrose solution. Once the bird fed from the wells several times, the hummingbird feeder was removed and the small plate was mounted at an angle of ca. 45° on a metal stake 80 cm high. Sucrose volume was reduced slowly to the volume that was used in the experiment over the course of several feedings. After each feeding the plate was moved ca. 1 m. The area in which the plate was positioned was approximately 16 m². The training plate was then replaced with a larger Plexiglas plate (described below) when the experiment proper began.

Trinary comparisons

Hummingbirds were presented with a baseline trinary choice of a flower-type with a nil variability and two other flower-types with the same mean volume as the nil variability type, but with different variability about the mean. Half of the hummingbirds experienced the low mean volume treatment (20 μ l) and the other half experienced the high mean volume treatment (30 μ l). The nectar volumes for the flower types used in the baseline treatments are presented in Table 2.1. The baseline treatment for each bird was terminated after 60 foraging bouts were completed. I considered a foraging bout to consist of a hummingbird foraging from several flowers on a plate and then departing. Hummingbirds usually returned to a favourite perch upon completing a foraging bout.

Immediately after the baseline treatment for each subject, the variance regimes were shifted either up or down. Half of the birds in each of the mean volume treatments experienced the shift down treatment, whereas the other half experienced the shift up treatment. The volume reward regimes for the shift treatments are presented in Table 2.1. The shift treatment always followed the baseline treatment for each bird and was also terminated after 60 foraging bouts.

Nectar was presented to the subjects on a single Plexiglas plate ($28 \times 21.5 \times 1.2$ cm) with 18 wells. The wells were arranged in a hexagonal pattern with a nearest neighbour distance of 5.2cm. Each well was considered a flower and marked with a coloured reinforcement ring to indicate the variance reward contained within. To ensure that subjects associated reward volume with flower colour, and not with spatial location, randomized colour patterns were assigned to the plates. The three colours were randomly assigned to the 18 wells. Each plate was used for four foraging bouts and was rotated 90° after each bout and moved approximately 1m. As well, after each bout the wells that were visited were cleaned and refilled with the appropriate volumes. After four foraging bouts a different plate with a new randomized colour pattern was presented. Six colours, divided into two groups of three contrasting colours, were used in the experiment. One colour group consisted of: red, yellow, and purple; and the other group consisted of: blue, orange, and green. Colour groups were assigned randomly to either the baseline or shift treatment for each subject and balanced across subjects. Colours were randomly assigned to each of the flower types of the treatment. In the event that a subject sampled a flower type fewer than four times during the first 18 visits, the subject was forced to visit the non-chosen flower. Forced bouts consisted of a single plate with 18 of the non-chosen

flower. The subject had to visit at least six flowers before the experiment was restarted. When the forced bouts were for a variable flower, half the flower contained the lower volume and the other half contained the higher. Volumes were randomly assigned to the 18 wells. All wells contained the same volume if the correction was for the nil reward. Out of the 40 treatments (2 treatments per hummingbird X 20 hummingbirds) 24 treatments required a flower colour correction. The experiment was started over after the correction. Flower visits made before and during the correction were not included in the analysis.

Analysis

Data were analyzed using JMP 4.0 (JMP 2000) software. Proportion of visits to each flower type was used as a measure of preference. A mixed-model ANOVA employed mean volume (low or high), shift direction (up or down), foraging environment (baseline or shift) and flower type (nil, intermediate or highest) as fixed variables, and subject nested within mean volume and shift direction as a random variable. For the analysis variable flowers were grouped into intermediate and highest levels of variability. Tukey-Kramer's hsd post-hoc test was used to determine which group means differed significantly at $P = 0.05$. Variation around means is reported as ± 1 standard error.

Results

Subjects visited similar numbers of flowers in both the baseline and shift treatments (MANOVA: $F_{1,18} = 1.25$, $P = 0.2778$: Table 2.2). Subjects that experienced the high-volume treatments visited 4.23 ± 0.26 flowers per bout for the baseline treatment and 4.61 ± 0.38 flowers per bout in the shift treatments. In the low-volume treatments, subjects visited 6.07 ± 0.26 flowers per bout in the baseline treatment and 6.06 ± 0.29

flowers in the shift treatment. Overall subjects visited more flowers when the mean volume was low (MANOVA: $F_{1,18} = 19.55$, $P = 0.0003$).

Subjects consumed far less sucrose per bout than the amount available from the foraging plate (Low volume: Sucrose available = 360 μ l, amount consumed: Baseline: 122.40 ± 5.54 μ l, Shift: 123.84 ± 6.30 μ l; High Volume: Sucrose available = 540 μ l, amount consumed: Baseline: 129.96 ± 5.82 μ l, Shift: 140.20 ± 12.00 μ l). There was no significant difference in the volume consumed between volume treatments (20 μ l or 30 μ l) (ANOVA: $F_{1,36} = 2.3043$, $P = 0.1378$), or environment treatments (baseline or shift) (ANOVA: $F_{1,36} = 0.5493$, $P = 0.4634$). The interaction between mean volume and treatment was also not significant (ANOVA: $F_{1,36} = 3116$, $P = 0.5801$).

Nectar volumes experienced by birds

To assess whether birds consumed a similar mean volume similar to the volume of the Nil flower, I compared the mean volume of each flower type experienced by each subject per bout. However, there is a complication in this comparison. When the last flower was a variable flower, hummingbirds more often departed when the flower was a 'Bonanza' (high volume) flower rather than a 'Bust' (low volume) flower (chi square: Low mean volume: $\chi^2_1 = 64.52$, $P < 0.0001$; High mean volume: $\chi^2_1 = 41.13$, $P < 0.0001$; Figure 2.2 (none of the 20 subjects represented more than 8% of the data used in this analysis; range = 2.3% - 7.3%)). This strong association represents a sort of sampling bias and would increase the mean volume received from the variable flowers. Therefore, the last flower was not included in the analysis of the nectar volume that the birds experienced, as it would artificially increase the mean volume experienced.

Given this modification mean nectar volumes consumed per flower did not differ significantly among flower types (Wilcoxon / Kruskal – Wallis: low volume: $\chi^2_4 = 1.4158$, $P = 0.8414$; high volume: $\chi^2_4 = 1.7956$, $P = 0.7733$; Figure 2.3: nonparametric test used because of unequal variances).

One-sample t-tests were used to determine if the long-term mean nectar volume experienced by subjects from variable flower types differed from that of nil flower types (Table 2.3). These tests were done to ensure that subjects were not using visual or olfactory cues to identify, and subsequently forage exclusively from, the high volume flowers of the variable type. The mean volume consumed from variable flower did not differ from the nil flower type volume. Therefore, it is likely that subjects were making risk-sensitive decisions based on nectar volume variance as they experienced it while feeding; and this study is an appropriate test of risk-sensitive foraging.

Test of the twin-threshold model

There was a significant 2-way interaction between Flower type and Environment (ANOVA: $F_{2,32} = 4.11$, $P = 0.0257$). However, the 3-way interaction between Mean volume, Environment, and Flower type was also significant (ANOVA: $F_{2,32} = 4.93$, $P = 0.0136$; Figure 2.4). In the baseline environment when the mean volume was low, hummingbirds preferred nil flowers types over the Moderate flower types (Tukey-Kramer hsd ($P = 0.05$)). Furthermore, hummingbirds chose the Nil flower option significantly more than expected by chance (one-sample t-test against a random expectation of 0.33: $t_9 = 2.62$, $P = 0.004$). When the mean flower volume was high, hummingbirds ranked the rewards as follows: Moderate>High>Nil (Tukey-Kramer hsd ($P = 0.05$)). The Moderate flower type was chosen more often than expected by chance when the mean volume was

high (one-sample t-test against a random expectation of 0.33: $t_9 = 3.27$, $P = 0.014$).

Overall, in the baseline environment, hummingbirds that experienced the low mean volume flowers preferred the nil option and hummingbirds that experienced the high mean volume flowers preferred the moderately variable option. The results from the baseline environment support the predictions of the twin-threshold model of risk-sensitive foraging.

The shift environment always conducted first followed by the baseline environment. I initially predicted that preference for the Nil flower in the low mean volume shift-up environment would be greater than preference for the Nil flower in the high mean volume shift up environment. As well, I predicted that preference for Nil in the low mean volume shift down environment to be lower than the preference for Nil in the low mean shift-up environment. In both cases there was no significant change in preference for nil between the two environments (Tukey-Kramer hsd ($P = 0.05$)). Changing the standard deviation of one of the variable flowers had no systematic effect on flower preference (interaction of Flower and Shift direction: ANOVA: $F_{2,32} = 1.28$, $P = 0.2906$). In the shift environment, hummingbirds preferred the Nil flower over the variable reward flowers when the mean volume was high (Tukey-Kramer hsd ($P = 0.05$)) and a similar trend was evident when the mean volume was low. In both cases preference for the Nil option was greater than expected by chance (one-sample t-test against a random expectation of 0.33: High mean volume; $t_9 = 3.32$, $P < 0.089$; Low mean volume: $t_9 = 2.64$, $P < 0.027$). The preferences of hummingbirds that experienced both environments at a low mean were consistent across environments (preference for Nil). However, the preferences of hummingbirds that experienced the environments at a high

mean volume changed across environments. These hummingbirds preferred the Intermediate option in the baseline but preferred the Nil option in the shift environment. The interaction between Mean volume, Environment, and Flower type cannot be interpreted within the context of the twin-threshold model. Rather, it appears that shifting the variability of flowers caused the birds to prefer the most certain reward, regardless of the mean reward volume.

Discussion

Rufous hummingbirds preferred the moderately variable option only when the mean volume of the nectar rewards was high and they had experienced no other artificial flower environments. That is, only hummingbirds in the high volume baseline environment preferred the moderately variable option. When the standard deviation of one of the variable options changed, or the mean volume was low, hummingbirds preferred the nil variable option. The change in preference of hummingbirds foraging at a high mean in the shift environment is a novel result and not predicted by the twin-threshold model.

Why are thresholds important?

Why do hummingbirds respond in a risk sensitive manner when there was a surplus of resources available from the artificial flowers? Hummingbirds in the low volume treatment had access to a total of 360 μ l of nectar available and subjects in the high volume treatment had access to a total of 540 μ l of nectar available to them. Hummingbirds harvested approximately 30% of the available nectar from the foraging plate; obviously there was enough nectar to surpass all critical thresholds. One must assume that hummingbirds foraging at artificial flowers in my experiment exhibit

behavioural adaptations that have evolved in the natural environment and therefore, respond to variation in nectar volume even when energy is not limited (McNamara 1996).

Foraging time may have been restricted by the time needed for other activities that affect overall fitness. Wild hummingbirds in this study were free to participate in courtship and territorial defense activities, which may have constrained their foraging activities. Suarez and Gass (1999) suggested that hummingbirds limit foraging flights to < 1 minute to ensure that carbohydrates, and not fats, are used to fuel foraging flight. Using fat to fuel foraging flight is 16% less efficient than directly oxidizing carbohydrates (Suarez et al 1990). Such biochemical regulatory control would increase the rate of net fat deposition, which is used to sustain courtship and territorial defense activities, overnight metabolism, and migratory flight.

Hummingbirds may also be limited by the amount of nectar they can transport while foraging. The average nectar load per bout represented 4.36% of the mass of a male rufous hummingbird (3.22 g n=20) (Johnsgard 1997). The accumulating nectar load would increase the cost of foraging and may cause the hummingbird to end a foraging bout. Another limitation may be crop capacity. However, hummingbirds did not seem to be restricted by crop capacity. The mean maximum nectar load was $275.50 \pm 20.05 \mu\text{l}$, and hummingbirds usually harvested $139.46 \pm 7.70 \mu\text{l}$.

Hummingbirds may also be physiologically constrained with feeding intake. Digestive processes may impose severe challenges to maintaining a constant energy budget. McWhorter and Martínez del Rio (2000) demonstrated that broad-tailed hummingbirds (*Selasphorus platycercus*) did not increase their intake rate when foraging at 10°C compared to 22°C. They concluded that hummingbirds were constrained by the

uptake of fructose and glucose from the intestine. To compensate for increased energy output, when constrained by energy acquisition, McWhorter and Martínez del Rio (2000) observed that hummingbirds increased their use of nocturnal torpor and flew less during the cold temperature treatment to conserve energy. Hummingbirds may have consumed very little of the available sucrose from the artificial flowers because they were constrained by physiological factors. These constraints may limit the amount of sucrose consumed during each foraging bout and, therefore, thresholds may exert real effects within the experimental set-up.

Individual variation

Predictions of the twin-threshold model are based on the energy state of the forager in relation to the two thresholds. I did not determine energy state of individuals involved in this experiment. The energy state of the forager should determine how they respond to the reward distributions. The low and the high mean used in this experiment were chosen based on previous results with rufous hummingbirds (Hurly and Oseen 1999, Hurly 2003). The low mean volume would be closer to the starvation threshold and the high mean volume would be closer to the reproductive threshold. However, a subject surviving a cold night may start foraging with a very low energy state, so that even the high mean volume may represent an energy state that is closer to the starvation threshold than the higher reproduction threshold. Results presented in Table 2.4 show little concordance in ranking of the flower options between subjects. These differences in ranking may be a result of different energy states of the individuals involved in the experiment. The variable weather of the Rocky Mountains may cause considerable variation between days of energy states in individual hummingbirds.

Most hummingbirds in the high mean volume baseline treatment preferred the moderate flower type (Table 2.4). However, in the low mean volume baseline treatment several hummingbirds significantly preferred the nil option and several significantly preferred the high option. Individual differences in the relative importance of starvation and reproduction may explain the variability in flower ranking in the low mean volume baseline. For example, for an older bird, that may not survive the season, reproduction may contribute more to overall fitness than it would for a bird that could participate in several more breeding seasons. When reproduction is important, an individual may be more willing to 'gamble' on the variable option providing an energy state high enough to reproduce. The twin-threshold model suggests that when reproduction has a greater effect on fitness the best option may be a variable reward distribution. I have no data on the age of the hummingbirds used in my experiment and therefore, have no data to test this hypothesis. The relationship between age and risk-sensitivity remains largely unexplored.

Test of the twin-threshold model

In the baseline treatment, hummingbirds that received the trinary comparison with the low mean volume were risk-averse. When the common mean volume of the rewards was low, hummingbirds responded as if their energy state was closer to the starvation threshold than to the reproductive threshold and preferred the nil flower option. Foraging preferentially from the nil flowers would decrease a bird's probability of falling below a starvation threshold. Hummingbirds that experienced the baseline comparison at the high mean volume preferred the moderately variable option. These hummingbirds in the high mean baseline treatment responded as if their energetic state was closer to the higher

reproductive threshold. I interpret this preference for the moderate option as an adaptation to increase the probability of reproduction. This difference in preference between hummingbirds foraging in a poor environment (low mean volume) versus a rich environment (high mean volume) is consistent with the predictions of the twin-threshold model. This results replicates the results of Hurly (2003); however, not directly because different subjects experienced contrasting environments in this study, whereas each subject in Hurly's (2003) experienced both environments.

The results of two other studies also support the twin-threshold model. Waser and McRobert (1998) conducted a field experiment with unmarked wild rufous hummingbirds and broad tailed hummingbirds in which weak risk-aversion was found at both the patch and individual plant level. Overall, the low variance patch was visited more often, although not significantly so (approximately 9% more visits) and hummingbirds visited more flowers on the low variance plants than on the high variance plants. However, hummingbirds exhibited risk prone behaviour on 5 of the 12 days of this study. Decreasing risk-aversion with increasing energy state has also been observed in European starlings (Bateson 2002). Starlings became less risk-averse as ambient temperature in the laboratory increased. However Bateson's (2002) data must be interpreted cautiously because temperature was not a manipulated variable in the experiment; instead, changes in temperature resulted from poor temperature control in the laboratory. Therefore, the relationship between increased temperature and decreased risk-aversion is only a correlation and cannot be seen as a causative effect.

After foraging from the baseline environments the standard deviation of one of the flowers was either increased or decreased. The overall trend was risk-aversion after

the standard deviation of one flower was changed. The direction of the shift had no effect on preference. Preferences of hummingbirds that received the treatments with the low mean volume remained risk-averse. However, there was a change in flower preference between environments of hummingbirds in the high mean volume treatment. Hummingbirds in the high mean volume baseline treatment preferred the moderate level of variance, but after the standard deviation of one of the variable options was changed, hummingbirds preferred the nil option. The results from the high mean volume shift treatment are not consistent with the predictions of the twin-threshold model. Based on the results from the baseline treatment of this experiment and results from past studies (Hurly and Oseen 1999; Hurly 2003) a mean volume of 30 μl should have resulted in an energy state closer to a higher reproduction threshold than to the lower starvation threshold. When the mean volume is close to the reproduction threshold, the twin-threshold model predicts preference for variability. Changing the standard deviation of one flower in the choice set caused the birds to prefer the most certain option regardless of mean volume.

The newly introduced options in the shift environment were the least preferred foraging option. In the shift down environment hummingbirds ranked the options as follows: nil > moderate > low. The proportion of visits to the nil option was significantly higher than that of the low option (Tukey-Kramer hsd, $P = 0.05$). This avoidance of the new option in the trinary comparison was also evident in the shift up environment. In the shift up environment hummingbirds ranked the flowers as follows: nil > high > extreme. Again, the proportion of visits to the nil option was significantly greater than the proportion of visits to the extreme option (Tukey-Kramer hsd, $P = 0.05$). The shift in the

standard deviation of one of the options may have caused the hummingbirds to perceive the new foraging environment as uncertain.

The overall preference of subjects in the shift treatment may be the result of subjects responding to uncertainty in the environment. Risk sensitive preferences are due to uncertainty in the environment and not just to variance around a mean, which at times can be predictable (Kacelnik and Bateson 1996). To guard against uncertainty hummingbirds could exploit the new foraging option to gain information about it, or hummingbirds could insure themselves against uncertainty by increasing their energy reserves and forage from known rewards (Dall and Johnston 2002). Hummingbirds were not only familiar with the nil option volume, from experience gained in the baseline treatment, but the nil option was also certain. Every time they foraged from the nil option they received 30 μ l of nectar. Foraging from the nil option would have allowed the hummingbird to maintain its energy reserves with little risk of starvation. In order to reap the possible benefits associated with the new variable reward (i.e., increased probability of reproduction) hummingbirds must insure themselves (energetically) against a possible initial increase in risk and corresponding probability of an energy shortfall, if they forage from several low volume flowers of the variable flower. Dall and Johnstone's (2002) model indicates that when foraging in an uncertain environment a robust response is 'insurance first and foremost, and information if affordable'.

The need to learn the value of a variable option should reduce risk-prone behaviour in risk-sensitivity studies (McNamara 1996). The variable options in risk-sensitivity experiments yield less information per unit of time foraging, therefore, making it hard to learn the value of the reward. The new options in the shift treatment would

need to be sampled several times before the value was determined. Hummingbirds may shift their preference in experiments dealing with risk as they learn about the quality of the patch in which they are foraging. I analyzed this possibility by comparing the proportion of visits to the new flower at the beginning of the shift treatment (first 30 bouts) and at the end of the shift treatment (last 30 bouts). There was no significant difference between proportion of visits to the new flower at the beginning versus end of the treatment (MANOVA: Low: $F_{1,18} = 0.88, P = 0.3600$; Extreme: $F_{1,18} = 0.26, P = 0.6180$).

Summary

When the common mean of the rewards was high in the baseline environment hummingbirds preferred the moderately variable option, a result consistent with the prediction of the twin-threshold model. When the common mean of the rewards was low in the baseline environment hummingbirds preferred the nil variable option, also consistent with the predictions of the twin-threshold model. However, shifting the standard deviation of one flower type resulted in some results that are not predicted by the twin-threshold model. The general trend in the shift environment was preference for the most certain option. Hummingbirds in the low volume treatment maintained their preference for nil, but hummingbirds in the high volume treatment changed their preference from the moderately variable option in the baseline environment to the nil option in the shift environment. Hummingbirds avoided the new option that replaced one of the options from the baseline. This avoidance can be interpreted as a response to dealing with uncertainty. Hummingbirds may 'play it safe' by foraging predominantly from options that they have experienced. Avoiding a new uncertain foraging option

would reduce the risk of an energy shortfall. Over time the new option may be included in the diet when energy reserves are sufficiently high to insure against an energy shortfall while foraging from the new risky option. Such a global change in the environment may have a more profound effect on fitness than does local variability. Hummingbirds may be more sensitive to changes in the greater environment, such as extreme weather or changes in the local abundance of certain flower species, than to slight nectar variation within a plant species.

References

- Barkan, C.P.L.** 1990. A field-test of risk-sensitive foraging in black-capped chickadees (*Parus atricapillus*). *Ecology*, **71**, 391-400.
- Bateson, M.** 2002. Context-dependent foraging choices in risk-sensitive starlings. *Animal Behaviour*, **64**, 251-260.
- Bednekoff, P.A.** 1996. Risk-sensitive foraging, fitness, and life histories: where does reproduction fit into the big picture? *American Zoologist*, **36**, 471-483.
- Biernaskie, J.M., Cartar, R.V. and Hurly, T.A.** 2002. Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar volumes? *Oikos*, **98**, 98-104.
- Caraco, T., Martindale, S. and Whittam, T.S.** 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour*, **28**, 820-830.
- Caraco, T.** 1983. White crowned sparrows (*Zonotrichia leucophrys*) foraging preferences in a risky environment. *Animal Behaviour*, **30**, 719-727.
- Caraco, T., and Gillespie, R.G.** 1986. Risk-sensitivity: foraging mode in an ambush predator. *Ecology*, **67**, 1180-1185.
- Cartar, R.V.** 1991. A test of risk-sensitive foraging in wild bumblebees. *Ecology*, **7**, 888-895.
- Dall, S.R.X., and R.A. Johnstone.** 2002. Managing uncertainty: information and insurance under the risk of starvation. *Philosophical Transactions of the Royal Society London B.*, **357**, 1519-1526.
- Hurly, T.A.** 2003. The twin-threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Animal Behaviour*, **66**, 751-761.
- Hurly, T.A., and Oseen, M.D.** 1999. Context dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Animal Behaviour*, **58**, 59-66.
- JMP 4.0.** 2000. SAS Institute, NC.
- Johnsgard, P.A.** 1997. The hummingbirds of North America 2nd Edition. Smithsonian Institution Press. Washington, D.C.
- Kacelnik, A., and Bateson, M.** 1996. Risky theories – The effects of variance on foraging decisions. *American Zoologist*, **36**, 402-434.

- McNamara, J.M.** 1996. Risk-prone behaviour under rules that have evolved in a changing environment. *American Zoologist*, **36**, 484-495.
- McNamara, J.M., Merad, S. and Houston, A.I.** 1991. a model of risk-sensitive foraging for a reproducing animal. *Animal Behaviour*, **41**, 787-792.
- McWhorter, T.J., and Martínez del Rio, C.** 2000. Does gut function limit hummingbird food intake? *Physiological and Biochemical Zoology*, **73**, 313-324.
- Real, L.A.** 1980. Uncertainty and pollinator-plant interactions: the foraging behaviour of bees and wasps on artificial flowers. *Ecology*, **62**, 20-26.
- Schimitz, O.J., and Ritchie, M.E.** 1991. Optimal diet selection with variable nutrient intake: Balancing reproduction with risk of starvation. *Theoretical Population Biology*, **39**, 100-114.
- Schuck-Paim, C., and Kacelnik, A.** 2002. Rationality in risk-sensitive foraging choices by starlings. *Animal Behaviour*, **64**, 869-879.
- Stephens, D.W.** 1981. The logic of risk-sensitive foraging preferences. *Animal Behaviour*, **29**, 628-629.
- Stephens, D.W. and Krebs, J.R.** 1986. *Foraging Theory*. Princeton: Princeton University Press.
- Stephens, D.W., and Paton, S.R.** 1986. How constant is the constant of risk-aversion? *Animal Behaviour*, **34**, 1659-1667.
- Suarez, R.K., Lighton, J.R.B. Moyes, C.D., Brown, G.S., Gass, C.L., and Hochachka, P.W.** 1990. Fuel selection in rufous hummingbirds: Ecological implications of metabolic biochemistry. *Proceedings of the National Academy of Science USA*, **87**, 9207-9210.
- Suarez, R.K., and Gass, C.L.** 2002. Hummingbird foraging and the relation between bioenergetics and behaviour. *Comparative Biochemistry and Physiology Part A*, **133**, 335-343.
- Waser, N.M., and McRoberts, J.A.** 1998. Hummingbird foraging at experimental patches of flowers: evidence for weak risk-aversion. *Journal of Avian Biology*, **29**, 305-313.

Table 2.1. Nectar volumes for the three flower types used in the trinary comparisons. Quantity refers to the total number of each flower type presented on one plate. Each plate consisted of 18 flowers with six flowers of each type.

Mean Volume	Baseline			Shift Down			Shift Up		
	Flower	Quantity	Volume (μ l)	Flower	Quantity	Volume (μ l)	Flower	Quantity	Volume (μ l)
Low (20μl)	Nil	6	20	Nil	6	20	Nil	6	20
	Moderate	3	10	Low	3	15	High	3	5
		3	30		3	25		3	35
	High	3	5	Moderate	3	10	Extreme	3	0
		3	35		3	30		3	40
	High (30μl)	Nil	6	30	Nil	6	30	Nil	6
Moderate		3	20	Low	3	25	High	3	15
		3	40		3	35		3	45
High		3	15	Moderate	3	20	Extreme	3	10
		3	45		3	40		3	50

Table 2.2. Mean (\pm SE) number of flowers visited per bout for both baseline and shift treatment according to mean volume (low or high).

Subject	Mean volume	Baseline	SE	Shift	SE
B22-03	Low	5.68	0.24	5.18	0.27
B26-03	Low	4.98	0.20	5.35	0.16
B30-04	Low	6.75	0.33	6.40	0.27
B3-03	Low	7.07	0.23	6.73	0.19
PI25-03	Low	5.93	0.23	5.25	0.16
PU5-03	Low	6.92	0.35	5.90	0.33
R15-03	Low	5.27	0.26	6.00	0.29
R19-03	Low	4.93	0.27	4.90	0.26
R27-03	Low	6.90	0.34	7.35	0.36
R8-04	Low	6.30	0.23	7.55	0.28
B14-03	High	4.12	0.14	3.98	0.12
B30-03	High	4.58	0.26	6.60	0.36
G1-03	High	3.95	0.18	3.27	0.15
G1-04	High	4.47	0.19	4.55	0.23
G18-03	High	5.35	0.34	6.43	0.29
PI2-03	High	4.33	0.24	4.52	0.22
PI29-03	High	3.62	0.16	3.37	0.15
PU20-03	High	3.45	0.16	3.73	0.16
R12-03	High	3.72	0.16	4.10	0.18
R23-04	High	4.70	0.17	5.53	0.30
Overall	Low	6.07	0.26	6.06	0.29
	High	4.23	0.18	4.61	0.38

Table 2.3. Mean (\pm SE) volume of sugar solution consumed per bout from each flower type for both the low and high mean volume treatments. The mean volume should be close to that of the nil flower type.

Mean Volume (μ l)	Flower	Mean volume consumed per bout	t statistic	df	p
20	Low	19.94 \pm 0.13	-0.471	4	0.6622
	Moderate	19.85 \pm 0.21	-0.6947	14	0.4986
	High	19.88 \pm 0.41	-0.3053	14	0.7647
	Extreme	19.35 \pm 0.86	-0.7497	4	0.4951
30	Low	30.11 \pm 0.15	0.744	4	0.4982
	Moderate	29.90 \pm 0.30	-0.3445	14	0.7356
	High	30.02 \pm 0.66	0.0232	14	0.9818
	Extreme	28.71 \pm 1.21	-1.0655	4	0.3467

Table 2.4. Individual flower rankings for both mean volume treatments and foraging environments (Baseline, Shift Down, and Shift Up).

Mean Volume	Bird	Baseline	Shift Down	Shift Up
Low (20 μ l)	B22-03	H>N>M*	N>M>L*	--
	B26-03	N>M>H*	N>L>M*	--
	PI25-03	N=H>M	L>M>N	--
	PU5-03	N>H>M*	M>N>L*	--
	B30-04	M>N>H	N>M>L*	--
	B3-03	M>N>H	--	N>H>E•
	R15-03	H>N>M*	--	H>N>E*
	R19-03	H>N>M*	--	E>N>H
	R27-03	M>N>H•	--	H>N>E
	R8-04	N>M>H*	--	E>N>H
High (30 μ l)	B14-03	M>H>N*	N>L>M*	--
	B30-03	M>H>N	M>N>L*	--
	G1-03	M>H>N•	N>L>M	--
	PI29-03	N>M>H	M>L>N	--
	G1-04	M>H>N*	M>N>L	--
	G18-03	M>H>N*	--	H>N>E
	PI2-03	M>N>H	--	N>E>H*
	PU20-03	M>H>N*	--	N>E>H*
	R12-03	N>M>H	--	H>N>E*
	R23-04	N>M>H*	--	E>N>H

• $P < 0.1$; * $P < 0.05$; chi square test

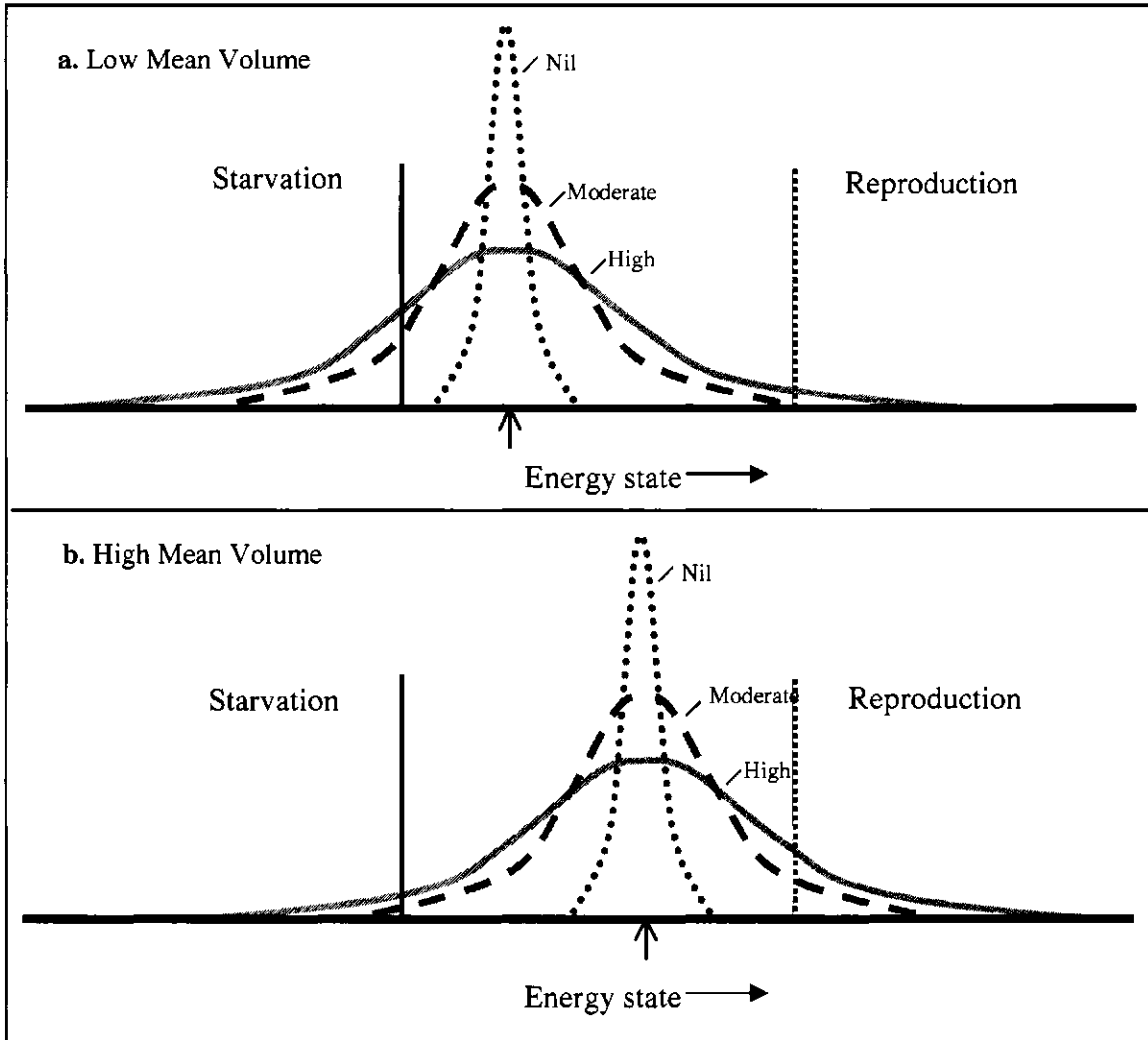


Figure 2. 1. Graphical presentation of the twin-threshold model. Distributions are the possible energy states of a forager feeding from a particular distribution. When the mean energy state of the forager is close to the starvation threshold (as in a. low mean volume) the optimal choice is the constant option (Nil). When a forager's energy state is closer to the reproduction threshold (as in b. high mean volume) the optimal choice is a variable option (Moderate or High). \uparrow represents the mean energy state of the animal foraging from the reward distributions.

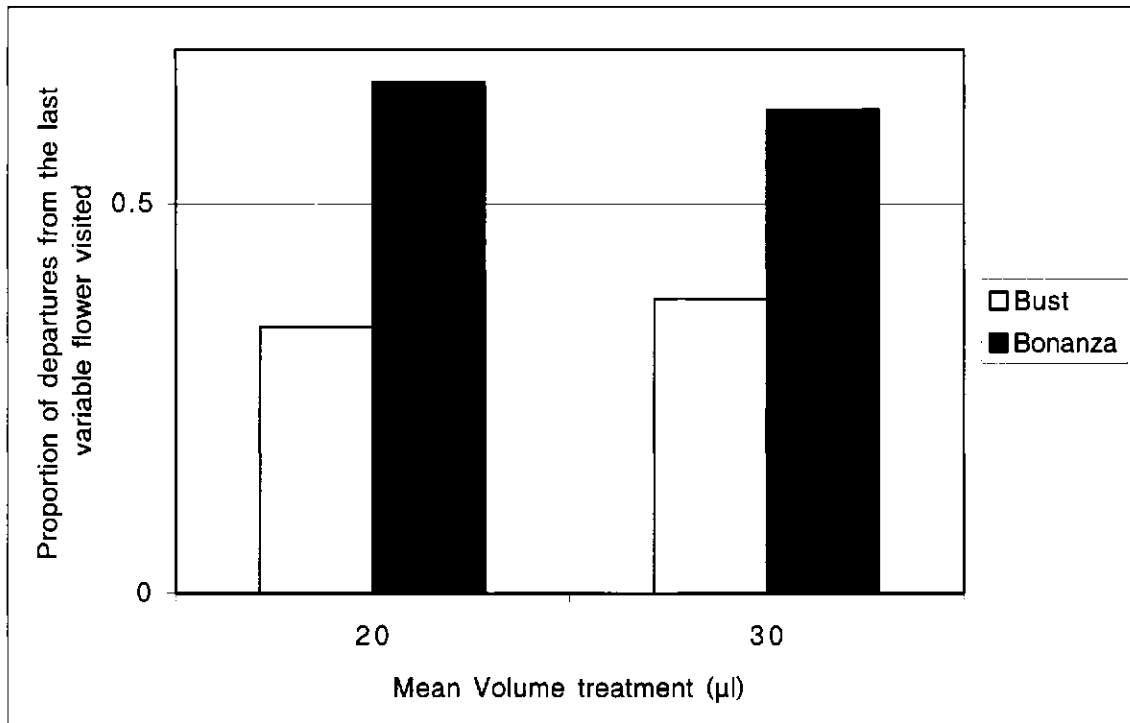


Figure 2. 2. Proportion of visits to a variable flower when the variable flower was the last flower visited. A strong association exists between departure and the volume of the variable flower (bust (lower volume) or bonanza (higher volume)). Subjects ended more bouts after visiting a bonanza flower than after a bust flower ($n = 20$).

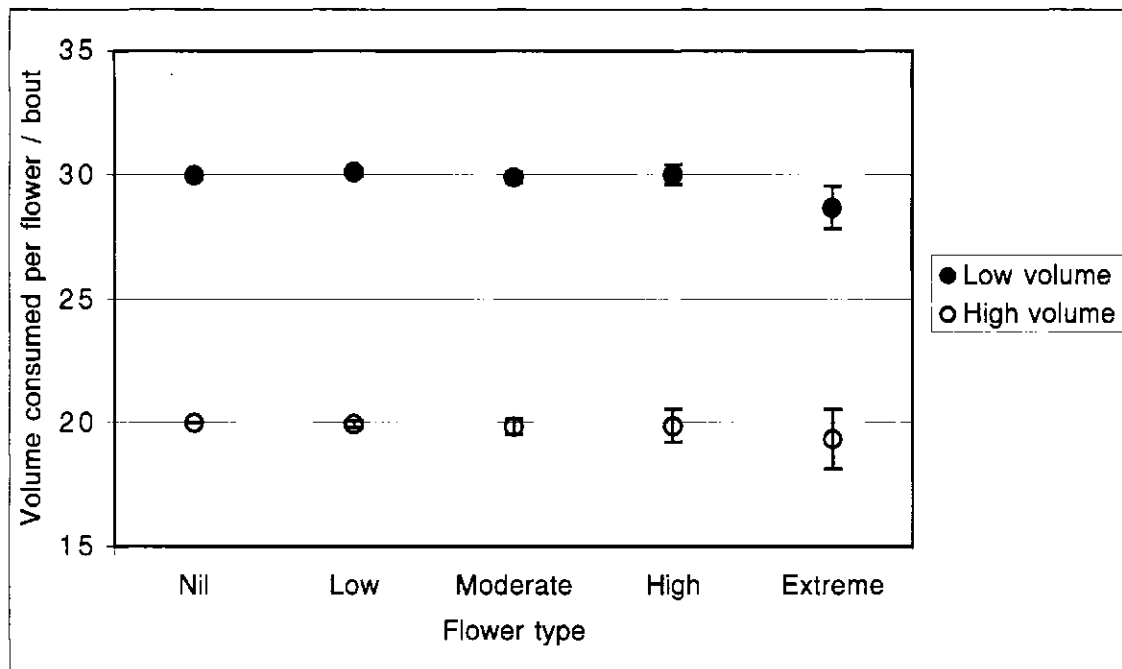


Figure 2. 3. Mean (\pm SE) volume of sucrose consumed from each flower type per bout. The nil flower type must be 20 μ l (low volume treatment) and 30 μ l (high volume treatment), averages for the variable flowers should equal that of the nil flower type of the same volume treatment (Nil: n = 20; Low: n = 10; Moderate: n = 20; High: n = 20; Extreme: n = 10).

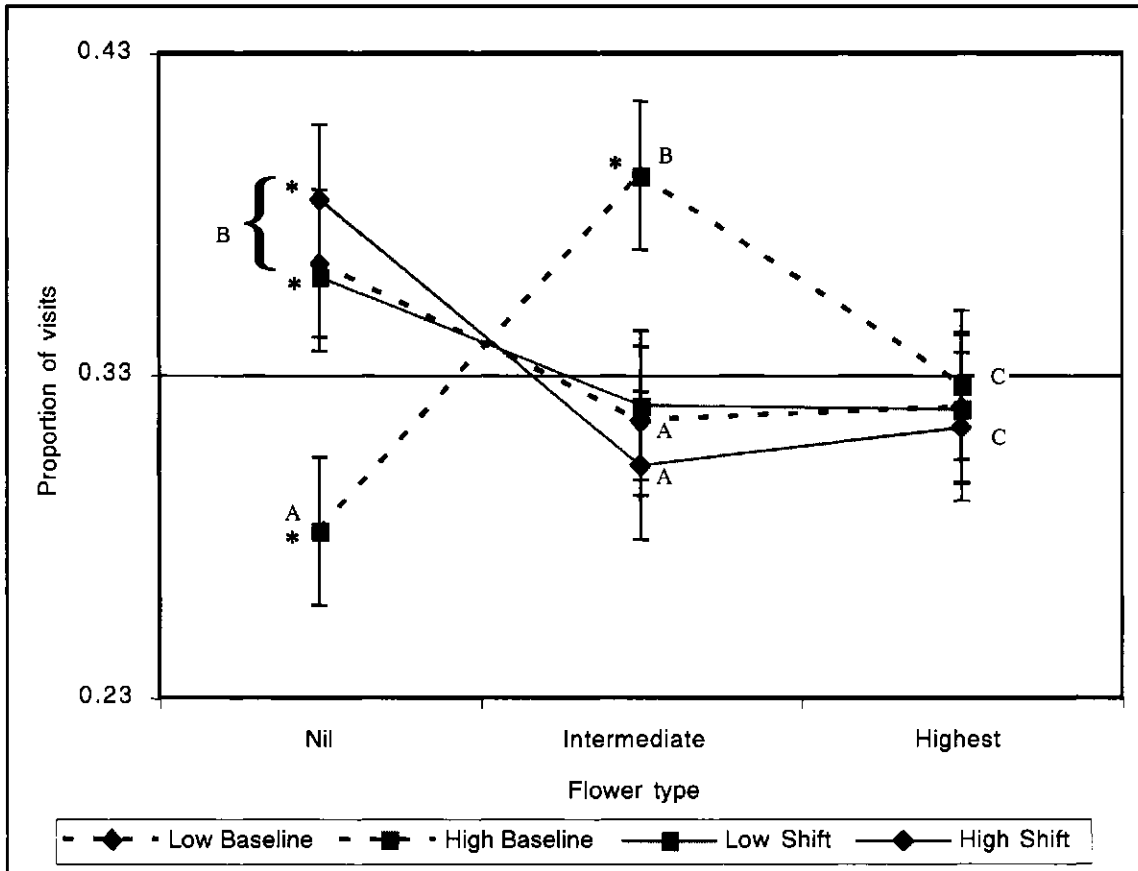


Figure 2. 4. Least square mean (\pm SE) proportion of visits to each flower type according to mean volume (high or low) and environment (baseline or shift). * indicates different from random (0.33). Letters represent least square means that are significantly different (Tukey-Kramer hsd ($P = 0.05$)) ($n = 10$).

Chapter 3

Risk-sensitive inflorescence departure: a test of the twin-threshold model

Abstract

This study tests predictions of the twin-threshold model of risk-sensitivity, which considers two energetic thresholds, a lower starvation threshold and a high reproductive threshold. The model predicts that when a forager's energy state slightly exceeds the starvation threshold the forager should respond in a risk-averse manner. When the forager's energy state is slightly below the higher reproductive threshold the forager should respond in a risk-prone manner. I tested these predictions with wild rufous hummingbirds (*Selasphorus rufus*) in southwestern Alberta, Canada. Hummingbirds were presented with a trinary comparison of artificial inflorescences with nil, moderate, and high variability in nectar volume, among flowers, but shared a common mean. To manipulate the energy state of the hummingbirds towards one of the energy thresholds I altered the cost of foraging. Hummingbirds experienced the trinary comparison with artificial inflorescences composed of flowers with long corollas (high cost of foraging) and short corollas (low cost of foraging). Risk-sensitive preferences were measured in terms of patch departure, based on the assumption that birds visit more flowers on inflorescences containing rewards they preferred than on inflorescences with rewards that were not preferred. When foraging from long corolla flowers hummingbirds preferred high variance inflorescences. However, when foraging from the short corolla flowers hummingbirds preferred both the moderate and high variance inflorescence. The preference for variance in both corolla treatments is consistent with models of risk-

sensitive foraging that include a reproductive threshold. The twin-threshold model accounts for the change in the number of flowers visited on inflorescences with moderate variance between the corolla treatments if specific assumptions of the energetic states of the hummingbirds and thresholds are met.

Introduction

An inflorescence is a set of flowers produced on a common stalk. From the perspective of a nectar-feeding animal, an inflorescence may be viewed as a patch (Pyke 1978; Cartar and Abrahams 1996). The optimal number of flowers visited on an inflorescence may be different depending on 'whose' perspective one takes, that of the animal or the plant. Pollinators visit large floral displays more often than they visit small floral displays (Klinkhammer et al. 1989, Ohara, and Higashi 1994). Plants may try to limit the number of flowers visited to decrease geitonogamy (within plant pollen transfer). Geitonogamy may lead to inbreeding depression of selfed progeny (Charlesworth and Charlesworth 1987) as well as a decrease in pollen export (decreased male fitness) (Klinkhammer and deJong 1993). Foraging theory, specifically the patch departure model, predicts that because a forager's rate of energy gain declines as the number of flowers probed increases, it should leave an inflorescence when the rate of gain is below the marginal rate of return (Stephens and Krebs 1986). However, a forager that is sensitive to variance around the mean reward (i.e., a risk-sensitive forager) may act to minimize the probability of an energy shortfall, a strategy that may not result in the highest net rate of energy gain. A risk-sensitive forager may minimize its risk of energy shortfall by visiting more flowers on an inflorescence whose flowers provide a constant nectar volume. Preference for inflorescence with either constant or variable nectar

volumes may be expressed by patch departure, that is, the number of flowers visited. Therefore, if nectar-feeding pollinators respond in a risk-sensitive manner, plants may produce variable nectar volumes within inflorescences to encourage early patch departure (Rathcke 1992; Pappers et al. 1999, Biernaskie and Cartar 2004).

Within-plant variation in nectar production could be an adaptive trait in plants (Feinsinger 1978; Pleasants 1983; Rathcke 1992; Pappers et al. 1999). Plants could use nectar variation to increase the rate of pollinator departure, and therefore, decrease geitonogamy. A plant could display several open flowers to attract foragers, but then encourage quick departure of risk-averse pollinators by presenting highly variable nectar content among flowers. Indeed, a relationship exists between nectar reward variation and floral display size. Biernaskie and Cartar (2004) observed a positive correlation between nectar reward variation and the number of open flowers on the inflorescence. If pollinators are risk-averse foragers, for which there is ample evidence (for a review see Perez and Waddington, 1996), then presenting an inflorescence of variable nectar volumes will encourage pollinators to depart early. Biernaskie et al. (2002) demonstrated that both rufous hummingbirds (*Selasphorus rufus*) and bumblebees (*Bombus flavifrons*) expressed preference for constancy by visiting more flowers on constantly rewarding inflorescence than on the variably rewarding inflorescence. Biernaskie et al. (2002) interpreted this behaviour as an adaptation to minimize the probability of falling below an energy threshold. However, Cartar and Abrahams (1996) found no evidence of risk-sensitive patch departure and concluded that shortfall-minimization does not explain patch departure by bees.

The energy-budget rule of risk sensitive foraging predicts that a forager on a negative energy trajectory should be risk-prone and when on a positive energy trajectory should be risk-averse when given the binary choice between constant and variable reward options (energy budget rule: Stephens 1981). A recent model of risk-sensitive foraging, the twin- threshold model, suggests that risk-prone behaviour may have added fitness benefits for a forager experiencing a positive energy budget (Hurly 2003; Figure 3.1). The twin-threshold model includes both a starvation threshold and a higher reproductive threshold and predicts risk-aversion when the forager's energy state exceeds the starvation threshold, but is closer to the lower starvation threshold than the higher reproduction threshold. When the forager's energy state is closer to the reproduction threshold, the model predicts risk-prone behaviour. However, there exists an energetic state between the two thresholds where the model predicts preference for a moderately variable flower. The logic of these predictions is presented graphically in Figure 3.1.

A forager's energy state could be manipulated by changing either the mean foraging return per patch or the cost of foraging. Foraging costs could be altered in several different ways (e.g., distance between inflorescences, corolla length). In hummingbirds, the cost of hovering flight is more energetically expensive than forward flight (Tamm 1989). Therefore, manipulating the time spent hovering will have a greater impact on energetic state than manipulating the distance between inflorescences, which only involves forward flight. Both gross and net energy intake rates vary negatively with corolla length (Montgomerie 1984). Given the choice, hummingbirds should forage preferentially from flowers with the shortest corolla, all else being equal. Long corollas are more costly and would also be a more hazardous option in terms of predator

avoidance because the longer access time to reach the nectar would increase the time needed to withdraw from the flower and avoid a predator.

Hurly (2003) tested the predictions of the twin-threshold model with rufous hummingbirds by increasing or decreasing the mean nectar volume of the rewards after subjects had foraged from flower types with nil, moderate, and high variability in nectar volume, but all with the same mean volume. After the baseline comparison, the common mean was either increased or decreased for each subject. Rufous hummingbirds responded in a manner consistent with the predictions of the twin-threshold model; increasing their preference for the high variance option when mean nectar volume was increased, but increasing their preference for the nil variance option when the mean nectar volume was decreased. In another study, conducted to replicate the results of Hurly and Oseen (1999), Bateson, (2002) employed the logic of the twin-threshold model to explain the decrease in risk-prone foraging of European starlings (*Sturnus vulgaris*) at warmer temperatures.

Here I present a novel test of the twin-threshold model in which I manipulated the cost of foraging by altering the corolla length of artificial flowers. The twin-threshold model predicts more risk-averse foraging when birds forage from flowers with long corollas and more risk-prone foraging when they forage from flowers with short corollas. The effect on net energy intake of foraging from flowers with either long or short corollas is the same as decreasing or increasing the mean volume of the foraging reward respectively. Typically, preferences in risk-sensitive studies are expressed as the proportion of visits to either the constant or variable option (Caraco 1980; Caraco 1982; Hurly and Oseen 1999; Hurly 2003). However, as mentioned above, risk-sensitive

preferences may also be expressed in terms of patch departure (Stephens and Charnov 1982; Bernard and Brown 1987; Abraham and Cartar 1996; Biernaskie et al. 2002). I tested the predictions of the twin-threshold model using both inflorescence choice and patch departure as measures of risk-sensitivity. If hummingbirds express risk-sensitive preferences in terms of patch departure, then they would demonstrate risk-prone behaviour by visiting more flowers on a high-variance inflorescence, whereas they would demonstrate risk aversion by visiting more flowers on a nil inflorescence. The inclusion of a second variable (moderate) option in the choice set, made the foraging environment more realistic (i.e., more than two flower types to choose from). Also, the context in which rewards are presented to hummingbirds may influence the perceived utility of each option (Hurly and Oseen 1999). The twin-threshold model predicts that for some energy states between the starvation and reproduction thresholds the moderate option may be the superior option in terms of fitness maximization.

Methods

Study Site and Study Animals

The experiment was conducted in the Westcastle River valley (49° 29' N, 114° 23' W; elevation 1400 m) in the eastern slopes of the Rocky Mountains west of Pincher Creek, AB, Canada. The subjects were 9 male rufous hummingbirds that established territories around commercial hummingbird feeders. Feeders were placed throughout the valley during May and were spaced at least 100 m apart. Subjects were identified individually by a small mark of non-toxic ink sprayed onto the subject's breast. Data were collected between 0600h – 2000h during June and July 2004.

Training

Hummingbirds were trained to drink 20% sucrose from artificial inflorescences. Inflorescences were made from wooden doweling 90 cm long with 12 artificial flowers, four columns of three in each cardinal direction. Artificial flowers consisted of a plastic pipette tip inserted through the center of a coloured paper disk (diameter= 24mm). Pipette tips were crimped at the end to prevent sucrose from draining out. Flowers were inserted into corks that were attached to the wooden dowel at an angle of 45° above the horizontal. Flowers started 10 cm from the top of the doweling and consecutive flowers were spaced 10 cm apart.

Trinary choice

The experiment contrasted two treatments of trinary comparisons. Trinary comparisons were between inflorescences with nil, moderate, and high variance in nectar volume. Inflorescences in one treatment had artificial flowers with short corollas (15mm) , whereas the other treatment had artificial flowers with long corollas (25mm). Corolla lengths were chosen following Montgomerie et al. (1984) who demonstrated that drink time increased drastically when the corolla exceeded a hummingbird's culmen. Therefore, corolla lengths were chosen based on the average culmen length of rufous hummingbirds (16.5 mm (n=18) (Johnsgard 1997)) one corolla length less than the average culmen length and one greater. To confirm that corolla length increased ingestion time, and thus net energy intake, I recorded the ingestion time of one hummingbird foraging from four different corolla lengths (10, 15, 25, and 30mm) in a laboratory setting. Drink times from the 25 and 30mm corolla flowers were significantly greater than drinks times from 10 and 15mm corollas (10mm: 0.77s ± 0.11, 15mm: 0.91s

± 0.07 , 25mm: 1.37 ± 0.19 , 30mm: 1.38 ± 0.25 , (Mean \pm SD); ANOVA: $F_{3,116} = 98.74$, $P < 0.0001$). In the experiment, short corolla length was 15mm long corolla length was 25 mm so that the cost of foraging from deep flowers should be about 50% greater than from shallow flowers. Hummingbirds were able to harvest all the nectar from both corolla lengths.

The order of the corolla treatments was assigned randomly to each bird, with 5 birds experiencing short corollas first and 4 birds experiencing long corollas first. Each treatment lasted for 72 foraging bouts. Each visit to the inflorescence patch was considered a foraging bout. The order in which inflorescences were visited and the number of flowers visited per inflorescence were recorded for each foraging bout.

Birds foraged from an array of 6 inflorescences, 2 of each variance level, each containing 12 flowers. Inflorescences were arranged in a hexagonal pattern with a nearest neighbour distance of 30 cm. Three inflorescence arrangements were used throughout the experiment, with a different arrangement being used after every six bouts. The entire array was moved at least 1m and rotated 90° after every foraging bout.

All the flowers on a nil variance inflorescence contained $10\mu\text{l}$ of 20% sucrose solution. Half of the flowers on a moderate variance inflorescence contained $5\mu\text{l}$ and the other half contained $15\mu\text{l}$. On a high variance inflorescence half the flowers contained $0\mu\text{l}$ and the other half contained $20\mu\text{l}$. Therefore, all three inflorescence types offered the same mean reward. To ensure that birds did not learn the position of the high-volume flowers on variable inflorescences, the high and low volumes were assigned randomly to each flower. A different random order was used for both the moderate and high inflorescences, which was changed after every 6 foraging bouts.

After the first 18 bouts the data were checked to determine that the bird had experienced each inflorescence type. If one inflorescence type had been visited three times or fewer the bird was forced to visit the avoided inflorescence. Three stalks of the avoided inflorescence type were presented to the subject in isolation. Once the subjects visited the avoided inflorescence type three times (approximately 2 foraging bouts) the experiment proper was restarted. Two birds needed the correction for one treatment each, therefore the correction was needed only twice out of 18 treatments.

Analysis

To assess the effect of corolla length on departure behaviour, mean number of flower visits per inflorescence were analyzed using a mixed model ANOVA with two within-subject factors (Inflorescence variance: Nil, Moderate, and High; and Corolla length; Short and Long) and one between-subject factor (Order: Short corolla – Long corolla and Long corolla – Short corolla). Subject was included as a random effect. The effect of corolla length on inflorescence choice was analyzed using a mixed model ANOVA with two within-subject factors (Inflorescence: Nil, Moderate, and High; and Corolla length; Short and Long) and one between-subject factor (Order: Short corolla – Long corolla and Long corolla – Short corolla). Tukey-Kramer's hsd post-hoc test was used to determine which group means differed significantly at $P = 0.05$. *Wilcoxon* signed-rank test was used, instead of a one-sample t-test, to test inflorescence choices against a random expectation of 0.33 because data were not normally distributed. Data were analyzed using JMP 4.0 (JMP 2000). Where means are reported, variation is ± 1 standard error.

Results

A hummingbird visited the inflorescence patch every 4-30 minutes throughout the day. While at the inflorescence patch hummingbirds visited 2.57 ± 0.03 inflorescences per bout and a total of 13.12 ± 0.15 flowers per foraging bout (see Table 3.1 for individual hummingbird data). From the available 720 μl of sucrose hummingbirds consumed 129.02 ± 8.45 μl per foraging bout.

Nectar volumes experienced by birds

The mean nectar volume consumed from flowers on the variable inflorescences should equal the nectar volume consumed from flowers on the nil inflorescence. There was no significant difference between mean nectar volumes consumed per flower from the three different inflorescence types (ANOVA: $F_{2,24} = 1.81$, $P = 0.1851$).

To confirm that subjects did not use visual or olfactory cues to identify, and subsequently forage exclusively from, high-volume flowers on variable inflorescences I also tested whether the mean volume consumed per flower per inflorescence per foraging bout on a variable inflorescence differed from 10 μl . The mean flower volume of the moderate and high variance inflorescence did not differ from 10 μl (one sample t- tests: moderate: $t_8 = -1.6696$, $P = 0.1336$; high: $t_8 = 0.53$, $P = 0.6083$; Figure 3.2). Therefore, differences observed in the number of flowers visited per inflorescences type and inflorescence choice are likely to be attributed to risk-sensitive foraging behaviour.

Individual preferences

Hummingbirds significantly preferred specific inflorescence type, but preferences varied between birds. Subjects ranked the nil, moderate and high variance inflorescences in several different orders (Table 3.2). Of the 18 trinary comparisons (Short and Long

corolla treatment for all subjects) all but two of the comparisons showed a significant difference in the total number of flowers visited to each inflorescence type (Table 3.2). Even though there was little concordance between hummingbirds, hummingbirds developed significant preferences within the treatments.

Number of flowers visited before departure

A clear effect of corolla length is indicated by a significant interaction between Corolla depth and Inflorescence variance (ANOVA: $F_{2,14} = 4.38$, $P = 0.0299$; Figure 3.3). Hummingbirds visited more flowers on moderate variance inflorescences with short corollas than with long corollas. When foraging from inflorescences with short corollas hummingbirds visited more flowers on moderate and high variance inflorescences than on nil variance inflorescences (Tukey-Kramer hsd ($P = 0.05$)). On inflorescences with long corollas, hummingbirds visited more flowers on high variance inflorescences than on moderate and nil variance inflorescences.

The number of flowers that birds visited on the inflorescences depended jointly on the order in which subjects experienced the corolla treatments and corolla depth (ANOVA: $F_{1,7} = 5.54$, $P = 0.0490$; Figure 3.4). Subjects that experienced the long corolla treatment first visited more flowers per inflorescence when corollas were short (Tukey-Kramer hsd ($P = 0.05$)). This difference in the number of flowers visited between corolla treatments was not evident for subjects that experienced the short corollas first.

Inflorescence choice

Preference measured by the proportion of inflorescence type visited per bout as the dependent variable produced results that parallel the number of flowers visited, but neither main effects nor interactions were statistically significant. Despite the lack of

primary effects in the main analysis, subjects visited the nil variance inflorescence less often than expected by random chance (Wilcoxon signed-rank test against random expectation of 0.33: $W_8 = -19.50$, $P = 0.0200$) and visited the moderate variance inflorescence more often than expected by chance in the short corolla treatment (Wilcoxon signed-rank test against random expectation of 0.33: $W_8 = 18.50$, $P = 0.0270$) (Figure 3.5). The change in the proportion of visits to the moderate variance inflorescences was also parallel to the inflorescence departure results reported above. Proportion of visits to the moderate variance inflorescence was higher in the short corolla treatment than in the long corolla treatment (Tukey-Kramer hsd ($P = 0.05$)).

Discussion

Hummingbirds foraging from artificial flowers with short corollas visited more flowers on moderate and high inflorescences than on nil variance inflorescences. That is, hummingbirds were risk preferring when the cost of foraging was low. When foraging from flowers with long corollas, hummingbirds visited a similar number of flowers on high variance inflorescences as when corollas were short. However, hummingbirds visited fewer flowers on moderate variance inflorescences when corollas were long.

Why did hummingbirds leave an inflorescence for another inflorescence before visiting all flowers on the first inflorescence? Inflorescences were presented twelve flowers, but on average hummingbirds visited only 5.63 ± 0.27 flowers per inflorescence and left approximately 60 μ l of nectar remaining. One possible explanation is that the birds may have departed after becoming satiated, but if this were the case, they could have visited more flowers on one inflorescence. On average hummingbirds visited 2.57

± 0.03 inflorescences per bout (see Table 1). The male hummingbirds in this study were defending breeding territories and were free to engage in reproductive activities. Therefore, birds may have left the inflorescences early to chase away intruders or to engage in courtship displays and mating. Such departure may have happened a few times; however, most foraging bouts ended with the hummingbird returning to a perch until the next foraging bout (personal observation).

The marginal value theorem predicts that a forager should leave a patch when net energy intake from the patch falls below the marginal rate of energy return for the entire habitat (Charnov 1976). Therefore, for patch depression to account for early departure, the rate of energy intake would have to decline as the hummingbirds visited more flowers on an inflorescence. Ohashi and Yahara (2001) suggested two mechanisms that could cause patch depression within an inflorescence. One possibility is that nonrandom foraging behaviour of pollinators may be coupled with variation in nectar production of plants. For example, nectar production decreases within an inflorescence from bottom to top, and a pollinator starts foraging at the bottom and move upward, the pollinator would experience a decrease in energy gain per flower. Such an explanation is not applicable in this study, nectar volumes were assigned randomly to flowers and volumes did not vary systematically within inflorescences. To ensure that hummingbirds would not learn the position of the 'bonanza' flowers on the variable inflorescence, flower volume assignments were changed after every six foraging bouts and the entire inflorescence array was rotated after every bout. Furthermore, the nil variance inflorescence provided the same volume in all flowers within the inflorescence and birds departed earlier from

this inflorescence type than from any other. Therefore, inflorescence departure was not coupled with a pattern of nectar variation within the artificial inflorescence.

A second possible cause of patch depression can also occur if the probability of revisitation increases with the number of flowers probed on an inflorescence. Ohashi and Yahara (1999) modeled the optimal number of flowers a pollinator should visit on an inflorescence with probability of revisitation as a major factor. In the present study, and in other studies with the same system (Hurly and Oseen 1999), the number of flower revisits was low (<1%) and probably did not cause patch depression in the artificial inflorescences.

A third possible cause of patch depression, suggested by Tamm (1989), is that the accumulating nectar load while foraging increases the overall mass of the hummingbird and therefore, increases the cost of foraging throughout the bout. According to this explanation the number of flowers visited on each inflorescence type should be the same, because they all offered the same long-term rate of energy intake. However, the number of flower visits differed between inflorescence types in the present study. Increasing nectar load mass probably had little effect on inflorescence departure in this study.

Variability in nectar volume may also affect the departure of hummingbirds. In a simulation model with bumblebees Pappas et al. (1999) demonstrated that variability in nectar rewards causes risk-averse departure and shortened the stay on inflorescences. In a field experiment, Biernaskie et al. (2002) too found that bumblebees (*Bombus flavifrons*) and rufous hummingbirds presented with a binary choice set of constant and variable inflorescences (2 of each type), visited more flowers on constant inflorescences than on variable inflorescences. They interpreted this behaviour as a strategy to minimize

the probability of falling below a critical starvation threshold. That is, bumble bees and hummingbirds responded in a manner consistent with the energy-budget model of risk sensitivity. Biernaskie et al. (2002) suggested that by leaving an inflorescence early, both species accepted a lower long-term rate of energy intake to attain less variability in energy intake.

The twin-threshold model of risk-sensitivity predicts that when the cost of foraging is high, a forager should prefer the nil option. Hummingbirds foraging from long corollas (relative high cost of foraging) did not prefer, nor increase their preference for, the nil variance option. When the cost of foraging was relatively high hummingbirds maintained their preference for the high variance option and decreased their preference for the moderate option, a result not predicted by the twin-threshold model. The preference for the moderate and high flower options exhibited by hummingbirds in the present study is consistent with the results of several risk-sensitive models that include a reproductive threshold (Caraco and Gillespie 1986; Gillespie and Caraco 1987; Schmitz and Ritchie 1991; Bednekoff 1996; McNamara et al. 1991; Hurly 2003). Generally, these models predict that if a forager energy state is just below a reproduction threshold (and the risk of starvation is low) the superior policy is to be risk-prone. I interpret this risk-prone behaviour of rufous hummingbirds as an adaptation to maximize the probability of reproduction.

Do the data from this experiment provide any support for the idea that two energetic thresholds influence hummingbird foraging behaviour? Yes, there are three aspects of foraging behaviour that could be considered to be consistent with animals trading-off costs and benefits resulting from two thresholds. First, the tendency of

hummingbirds to prefer the variable options is consistent with the predictions of the model. When the energy state of a hummingbird is slightly below the reproductive threshold the model predicts preference for variability (see also: Caraco and Gillespie 1986; Gillespie and Caraco 1987; Schmitz and Ritchie 1991; Bednekoff 1996; McNamara et al. 1991). I interpret this preference for variability by rufous hummingbirds as an adaptation to maximize the probability of reproduction. Second, the behaviour that changed most between the corolla treatments was the number of flowers visited on moderate inflorescences, with birds visiting more flowers on moderate variance inflorescences when corollas were short than when corollas were long. Essentially, the subjects were more risk-averse when the corollas were long and more risk-prone when corollas were short, as predicted by the twin-threshold model. Third, the maintenance of nil and high departure values between corolla treatments seems unusual. The most straight-forward interpretation of the twin-threshold model predicts that when corollas were long the birds should visit more flowers on the nil variance inflorescences and when the corollas were short they should visit more flowers on the high variance inflorescences. However, a very specific configuration of the twin-threshold model could account for the difference in the number of flowers visited on moderate inflorescences and the maintenance of nil and high departure values between corolla treatments.

Predictions of the twin-threshold model depend on the relation of an animal's energy state to the starvation and reproductive thresholds. However, I do not know either the exact energy state of the hummingbirds or the position of the thresholds. I assumed that increasing the corolla length by 10 mm would shift the energy state of the

hummingbirds below the midpoint between the two thresholds, a situation in which the twin-threshold model predicts risk-averse foraging. However, hummingbirds responded as if their energy state had only decreased enough that moderate variance inflorescences offered little chance of an energy state exceeding the reproductive threshold when corolla length was long (see Figure 3.6). Hummingbirds behaved as if their energy state was closer to the reproductive threshold than to the starvation threshold in both corolla treatments. Whereas this interpretation is consistent with the twin-threshold model, it is important to note that further tests of the model are required to increase confidence in this interpretation.

The change in corolla length may not have had a profound effect on net energy gain between the two corolla treatments. Montgomerie (1984) found that corollas up to a few mm longer than the hummingbirds' bill had little effect on handling time. A marked increase in handling time was only evident when the corolla length was considerably greater than the culmen length of the bird. Increased tongue extension with these long corollas most probably caused the marked increase in handling time (Montgomerie 1984). The average culmen length of male rufous hummingbirds is 16.5 mm (n=18) (Johnsgard 1997). The corolla lengths used in the present study were 15mm and 25 mm. These corolla lengths appear to be on different sides of the 'marked increase in handling time' noted by Montgomerie (1984). However, the corollas appeared to have altered the energy state only slightly. A more extreme corolla length may have created a larger shift in energy state of the hummingbirds. However, an initial trial with a long corolla length of 30mm resulted in no nectar being removed from the flowers. Hummingbirds seemed reluctant to forage from long artificial corollas in the wild. In future studies, training

hummingbirds to probe more deeply may allow for the use of longer corollas to manipulate the cost of foraging. The reluctance shown by wild hummingbirds to forage from long corollas strongly suggests that long corollas are costly to forage from and are therefore an appropriate manipulation of energy state.

The present study is similar to that of Biernaskie et al (2002) in that the response to nectar variation was measured in terms of inflorescence departure (see also: Barnard and Brown 1987; Cartar and Abraham 1996). However, the present study differs from Biernaskie et al (2002) in two ways. First, the cost of foraging was manipulated by altering corolla length. Second, hummingbirds were presented with a choice set of three rather than two foraging options. Hurly and Oseen (1999) suggest that the importance of variability on foraging decisions would be more convincing if the choice set included more than two foraging options. As well, broader choice would replicate a more natural setting in which hummingbirds experience more than two flower species at a time. The context in which an animal experiences a foraging reward also influences foraging preferences (Shafir 1994; Hurly and Oseen 1999; Bateson et al. 2002; Bateson et al. 2003; Hurly 2003). For example, the inclusion of a third option in the choice may alter the relative preferences of the initial options (Hurly and Oseen 1999; Bateson et al. 2002; Bateson et al. 2002). That is, the choices of animals may not be rational in that animals may not evaluate alternative foraging options using absolute currencies. Instead, animals may employ a relative or comparative evaluation mechanism in foraging decision making. The perceived utility of an option may be influenced by the characteristics of the other options in the choice set.

If hummingbirds employ a comparative evaluation mechanism, the difference in risk-preference between the present study (preference for variable) and that of Biernaskie et al. (2002) (preference for constant) may be partially accounted for. When presented with a binary choice between constant and variable inflorescences, hummingbirds preferred the constant option to the variable option (Hurly and Oseen 1999; Biernaskie et al. 2002). However, when presented with a choice set of three options (nil, moderate, and high levels of variance), hummingbirds frequently prefer the moderate option (Hurly and Oseen 1999) even though the nil option was preferred in a binary choice set of nil and moderate. The perceived utility of the moderate option may be dependent upon the presence of the high option. However, comparison between the present study and Biernaskie et al. (2002) is confounded by differences in the mean volume of the flower rewards. The mean volume in the present study was twice as high as that used in Biernaskie et al (2002). Mean volume of the flower rewards influence risk preferences (Hurly 2003; Klassen and Hurly unpublished data). Low mean volume would result in an energy state closer to the starvation threshold, a situation in which nil would provide the lowest threat of starvation. A high mean volume reward results in an energy state closer to the reproductive threshold, a situation in which preference for variability would increase the probability of reproduction.

With an increase in the cost of foraging hummingbirds should increase the number of flowers visited to compensate for the lower energy gain. However, there was no significant increase in the number of flowers visited in the long corolla treatment. In fact, there was a slight decrease, which is evident in Figure 3.3. The fewer flowers visited on moderate inflorescences make it appear as if the number of flowers visited

differed between the corolla treatments. This slight difference may be an artifact of the interaction between corolla and the order in which hummingbirds received the corolla treatments. In general, subjects visited more flower during the second treatment. However, the magnitude of the increase depended on the order in which hummingbirds received the corolla treatment. There was only a significant difference in number of flowers visited when hummingbirds experienced the short corolla treatment after the long corolla treatment. It is not clear why hummingbirds increased the number of flowers visited on the short corolla inflorescence after experiencing an inflorescence with long corolla flowers.

Inflorescence choice

Risk sensitive preferences were expressed in terms of patch departure and not demonstrated in inflorescence choice. Inflorescences were identified by colour and therefore hummingbirds could learn the association between colour and inflorescence variability. Inflorescence choice data were parallel to those of the patch departure data, but not statistically significant. However, the proportion of visits to the moderate inflorescence was significantly higher in the short corolla treatment than in the long corolla treatment. This change in the proportion of visits to the moderate inflorescence is also consistent with the specific configuration of the twin-threshold model described above that accounted for the change in moderate inflorescence departure values between corolla treatments. Again, more data are needed to increase the confidence of this interpretation of the twin-threshold model.

Summary

The present study is unique in that it tested the twin-threshold model of risk-sensitivity using an alternative measure of preference, that being patch departure. When hummingbirds were presented with three inflorescences that offered the same mean reward but differed in the variance around that mean, hummingbirds were risk preferring. When the cost of foraging was relatively low hummingbirds responded as if the variable options provided the greatest value, possibly because they offered the highest probability of reproduction. When the cost of foraging was relatively high hummingbirds responded as if they devalued the moderate reward and they departed earlier from the moderate inflorescence. The preference for variance is consistent with risk-sensitive models that include a reproductive threshold. Preference for the variable options may be an adaptation to maximize the probability of reproduction. If several specific energetic assumptions are made, the lower number of flowers visited on a moderate inflorescence in the long corolla treatment can be accounted for by the twin-threshold model. My results, along with the results of Biernaskie et al. (2002), further demonstrate that the foraging preferences of hummingbirds in risk-sensitive studies are context dependent (Hurly and Oseen), the addition of a second variable option influences the number of flowers visited on an inflorescence. However, risk-sensitive inflorescence departure may, and should also be dependent on the energy state of the forager.

References

- Barnard, C.J., and Brown, C.A.J.** 1987. Risk-sensitive foraging and patch residence time in common shrews, *Sorex araneus* L. *Animal Behaviour*, **35**, 1255-1257..
- Bateson, M.** 2002. Context-dependent foraging choices in risk-sensitive starlings. *Animal Behaviour*, **64**, 251-260.
- Bateson, M., Healy, S.D., and Hurly, T.A.** 2002. Irrational choices in hummingbird foraging behaviour. *Animal Behaviour*, **63**, 587-596.
- Bateson, M., Healy, S.D., and Hurly, T.A.** 2003. Context-dependent foraging decisions in rufous hummingbirds. *Proceedings of the Royal Society. London. B.*, **270**, 1271-1276.
- Biernaskie, J.M., and R.V. Cartar.** 2004. Variation in rate of nectar production depends on floral display size: a pollinator manipulation hypothesis. *Functional Ecology*, **18**, 125-129.
- Biernaskie, J.M., R.V. Cartar, and T.A. Hurly.** 2002. Risk-averse inflorescence departure in hummingbirds and bumblebee: could plants benefit from variable nectar volumes? *Oikos*, **98**, 98-104.
- Caraco, T.** 1980. On foraging time allocation in a stochastic environment. *Ecology*, **61**, 119-128.
- Caraco, T.** 1982. Aspects of risk-aversion in foraging white-crowned sparrows. *Animal Behaviour*, **30**, 719-727.
- Caraco, T, and Gillespie, R.G.** 1986. Risk-sensitivity: foraging mode in an ambush predator. *Ecology*, **67**, 1180-1185.
- Cartar, R.V., and M.V. Abrahams.** 1996. Risk-sensitive foraging in a patch departure context: A test with worker bumblebees. *American Zoologist*, **36**, 447-458.
- Charlesworth, D. and Charlesworth, B.** 1987. Inbreeding Depression and its Evolutionary Consequences. *Annual Review of Ecology and Systematics*, **18**, 237-268.
- Charnov, E.L.** 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-135.
- Feinsinger, P.** 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs*, **48**, 269-287.

- Gillespie, R.G., and Caraco, T.** 1987. Risk-sensitive foraging strategies of two spider populations. *Ecology*, **68**, 887-899.
- Hurly, T.A.** 2003. The twin-threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Animal Behaviour*, **66**, 751-761.
- Hurly, T.A., and Oseen, M.D.** 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Animal Behaviour*, **58**, 59-66.
- JMP 4.0.** 2000. SAS Institute, NC.
- Johnsgard, P.A.** 1997. *The hummingbirds of North America: Second Edition.* Smithsonian Institution Press, Washington, D.C.
- Klinkhamer, P.G.L., and deJong, T.J.** 1993. Attractiveness to pollinators: a plant's dilemma. *Oikos*, **66**, 180-184.
- Klinkhamer, P.G.L., deJong, T.J., and de Bruyn, G-J.** 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos*, **54**, 201-204.
- McNamara, J.M., Merad, S., and Houston, A.I.** 1991. A model of risk-sensitive foraging for a reproducing animal. *Animal Behaviour*, **41**, 787-792.
- Montgomerie, R.D.** 1984. Nectar extraction by hummingbirds: response to different floral characters. *Oecologia*, **63**, 229-236.
- Ohara, M., and Higashi, S.** 1994. Effects of inflorescence size on visits from pollinators and seed set of *Corydalis ambigua* (Papaveraceae). *Oecologia*, **98**, 25-30.
- Ohashi, K., and T. Yahara.** 1999. How long to stay on, and how often to visit a flowering plant? - a model for foraging strategy when floral displays vary in size. *Oikos*, **86**, 386-392.
- Ohashi, K., and T. Yahara.** 2001. Behavioral responses of pollinators to variation in floral display size and their influence on the evolution of floral traits. In: *Cognitive Ecology of Pollination* (Ed. By L. Chittka and J.D. Thomson), pp. 274-296. Cambridge: Cambridge University Press.
- Pappers, S.M., deJong, T.J., Klinkhamer, P.G.L., and Meelis, E.** 1999. Effects of nectar content on the number of bumblebee approaches and the length of visitation sequences in *Echium vulgare* (Boraginaceae). *Oikos*, **87**, 580-586.
- Perez, S.M., and Waddington, K.D.** 1996. Carpenter bee (*Xylocopa micans*) risk indifference and a review of nectarivore risk-sensitivity studies. *American Zoologist*, **36**, 435-446.

- Pleasant, J.M.** 1983. Nectar production patterns in *Ipomopsis aggregata* (Polemoniaceae). *American Journal of Botany*, **70**, 1468-1475.
- Pyke, G.H.** 1978. Optimal foraging in hummingbirds: testing the marginal value theorem. *American Zoologist*, **18**, 739-752.
- Rathcke, B.J.** 1992. Nectar distributions, pollinator behavior, and plant reproductive success. In: Hunter, M.D., Ohgushi, T. and Price, P.W. (eds), *Effects of resource distribution on animal-plant interactions*. Academic Press, pp. 114-138.
- Shafir, S.** 1994. Intransitivity of preferences in honey bees: support for 'comparative' evaluation of foraging options. *Animal Behaviour*, **48**, 55-67.
- Schmitz, O.J., and Ritchie, M.E.** 1991. Optimal diet selection with variable nutrient intake: balancing reproduction with risk of starvation. *Theoretical population biology*, **39**, 100-114.
- Stephens, D.W.** 1981. The logic of risk-sensitive foraging preferences. *Animal Behaviour*, **29**, 628-629.
- Stephens, D.W., and Charnov, E.L.** 1982. Optimal foraging: some simple stochastic models. *Behavioral Ecology and Sociobiology*, **10**, 251-263.
- Stephens, D.W., and Krebs, J.R.** 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Tamm, S.** 1989. Importance of energy costs in central place foraging hummingbirds. *Ecology*, **70**, 195-205.

Table 3.1. Mean number of inflorescences visited and number of flowers visited by each subject per bout.

Subject	N	Mean Number of Inflorescences Visited per bout	Standard Error	Mean Number of Flowers Visited per bout	Standard Error
Blue30	147	2.86	0.10	17.62	0.52
Green 1	148	3.12	0.09	17.76	0.49
Green 28	144	2.81	0.08	12.68	0.35
L22	152	2.52	0.08	11.95	0.28
Pink 2	143	2.28	0.08	8.71	0.26
Pink 22	144	2.78	0.08	13.16	0.38
Pink 29	145	1.94	0.07	9.87	0.34
Red 23	144	2.63	0.10	13.60	0.48
Red 8	144	2.18	0.07	12.63	0.31
Overall	1311	2.57	0.03	13.12	0.15

Table 3.2. Inflorescence rankings and chi square results of subjects for both long and short corolla treatments. $df = 2$ for all chi square tests.

Corolla	Subject	Preference	Chi Square	p value
Long	Blue30	H > M > N	118.7659	<0.0001
Long	Green 1	M > H > N	91.0234	<0.0001
Long	Green 28	N > M > H	41.2868	<0.0001
Long	L22	N > M > H	23.5173	<0.0001
Long	Pink 2	N > H > M	6.4551	0.0397
Long	Pink 22	H > M > N	3.3843	0.1841
Long	Pink 29	N > H > M	45.5654	<0.0001
Long	Red 23	M > N > H	9.0327	0.0109
Long	Red 8	M > N > H	13.0689	0.0015
Short	Blue30	M > H > N	232.6728	<0.0001
Short	Green 1	M > H > N	66.073	<0.0001
Short	Green 28	N > H > M	0.3511	0.839
Short	L22	M > H > N	5.9882	0.0501
Short	Pink 2	N > H > M	16.0665	0.0003
Short	Pink 22	H > M > N	14.556	0.0007
Short	Pink 29	H > M > N	121.6584	<0.0001
Short	Red 23	H > N > M	33.5091	<0.0001
Short	Red 8	M > H > N	23.5648	<0.0001

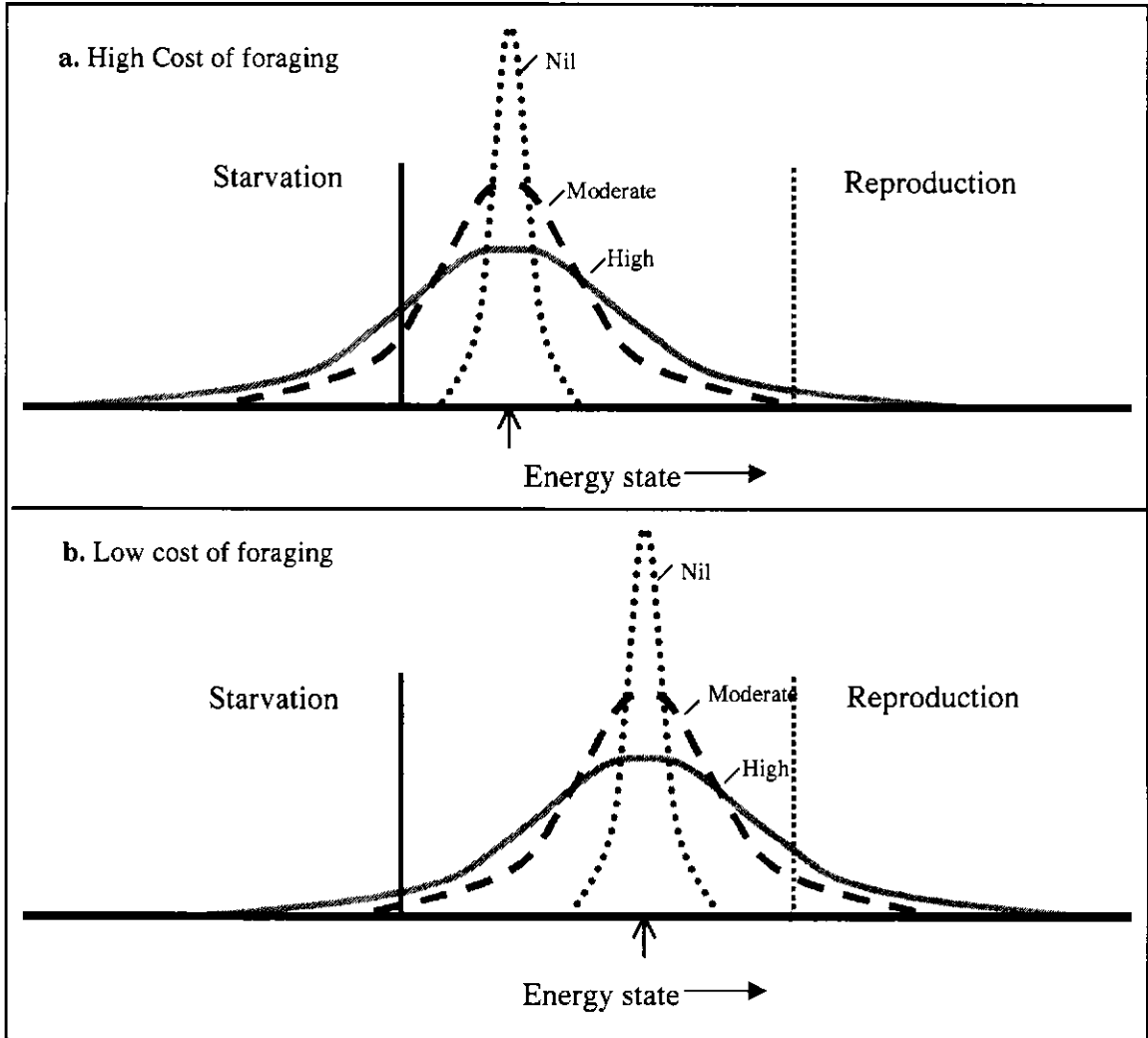


Figure 3. 1. Graphical presentation of the twin-threshold model. Distributions are the possible energy states of a forager feeding from a particular distribution. When the mean energy state of the forager is close to the starvation threshold (as in a. high cost of foraging) the optimal choice is the constant option (Nil). When a forager's energy state is closer to the reproduction threshold (as in b. low cost of foraging) the optimal choice is a variable option (Moderate or High). \uparrow represents the mean energy state of the animal foraging from the reward distributions.

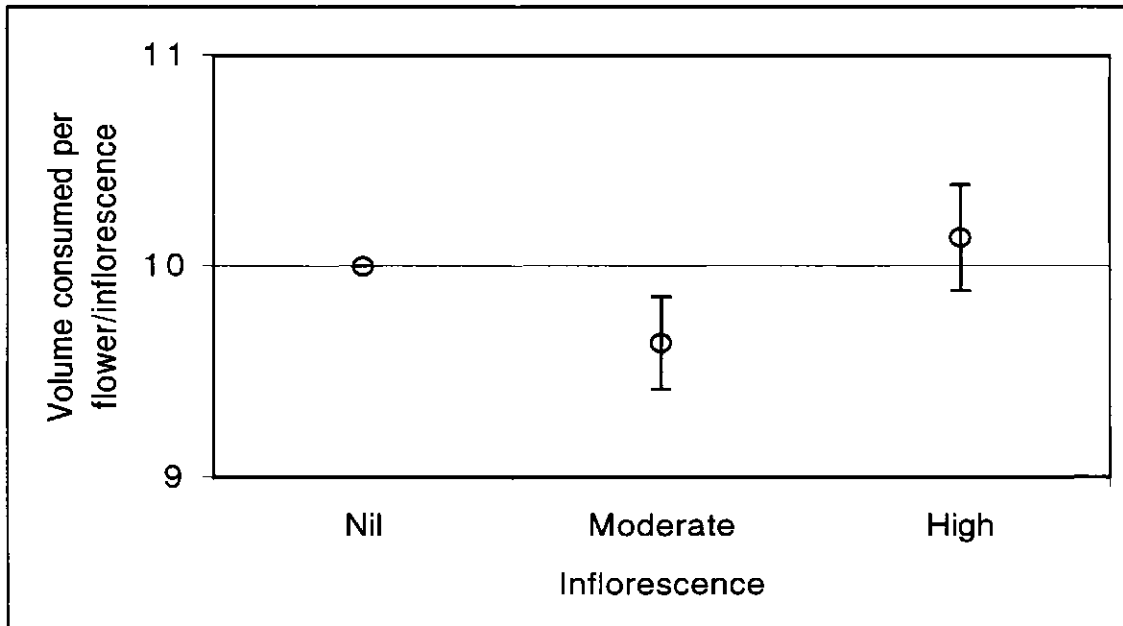


Figure 3. 2. Mean (\pm SE) volume of sucrose consumed per flower from each inflorescence type per bout. Mean volume for the nil inflorescence must be 10 μ l, and the average for both the moderate and high inflorescences should be 10 μ l.

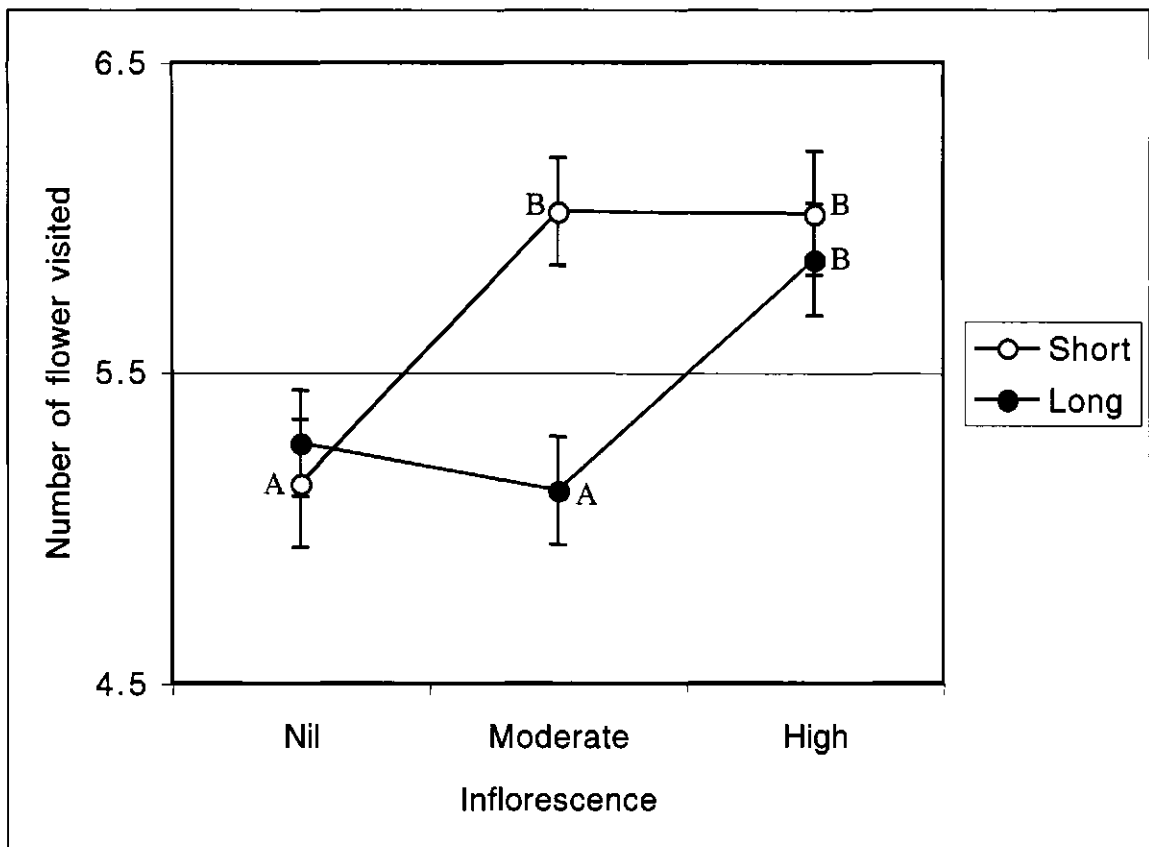


Figure 3. 3. Least square mean (\pm SE) number of flowers visited per inflorescence according to corolla length (Short and Long). Letters represent means that are different from each other (Tukey-Kramer hsd ($P = 0.05$)) ($N = 9$).

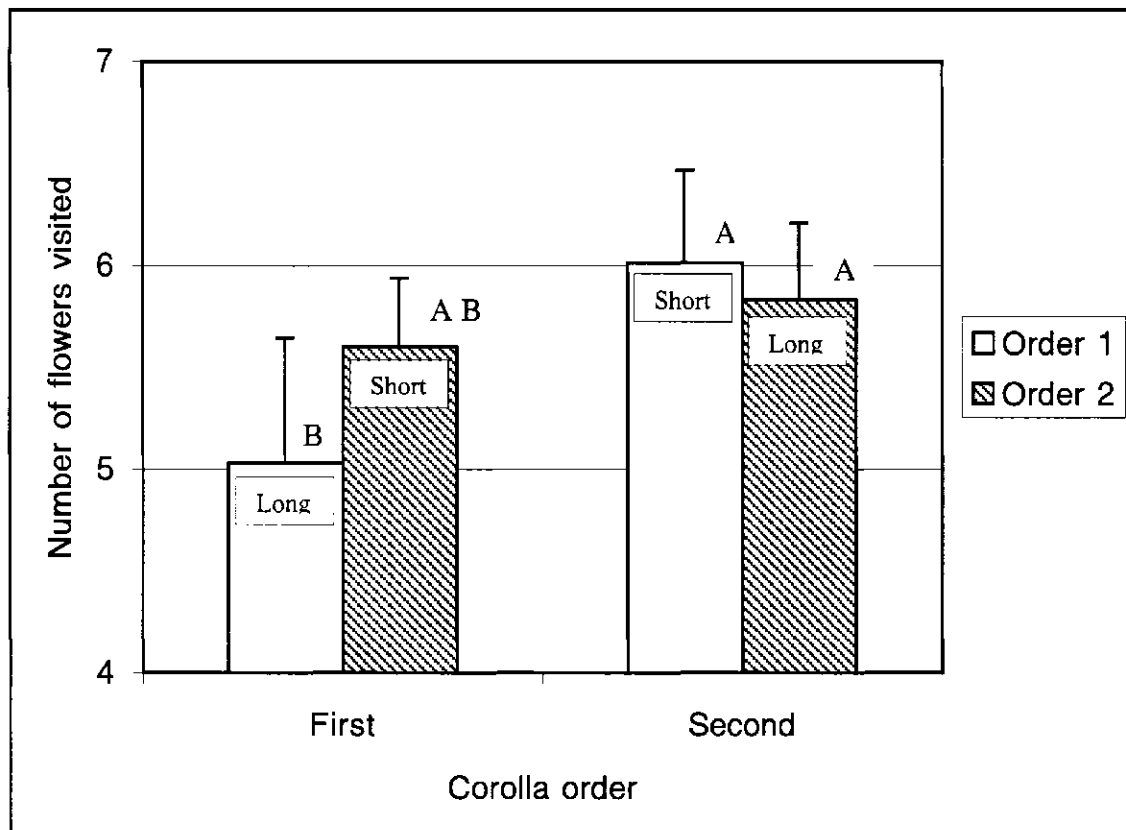


Figure 3. 4. Mean (\pm SE) number of flowers visited across inflorescences according to corolla length (short or long) and treatment order (Order 1: Long corolla followed by Short corolla and Order 2: Short corolla followed by Long corolla). Letters represent means that are different from each other (Tukey-Kramer hsd ($P = 0.05$)).

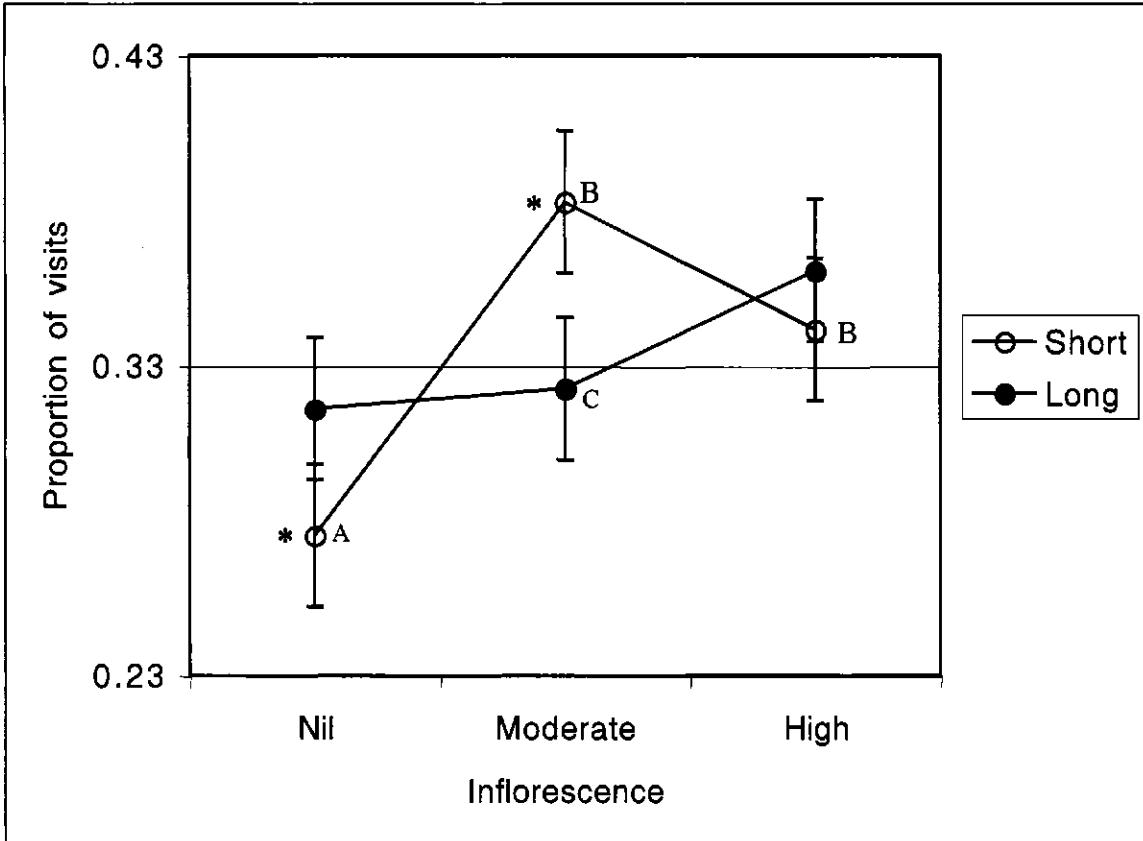


Figure 3. 5. Least square mean (\pm SE) proportion of visits to inflorescence type according to corolla length (Short and Long). * indicate means that are significantly different from random expectation (0.33). Letters represent means that are different from each other (Tukey-Kramer hsd ($P = 0.05$)) ($N = 9$).

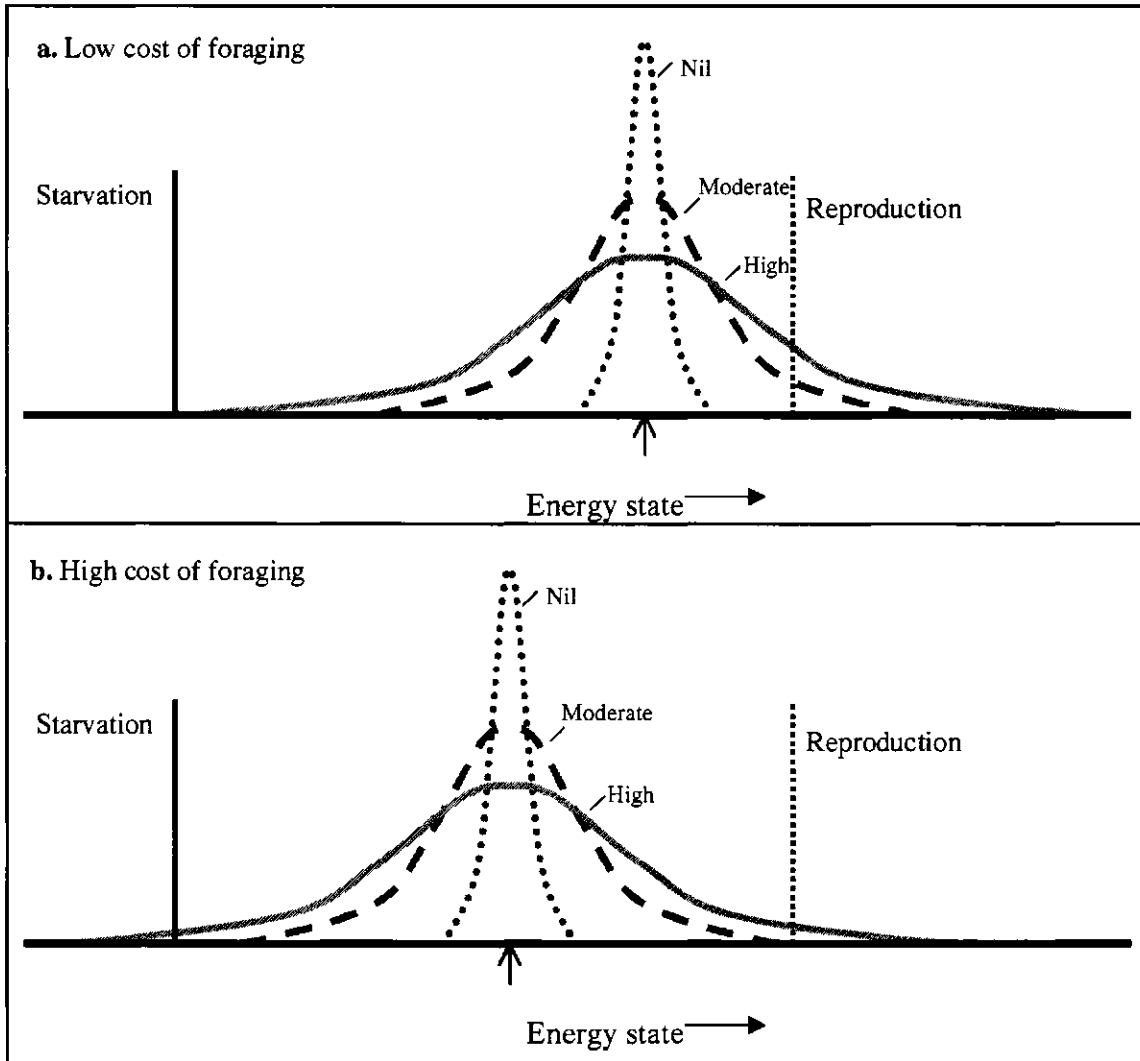


Figure 3. 6. Specific configuration of the twin-threshold model accounting for the change in the number of flowers visited on moderate inflorescence between corolla treatments (see text for details). Distributions are the possible energy states of a forager feeding from a particular distribution (Nil, Moderate or High). When the mean energy state of the forager is close to the reproduction (as in a. low cost of foraging (Short corolla) the optimal choice is a variable option (Moderate or High). When a foragers' energy state is closer to the starvation threshold (as in b. high cost of foraging (Long corolla) the High option may be of more value than the moderate option. ↑ represents the mean energy state of the animal foraging from the reward distributions.

Chapter 4

Conclusions and General Discussion

Introduction

Several models of risk-sensitive foraging consider only one energy threshold, including either starvation (Caraco 1980; Caraco et al.1980; Stephens 1981; Stephens and Charnov 1982), or reproductive (Caraco and Gillespie 1986; Schimitz and Ritchie 199; Bendnekoff 1996; but see: McNamara et al. (1991) for a model that considers two thresholds). In contrast the twin-threshold model (Hurly 2003) incorporates both thresholds simultaneously. The twin-threshold model makes predictions for an animal foraging from a choice set of two or more options, which have a common mean volume but the variability about the mean differs for all options (e.g., nil, moderate and high variance). According to this hypothesis foraging preferences will depend on the relations of the energy state distributions to both thresholds. The value of a specific reward is the sum of the probability of an energy state above the reproduction threshold and the probability of an energy state above the starvation threshold.

Like the energy-budget model, the twin-threshold model predicts preference for the variable option when the forager's energy state is below the starvation threshold. Predictions of the twin-threshold model start to differ from traditional models when the resultant energy state of the forager is between the two thresholds. Basically, when the energy state is below the midpoint between the two thresholds the model predicts preference for the nil option. When the energy state is above the midpoint of the two thresholds the model generally predicts preference for the high variance option.

However, an area exists where preference for the moderate option will provide the greatest fitness advantage.

To date, there is only one published test of the twin-threshold model; a study conducted using rufous hummingbirds (Hurly 2003). Rufous hummingbirds feeding from artificial flowers switched their flower preference when the mean volume of the foraging options was increased or decreased. Hummingbirds were presented with a baseline treatment of nil, moderate and high with a common mean of 25 μ l. In this baseline treatment hummingbirds preferred the moderately variable flower options. After the baseline treatment the common mean of the rewards was either decreased to 20 μ l (shift down) or increased to 30 μ l (shift up). Hummingbirds that received the shift down treatment switched from preferring the moderately variable flower to preferring the nil flowers. Hummingbirds that experienced the shift up treatment switched from preferring the moderately variable flower to preferring the highly variable flower. Hummingbirds in the shift down treatment responded as if the value of the moderate flower decreased when the reward distributions were shifted closer to the starvation threshold and offered an increased threat of starvation. With all the reward distributions shifted closer to the starvation threshold the values of the rewards were altered such that the value of the nil flower was superior. When the reward distributions were shifted up hummingbirds responded as if the value of the high option was greater than that of the moderate option. The high option offered an increased chance of reproduction now that the distribution was closer to the reproductive threshold. These results are consistent with the primary prediction of the twin-threshold model of risk-sensitivity.

One other published result in the literature is also consistent with the predictions of the twin-threshold model. In an experiment intended to replicate the results of Hurly and Oseen (1999), Bateson (2002a) presented European starlings (*Sturnus vulgaris*) with a trinary choice set of seed rewards with nil, moderate and high levels of variation, all with a common mean number of seeds. Individual preferences of European starlings for the moderate option were positively correlated with morning temperature in the laboratory. As well, the proportion of visits to the constant seed option significantly decreased with lower morning laboratory temperatures. However, it must be noted that differences in morning temperatures were because of natural fluctuations in laboratory temperature and were not controlled manipulation. These results contradict the results of Caraco et al. (1990) who found that yellow-eyed juncos (*Juncos phaeonotus*) exhibited risk-averse behaviour when laboratory temperature was warm, but exhibited risk-prone behaviour when laboratory temperature was cool. Caraco et al. (1990) interpreted this switch as a response to change in energy budget due to the different temperatures (warm temperature resulted in a positive energy budget, and cold temperature resulted in a negative energy budget), a result consistent with the energy budget rule (Stephens 1981). Experiments that manipulate temperature in order to manipulate energy state must be interpreted carefully. Temperature changes must cause the energy state of the forager to cross over the starvation threshold.

However, contrary to the energy-budget model, the twin-threshold model predicts increase preference for variability when temperature, and therefore energy state is increased. Bateson (2002b) employs the predictions of the twin-threshold model to explain the European starling behaviour presented in Bateson (2002a). The second,

higher threshold reverses the predictions of the energy-budget model (a single threshold model) and predicts that an animal should be more risk-averse when foraging at lower temperatures. Foraging at a lower temperature is analogous to an animal foraging in an environment where the mean value of the reward distribution has been decreased. Under these circumstances there is an increased threat of starvation when foraging from the variable rewards rather than from the nil reward. European starlings responded as if the lower temperatures resulted in an energy state closer to the starvation threshold and the probability of starvation was decreased when the starlings chose the nil variance seed option. Bateson (2002a) also reported preference for the moderately variable reward in a trinary comparison a result consistent with the twin-threshold model, which predicts preference for the moderately variable reward under some energy states (Hurly 2003). Aside from the mean volume manipulation test of the twin-threshold model by Hurly's (2003), the work presented in this thesis constitutes the only other experimentally controlled tests of the twin-threshold model.

Discussion

The behaviour exhibited by rufous hummingbirds provides further support for the twin-threshold model of risk-sensitivity (Hurly and Oseen 1999; Hurly 2003). As well, the model provides an *a posteriori* explanation of the behaviour exhibited by European starlings (Bateson 2002). However, in a test designed to investigate the effect of variance on departure, in the context of plants manipulating pollinator behaviour, bumblebees (*Bombus flavifrons*) failed to demonstrate preference for variability (J.M. Biernaskie, R.V. Cartar, and T.A. Hurly, unpublished data). Predictions of the twin-threshold model are dependent on the combination of reward distributions, and energy thresholds.

Therefore, tests of the model need to be conducted at several combinations of reward means and variance levels. The study with bumblebees was conducted at only one mean volume reward level therefore, this study does not provide insight into the twin-threshold model. Future tests of the twin-threshold model need to be conducted at several mean reward levels in order to manipulate the energy state of the forager closer to either the starvation threshold or the reproductive threshold.

Predictions of the twin-threshold model are based on the foragers' energy state relative to a lower starvation threshold and a higher reproduction threshold. However, the energy states of the hummingbirds used in the present studies were not known. I assume that hummingbirds were on a positive energy budget. The artificial flowers offered a substantial amount of nectar that was not totally consumed during a foraging bout and hummingbirds were also free to forage from wild flowers growing at the local field sites. With such an abundance of nectar sources it is doubtful that the hummingbirds used in the studies were on negative energy budgets. I also assume that hummingbirds had an energy state between the two thresholds and that energy manipulations resulted in the energy state of hummingbirds to shift towards one of the thresholds. That is, foraging from a low mean nectar volume would result in energy state closer to the starvation threshold and foraging from a high mean nectar volume would result in an energy state closer to the reproductive threshold. Along with data for the energy state of the forager, data are also required to determine the energy thresholds to make accurate quantitative predictions. I have no data on amount of energy needed to surpass the energy thresholds included in the twin-threshold model and or the energy state of the hummingbirds used in these experiments.

The twin-threshold model, along with other foraging models, is a simplification of the foraging behaviour exhibited by animals. The model considers the fitness consequences for a forager following a choice of a few foraging rewards that may have altered the energy state of the forager. Information is needed as to what time frame, or number of choices, a forager uses to base decisions on. As well, not knowing the starvation and reproductive thresholds and the energy state of the forager, and how choices specifically affect energy state, limit the quantitative predictions that can be made by the twin-threshold model.

The twin-threshold model may have interesting implications about Life History Theory. Thresholds may not be limited to being either starvation or reproduction, but could represent thresholds for a variety of life history events. For example, the upper threshold could represent the energy needed to maintain a territory of flowers or the energy needed for migration. For a juvenile hummingbird, a variable nectar volume flower may increase the probability of a successful migration. Foraging from a flower with a variable volume of nectar may result in an energy state far surpassing a migration energy threshold.

The foraging response to thresholds may also be affected by the age of the hummingbird. Survival may have a greater influence on foraging decision for a young bird than it does for an older bird. An older bird that may not survive to the next breeding season and, therefore, immediate reproduction may have a greater influence on foraging decisions. Older birds may be more willing to accept a higher risk of starvation, in order to increase the probability of reproduction, than would a younger bird, to increase overall fitness. For a young bird with several future breeding seasons, balancing

the tradeoff between surviving to the next breeding season and possible immediate reproduction may cause them to be more risk-averse.

There is a growing body of literature on rufous hummingbirds and risk-sensitive foraging behaviour (Stephen and Paton 1986; Waser and McRoberts 1998; Hurly and Oseen 1999; Biernaskie et al. 2002; Hurly 2003; M. Bateson, S.D. Healy, and T.A. Hurly, published data; M.E. Klassen and T.A. Hurly unpublished data, and see Chapters 2 and 3). Results from these studies provide strong support that rufous hummingbirds are risk-sensitive foragers. Studies conducted with rufous hummingbirds have reported preference for nil, moderate and high levels of variability. As well, preference switches have also been reported for rufous hummingbirds when energy state was manipulated (Hurly 2003; M.E. Klassen and T.A. Hurly, unpublished data, see also Chapters 2 and 3). Generally, when presented with a choice set of three options and the mean volume was high or cost of foraging was low, hummingbirds preferred a variable option and when the mean volume was low or costs were high hummingbirds preferred the nil option. Also, in a binary comparison between a constant and a variable option rufous hummingbirds changed their preference when the mean volume was manipulated. When the mean volume was high, hummingbirds were risk-prone and when the mean volume was low, hummingbirds were risk-averse (M.E. Klassen and T.A. Hurly, unpublished data). The relationship evident in hummingbirds between the direction of risk-sensitive preferences and energy state manipulations adds further support to a pattern evident in the risk literature. That is, the direction of risk-sensitive preferences is related to the forager's energy budget, especially for species of small mass (Kacelnik and Bateson 1996).

The expression of risk-sensitive preferences has been demonstrated in two different measures with rufous hummingbirds. Traditionally, preference was measured by analyzing the proportion of visits to each reward type (e.g., inflorescence or flower). An additional measure, one that may be more sensitive, is patch departure. Preference in terms of patch departure, in a hummingbird context, is based on the number of flowers visited on a particular inflorescence. The inflorescence with the highest average number of flower visits is the most preferred. Studies that have employed patch departure as a measure of preference, both conducted with rufous hummingbirds, detected risk-sensitive patch departure (Biernaskie et al. 2002; see also Chapter 3). Inflorescence choice results parallel inflorescence departure results, however, in both cases inflorescence choice results were not significant.

Clear patterns have emerged in the risk-sensitive literature (for a review see Kacelnik and Bateson 1996; Bateson 2002b). These patterns are: 1) direction of risk-sensitivity is influenced by the energy state of the forager, 2) direction is also affected by whether variability is in delay to the reward or in reward amount, 3) the magnitude of risk-sensitive preferences is related to the coefficient of variation of the variable reward, and 4) the number of foraging options presented simultaneously (e.g., two or three) may influence the direction of risk-sensitive preferences. The data presented in this thesis specifically address the effect energy budget has on hummingbird preferences. My results support the suggestion that an animal's energy budget has a role in determining the direction of risk-sensitive preferences.

The energy-budget model (Stephens 1981) provided a useful framework with which to explore how variability affects foraging decisions. The energy-budget model

has explained the preference shift between constant and variable options relative to a starvation threshold. However, the energy-budget model does not explain risk-sensitive preferences when variability is in delay to the food reward or some observations of risk-prone behaviour of animals on positive energy budgets. Similarly, the twin-threshold model has provided a framework to explore risk-sensitive foraging relative to multiple thresholds. Thus far the twin-threshold model has successfully explained preferences changes when reward means are manipulated or when foraging temperatures have changed in the lab situation. However, the twin-threshold model has not been successful with explaining the effect of shifting the variance levels of foraging rewards. More tests of the twin-threshold model are needed with other species to determine the generality of the model. To accurately test the twin-threshold model the energy state of the forager must be manipulated within the experiment. As well, more models are needed that consider concepts such as multiple thresholds and larger choice sets to further our understanding of risk-sensitive foraging.

References

- Bateson, M.** 2002a. Context-dependent foraging choice in risk-sensitive starlings. *Animal Behaviour*, **64**, 251-260.
- Bateson, M.** 2002b. Recent advances in our understanding of risk-sensitive foraging preferences. *Proceedings of the Nutritional Society*, **61**, 509-516.
- Bednekoff, P.A.** 1996. Risk-sensitive foraging, fitness, and life histories: where does reproduction fit into the big picture? *American Zoologist*, **36**, 471-483.
- Biernaskie, J.M., Cartar, R.V., and Hurly, T.A.** 2002. Risk-averse inflorescence departure in hummingbirds and bumblebees: could plants benefit from variable nectar volumes? *Oikos*, **98**, 98-104.
- Caraco, T.** 1980. On foraging time allocation in a stochastic environment. *Ecology*, **61**, 119-128.
- Caraco, T., Blanckenthorn, W.U., Gregory, G. M., Newman, J.A., Recer, G.M. and Zwicker, S.M.** 1990. Risk-sensitivity: ambient temperature affects foraging choice. *Animal Behaviour*, **39**, 338-345.
- Caraco, T., and Gillespie, R.G.** 1986. Risk-sensitivity: foraging mode in an ambush predator. *Ecology*, **67**, 1180-1185.
- Caraco, T., Martindale, S. and Whittam, T.S.** 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour*, **28**, 820-830.
- Hurly, T.A., and Oseen, M.D.** 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Animal Behaviour*, **58**, 59-66.
- Hurly, T.A.** 2003. Twin-threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Animal behaviour*, **66**, 751-761.
- Kacelnik, A., and Bateson, M.** 1996. Risky theories – The effect of variance on foraging decisions. *American Zoologist*, **36**, 402-434.
- McNamara, J.M., Merad, S., and Houston, A.I.** 1991. A model of risk-sensitive foraging for a reproducing animal. *Animal Behaviour*, **41**, 787-792.
- Schmitz, O.J., and Ritchie, M.E.** 1991. Optimal diet selection with variable nutrient intake: Balancing reproduction with risk of starvation. *Theoretical Population Biology*, **39**, 100-114.

- Stephens, D.W.** 1981. The logic of risk-sensitive foraging preferences. *Animal Behaviour*, **29**, 628-629.
- Stephens, D.W., and Charnov, E.L.** 1982. Optimal foraging: some simple stochastic models. *Behavioral Ecology and Sociobiology*, **10**, 251-263.
- Stephens, D.W., and Krebs, J.R.** 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Stephens, D.W., and Paton, S.R.** 1986. How constant is the constant of risk-aversion. *Animal Behaviour*, **34**, 1659-1667.
- Waser, N.M., and McRoberts, J.A.** 1998. Hummingbird foraging at experimental patches of flowers; evidence for weak risk-aversion. *Journal of Avian Biology*, **29**, 305-313.