Foraging behavior and risk assessment of six hummingbird species in Monteverde, Costa Rica

Emily Ellison

Department of Biology, Denison University

RESUMEN

La hipótesis de asignación de riesgo por depredación (ARD) dice que los animales demuestran mayor comportamientos anti-depredadores bajo situaciones de alto riesgo, y que gastan menos tiempo forrajeando en estas mismas situaciones. Los colobríes son forrajeadores sensibles al riesgo, y este estudio examina si diferentes especies pueden determinar riesgos, apoyando la ARD. Se le presentaron comederos a los colibríes en diferentes locaciones y obstrucciones visuales, y las preferencias y comportamientos de forrajeo se usaron para determinar la habilidad de los mismos para determinar el riesgo. Este estudio indica que los colibríes tienen la capacidad de determinar el riesgo, sin embargo las especies difieren en la habilidad dependiendo en el tipo y severidad de la situación. El colibrí Colirrayado, el Esmeralda Coronilla Cobriza, el colibrí Montañez Gorgimorado y el Ala de Sable Violaceo todos demuestran preferencias por comederos a ciertas alturas o posiciones. El Brillante Frentiverde gasta menos tiempo en los tres tratamientos de los comederos (obstrucción de la mirada) y escanea mas que las otras especies. Los colibríes escanean significativamente menos en los comederos normal y con obstrucción clara que en los comederos con obstrucción roja, lo que sugiere que la obstrucción de la visión es un riesgo para todos los colibríes mientras forrajean.

ABSTRACT

The predation risk allocation hypothesis (RAH) theorizes that animals display more anti-predator behavior in high-risk situations, and should spend less time foraging in high risk situations. Hummingbirds are risk sensitive foragers, and this study examines whether several different species of tropical hummingbirds can assess risk, supporting the RAH. Hummingbirds were presented with feeder location and view obstruction risk situations, and their preferences and foraging behaviors were used to determine their ability to assess risk. This study indicated that hummingbirds have the ability to assess risk, although species differed in their ability depending on the type and severity of the risk situation. Striped-Tailed, Coppery-headed Emerald, Purple-Throated Mountain Gem, and Violet Sabrewing all showed significant preferences for a certain feeder height and/or position. The Green-crowned Brilliant spent significantly less time at the three feeder treatments (view obstruction) and scanned significantly more than the other hummingbird species. Hummingbirds scanned significantly less at the normal and clear blinder flower type than the red blinder flower, which suggests view obstruction is a risk for all hummingbirds while foraging.

Introduction

Predation is a strong evolutionary force acting on prey animals causing their behaviors to change, especially when in more vulnerable situations, such as foraging (Lima and Dill 1990). The predation risk allocation hypothesis (RAH) predicts that animals should display more anti-predator behavior in high-risk situations than low-risk situations (Lima 1999). Two studies, one

done by Ferrari *et. al* (2007) and the other by Whitear and Stehlik (2009), have supported this aspect of the RAH in studies using fish and hummingbirds, respectively: the animals displayed more anti-predator behavior in high-risk situations. In terms of foraging in high-risk situations, animals should spend less time feeding and more time taking anti-predator precautions, whereas in low-risk foraging situations, the animal should spend more time actually feeding (Lima 1999). Animals that are cautious foragers are known as risk-sensitive foragers, and hummingbirds are thought to forage in this way (Montgomerie *et al.* 1984; Weissburg 1986, Bateson 2002).

Hummingbird species behave differently in their foraging behaviors: they prefer different nectar sources and locations, along with displaying different foraging techniques (Stiles and Skutch 1989, Fogden and Fogden 2005). There are trapliner and territorial hummingbird species, which differ in behavior based on their foraging techniques, along with different energy intakes, speed, and morphologies of hummingbirds that influence their foraging behaviors (Stiles 1975, Stiles and Skutch 1989, Fogden and Fogden 2005). Hummingbirds also differ in their foraging behaviors in regards to their foraging locations. The different locations can be geographic, such as the interior of a forest or the forest edge and varying elevations. The locations can also differ in preferred flower height; some hummingbird species prefer to forage on lower, understory plants, while others forage on canopy plants (Stiles and Skutch 1989, Fogden and Fogden 2005). Flower type and nectar concentration also influence different foraging behaviors between hummingbird species (Stiles and Skutch 1989, Fogden and Fogden 2005).

A study by Lima (1991) tested risk assessment in Anna's hummingbirds (*Calypte anna*), and found that these hummingbirds have the ability to assess risk while foraging and the risk is due to predation threat. Lima (1991) found that the hummingbirds preferred to feed at higher feeder versus lower feeders, and he also found that hummingbirds displayed more anti-predator vigilance behavior when their view was obstructed while feeding. This study suggests hummingbirds risk assessment was based on predation threat; thus hummingbirds changed foraging behavior due to predation risk (Lima 1991). These hummingbirds supported the RAH, although the behavioral foraging differences between species was not considered.

This study will examine whether hummingbirds have the ability to assess risk while foraging, and also whether hummingbird species from the Monteverde Cloud Forest Region differ in their ability to assess risk. The risk assessment of hummingbird foraging will take place on various levels where hummingbirds will be presented with risks, such as feeder location and view obstruction, similar to the Lima (1991) study with the addition of observations on differences in hummingbird species foraging behavior. Hummingbirds are likely to have the ability to assess risk while foraging, and species are likely to differ in their risk assessment due to differences in foraging behavior.

Materials and Methods

Study Site

This study was conducted at the Biological Station in Monteverde, Costa Rica at 1550m in a lower montane, tropical wet forest (Haber 2000). Three different feeder locations were used on a three day rotating schedule to avoid trap liner and territorial species from dominating the feeders, as seen during other studies in the same location. This deterred certain species from dominating the area by having an inconsistent feeder availability because the same location was only used once every third day; thus the birds could not rely on the feeder everyday and establish

a territory. Two of the three locations were forest edges 100m apart, while the third was in the interior of the forest, in which the forested mountain side separated the third from the other two, at least 50 m away from either one.

Observations were made from 6:30am to 9:30am for twenty days during the month of April 2011. Initially, feeders were placed at all three locations three days prior to the experiment to acclimate the hummingbirds to the three different experiment sites. The feeders were hung between two trees with a string 1.5 m above the ground: this feeder height acted as a control height because 1m and 2m feeder heights were used in the actual experiments. The feeders were filled with a 1:5 sugar to water concentration (20%) solution because it most closely matches the sugar content in flower nectar (Lima 1991, Lai 2010).

High vs. Low and Inner vs. Outer Feeders

The first experiment tested hummingbird risk assessment based on foraging preference for feeders located at different heights and positions. Two rows of four feeders (8 total feeders) were hung between two trees with a 1m space in between each feeder: one row of four feeders at 1m and the other row of four feeders at 2m above the ground. The two different height choices and the four different feeder positions were used to determine if either or both foraging height and location is a risk for hummingbirds while foraging. Hummingbird species and number of visits to each feeder were documented for four days. Five hummingbird species were considered for this part of the study: Violet Sabrewing (*Campylopterus hemileucurus*), Purple-throated Mountain Gem (*Lampornis calolaema*), Green Hermit (*Phaethornis guy*), Coppery-headed Emerald (*Elvira cupreiceps*), Striped-tailed (*Eupherusa eximia*). Depending on each species' feeder preference, it can be determined which feeder is safer (according to each species) and which feeder presents the greater risk for each species of hummingbirds while foraging.

Normal, clear blinder, and red blinder flowers

The following experiment tested hummingbirds risk assessment based on visibility while foraging. Three different feeder types were used to determine if visibility while feeding is a risk for hummingbirds while foraging. First, two normal (Fig.1 A) feeders were hung at 2m with a 1m space in between them, and species, visit time, and how many times the hummingbird scanned the area while feeding were documented for three days. A hummingbird was considered to be scanning when they took breaks while feeding to look at the area surrounding them: the scan could be as little as the hummingbird removing their head from the feeder to look around or as large as flying a few inches away from the feeder, hovering, and checking the area around them. The normal feeder was used to determine a baseline of how long hummingbirds would stay at a feeder without their vision being obstructed. For the next three days, two feeders were hung at 2m with 1m space in between them with red blinders attached to the feeder surrounding the drinking hole (Fig.1 C), which reduced the hummingbird's direct and peripheral vision while foraging. Visit time, species, and number of scans were recorded again to compare to the normal feeder to determine if foraging behavior changed with reduced visibility. The third flower type was a clear blinder (Fig.1 B), and was hung equivalent to the previous two tests. The clear blinder was used as a control to determine if the hummingbirds changed foraging behavior based on the bulk of the blinders or because of lack of visibility. Again, species, visit time, and scans were recorded for three days. Four hummingbird species were considered for the three

treatments: Violet Sabrewing, Purple-throated Mountain Gem, Green Hermit, and Green-crowned Brilliant (*Heliodoxa jacula*).

FIGURE 1: Three different hummingbird feeder types: (A) normal feeder, (B) clear blinder, and (C) red blinder type feeder.

Normal vs. Red blinder flower

The last experiment tested if hummingbirds, when presented with choice, have the ability to assess risk. One normal feeder and one red blinder feeder were hung at 2m with a 1m space separating them. Species, feeder preference, time of visit, and number of scans were recorded for three days. Six hummingbird species were considered (Violet Sabrewing, Purple-throated Mountain Gem, Green Hermit, Green-crowned Brilliant, Coppery-headed Emerald, and Striped-tailed), and the ability to assess risk was determined by preference for a certain feeder, or the time spent and number of scans at a certain feeder.

Results

High vs. Low and Inner vs. Outer Feeders

Both Striped-tailed (X^2, df=1, $p<0.0001$) and Coppery-headed Emerald (X^2, df=1, $p<0.0001$) preferred the high, outer feeders significantly more than the other feeder heights and positions (Table 1). The Purple-throated Mountain Gem significantly preferred the lower feeders, regardless of feeder position (X^2, df=1, $p=0.008$) (Table 1). Violet Sabrewing significantly showed a preference for the outer feeders, regardless of height (X^2, df=1, $p= 0.02$) (Table 1). The Green Hermit did not show any significant preference for feeder position or height.

TABLE 1: Hummingbird species and number of visits to the eight feeders at the high/low and inner/outer feeder positions at the three study sites for four days.

Hummingbird Species	Feeder Position	High Feeder	Low Feeder
Green Hermit	in	8	6
	out	7	8
Striped-tailed*	in	1	0
	out	27	2
Coppery-headed Emerald*	in	14	1
	out	33	2
Purple-throated Mountain Gem*	in	4	16
	out	10	11
Violet Sabrewing*	in	4	7
	out	13	11

*Significant differences $p < 0.02$.

Normal, Clear blinder, and Red blinder

The foraging time between feeder types, was significantly different between hummingbird species (ANOVA, $F=28.58$, $df= 3$, $p<0.0001$), but not significantly different between feeder type (Fig. 2). The Green-crowned Brilliant spent significantly less time at the three feeders than the other hummingbird species. For sample sizes and number of visits per feeder see Table 2.

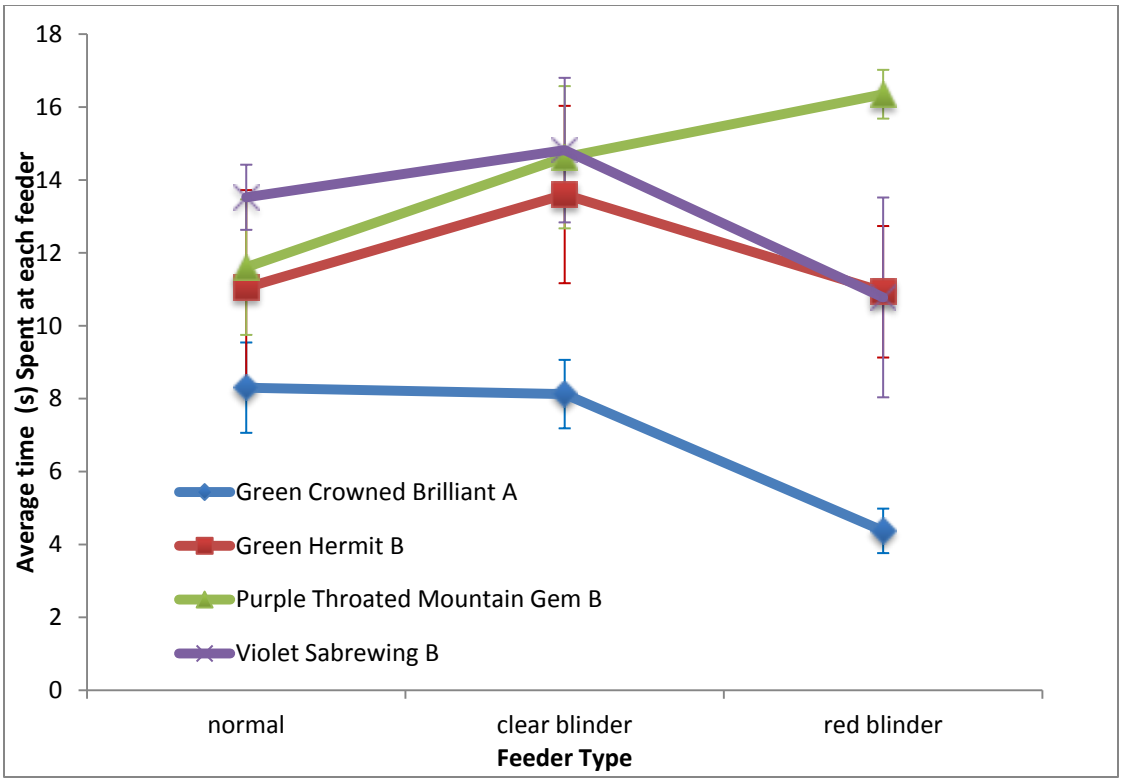

FIGURE 2: Average (±SE) foraging times on normal, clear blinder, and red blinder feeder types, of 4 hummingbird species in Monteverde. Green-crowned Brilliant (^{A}) differed significantly from all other hummingbird species (^{B}) (Tukey's HSD test, $p < 0.05$).

TABLE 2: Hummingbird species and number of visits to each of the three feeder types. Two feeders of each feeder type were at the three study sites for three days each.

	Flower Type		
Hummingbird Species	Normal	Clear blinder	Red blinder
Green-crowned Brilliant	13	27	62
Green Hermit	8	15	9
Purple-throated Mountain Gem	16	22	33
Violet Sabrewing	24	12	6
Total Visits	61	76	110

The average number of scans per second differed significantly for both feeder type (ANOVA, $F = 25.8$, $df = 2$, $p < 0.0001$) and hummingbird species (ANOVA, $F = 12.7$, $df = 3$, $p < 0.0001$). Normal and clear flower type feeders received significantly less average number of scans per second with means of 0.45 and 0.39 scans/second, respectively, compared to the red blinder feeder with an average mean of 0.69 scans/second (Fig. 3). Green-crowned Brilliant scanned significantly more per second than the Purple-throated Mountain Gem with average

means of 0.67 and 0.53, respectively (Fig. 3). The Purple-throated Mountain Gem scanned significantly more than both the Violet Sabrewing and Green Hermit with average means of 0.53, 0.39, and 0.34, respectively. Violet Sabrewing and Green Hermit did not differ significantly from each other in average number of scans per second while foraging.

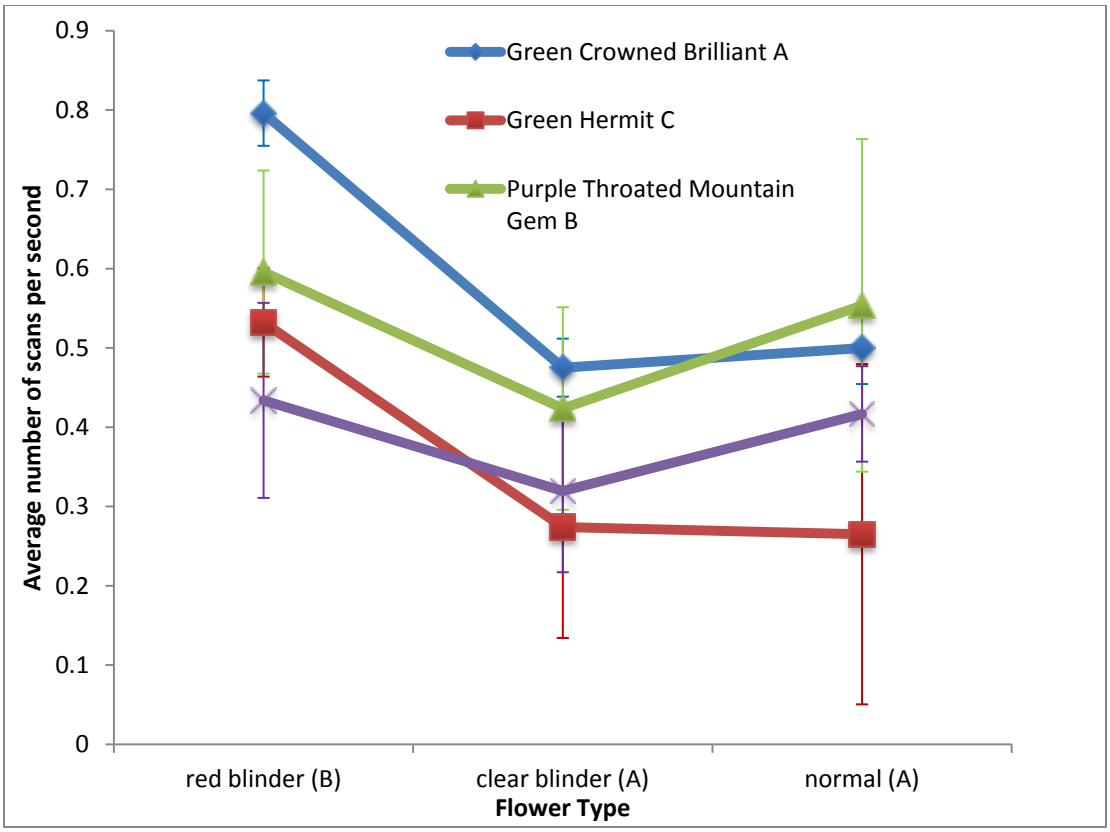

FIGURE 3: Average (±SE) number of scans per second on normal, clear blinder, and red blinder feeder types, of 4 hummingbird species in Monteverde. Green-crowned Brilliant (^{A}) differed significantly in average number of scans per second from the Purple-throated Mountain Gem (^{B}), and Purple-throated Mountain Gem (^{B}) differed significantly from Violet Sabrewing (^{C}) and Green Hermit(^{C}) (Tukey's HSD test, $p > 0.05$). The normal (^{A}) and clear blinder (^{A}) flower type feeder differed significantly from the red blinder flower feeder (^{B}) in the average number of scans per second during the foraging visit (Tukey's HSD test, $p<0.05$).

Normal vs. Red Blinder

None of the humming bird species differed significantly in their preference for the normal versus red blinder feeders, although Green Hermit almost showed significance in preference for the normal feeder over the red blinder feeder (X^2, df=1, p= 0.058, Table 3).

TABLE 3: Hummingbird species and number of visits to normal and red blinder feeder types. Both feeder types were at all three study sites in pairs of the same feeder type for three days each.

Hummingbird Species	Red Blinder	Normal Feeder
Coppery-headed Emerald	1	1
Green-crown Brilliant	10	9
Green Hermit	1	6
Purple-throated Mountain Gem	14	21
Strip Tailed	4	4
Violet Sabrewing	11	9
Total Visits	41	50

Discussion

This study found that the different species of hummingbirds in the Monteverde Cloud Forest each show different feeder preferences and foraging behaviors in different risk situations. Because hummingbirds did show preference for certain feeders, it can be concluded that hummingbirds are able to assess risk in certain situations, but not all of the hummingbirds assessed risk the same way in each risk situation. This can be explained by conclusions made by Lima (1998): because there is temporal variation in foraging risk predation, animals may behave differently based on risk level: the decision to feed and the length of the feed depend on the severity of the risk. Preference may be explained also by other factors, such as foraging techniques, preferred foraging locations, morphology, and energy intake, rather than risk assessment alone.

High vs. Low and Inner vs. Outer Feeders

The preference of the Striped-tailed and Coppery-headed Emerald for the high and outer feeders could be explained by risk assessment due to predation threat. They purposely chose to forage at higher feeders, closer to tree coverage to avoid and escape ground predators (Lima 1991). The Purple-throated Mountain Gem's preference for the lower feeders can be due to natural foraging preferences for shrub level plants, such as *Cephaelis* (Fogden and Fogden 2005). The outer feeder preference of the Violet Sabrewing can be explained by their natural tendency to forage at forest edges; they are used to feeding in an open area, but closest to the trees (Stiles and Skutch 1989). The Green Hermit did not display a feeder preference; thus, according to the data from this study, the Green Hermit does not assess risk for foraging height and position. Feeder height and position preference can be explained by both natural foraging behaviors and risk assessment.

Normal, Clear blinder, and Red blinder

The Green-crowned Brilliant was the only species to spend significantly less time at all three feeders, and also displayed the most anti-vigilance behavior at all three feeder types. These

results are conclusive with the Whitear and Stehlik (2009) study who considered foraging time in high-risk situations, and their results supported the RAH: less time is spent foraging in high risk situations. Both of these foraging behaviors could be due to their natural foraging behavior as well: they prefer to perch while feeding, and since they did not have access to a perch, they spent less time at the feeders (Stiles and Skutch 1989). Time spent visiting the feeder did not appear to be a severe risk for hummingbirds, but the hummingbirds did display different degrees of anti-predator vigilance behaviors (scanning) while foraging at the three feeder types. More scans per second were taken at the red blinder flower type feeder than the normal and the clear blinder flower type feeders, which implies that view obstruction while foraging is a risk for hummingbirds (Lima 1991). The Purple-throated Mountain Gem, Green Hermit, and Violet Sabrewing also demonstrated anti-predator vigilance behavior while at the three flower types, in different degrees, and thus are perceived as having the ability to assess risk (Lima 1991).

Normal vs. Red blinder

Although no hummingbird species preferred one feeder of the other in the normal versus red blinder flower experiment, the Green Hermit had a strong trend toward preferring the normal feeder. This foraging preference means that, for the Green Hermit, view obstruction is a risk because they tended to avoid the feeder where their view was blocked (Lima 1991). In general, for all of the other hummingbird species considered, view was not a risk in the sense that if their view was obstructed they would avoid the feeder completely, but it was a risk in a way that made them display more anti-predator vigilance behavior. Regardless of what the risk was, these data conclude that the hummingbirds are able to assess risk, but not all species assess risk to the same degree and risk assessment is dependent on the situation for each species.

Future Research

Further research is needed to fully determine the different abilities of the hummingbirds to assess risk. Since some of the risk-situations in this study did not seem to be a risk or risky enough for some of the hummingbirds, future studies are needed to determine which risk-situations are actually risks for hummingbirds. Future studies are also needed to determine if the foraging behavior is due to risk or if it caused by their natural foraging preferences. The research could potentially determine which hummingbird species are more prone to risk and what foraging behaviors are due to instinct, and thus shed light on hummingbird foraging behavior based on predation risk. Beyond the focus of foraging behavior, this research could help determine personality traits between similar, non-human species, such as hummingbirds, enriching our knowledge of animal behavior.

Acknowledgements

I would like to thank my project advisor Pablo Allen for guiding me through my project. I would also like to thank Anjali Kumar for presenting this project idea to me. Thanks to the Varela- Jimenez family for being Monteverde's best host family and providing me with a place to live during my project. Thanks to Estación Biológica for allowing me to use the property for my study site.

Literature Cited

Bateson, M. 2002. Recent advances in our understanding of risk-sensitive foraging preferences. Proceedings of the Nutrition Society. 61: 1-8.

Ferrari, M. C., A. C. Rive, C. J. MacNaughton, G. E. Brown, and D. P. Chivers. 2008. Fixed vs. random predictability of predation risk: an extension of the risk allocation hypothesis. Ethology. 114: 238-44.

Fogden, M. and P. Fogden. 2005. Hummingbirds of Costa Rica, pp. 9-131. Distribuidores Zona Tropical, South America.

Haber, W. A. 2000. Plants and Vegetation. *In*: N. M. Nadkarni and N. T. Wheelright (Ed.) Ecology and Conservation of a Tropical Forest, pp. 39-93. Oxford University Press, New York.

Lai, S. 2010. Feeder position preferences in response to potential and artificial predators in hummingbirds. Tropical Ecology and Conservation, CIEE. Fall: 116-123.

Lima, S. L. 1991. Energy, predators and the behavior of feeding hummingbirds. Evol. Ecol. 5: 220-30.

Lima, S. L. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior. 27: 215–90.

Lima, S. L. and P. A. Bednekoff, 1999. Temporal variation in danger drivers antipredator behavior: the predation risk allocation hypothesis. Am. Nat. 153: 649-59.

Lima, S. L. and L. M. Dill, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619-40.

Montgomerie, R.D., J.M. Eadie, and L.D. Harder. 1984. What do foraging hummingbirds maximise? Oecologia. 63: 357-63.

Stiles, F.G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology. 56: 285-301.

Stiles, F. G. and A. F. Skutch. 1989. A guide to the birds of Costa Rica, pp. 210-227. Comstock Publishing Associates, New York.

Weissburg, M. 1986. Risky Business: On the ecological relevance of risk-sensitive foraging. Oikos. 46: 261-62.

Whitear, A. K. and I. Stehlik, 2009. Use of auditory predation cues in the Ruby-throated hummingbird (*Archilochus colubris*). JULS. 3:47-49.