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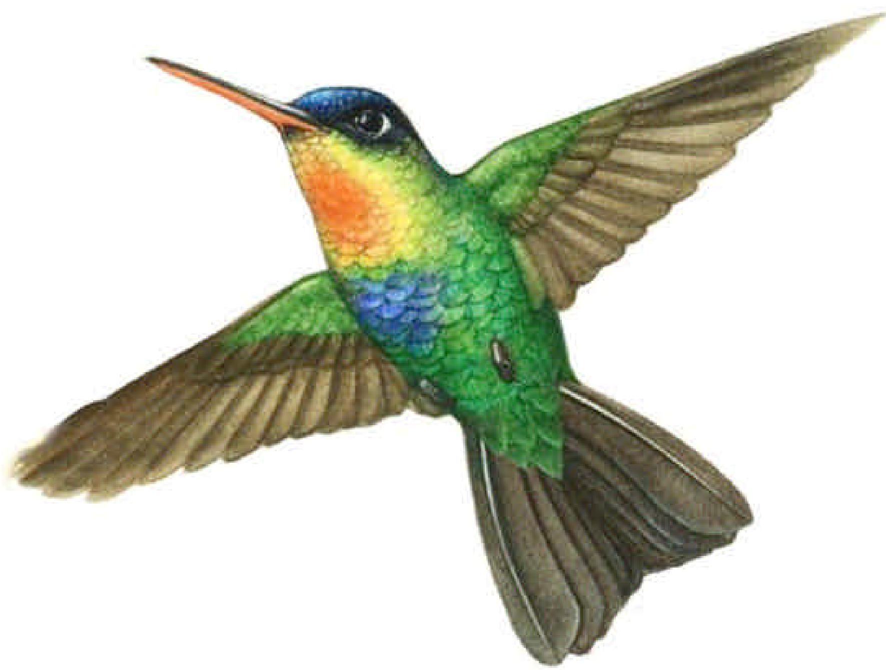
Research Program

Climate Change and the Hummingbirds of the Monteverde Cloud Forest, Costa Rica



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Abstract

It has been recently reported that the climate in Monteverde, Tilarán Mountain Range, Costa Rica, is changing rapidly, and that these changes have begun to affect wildlife populations in the region. Anecdotal evidence suggests that the distributions and abundances of hummingbird species are shifting. It is possible that these changes are related to climate. This paper investigates this potential link, examining how climate affects hummingbirds directly and how it affects their resources, namely nectar producing plants. Hummingbirds have complex effects on the plant community through pollination. In turn, nectar and flower production affects hummingbird behavior, population size, and life cycle. Climatic variables including precipitation, temperature, and cloud cover all affect nectar production. Research shows that precipitation also impacts hummingbirds directly. In Monteverde where the climatic trend is one of decreased precipitation, increased temperature, and increased cloud cover, the potential effects on hummingbird populations and the plants that support them are complex. It is possible that there will be a shift in the spatial and temporal distributions of both hummingbirds and plants and a change in the relative abundances of species. A decline in nectar resources resulting in a reduction of hummingbird diversity is possible. Because of the complexity of the potential effects, it is crucial to implement a monitoring program and conduct experiments to deepen our understanding of the relationship between climate change and wildlife biology. Chapter 2 describes a plan for undertaking this research at the Monteverde Cloud Forest Preserve. This includes determining the population sizes and relative abundances of hummingbirds in the region, identifying important flowering plant species, delineating their phenologies, and noting hummingbird visitation rates to these plants. Techniques for measuring nectar are described. Experiments to ascertain the effects of precipitation, temperature, and cloud cover on nectar production are outlined. Baseline data from earlier studies in the region can be compared to new data in order to determine the extent to which climate change has already begun to impact the hummingbirds of Monteverde. Chapter 3 discusses the pros and cons of using hummingbird feeders as a research tool, and recommends that feeders only be used in a limited capacity and in areas of high flower abundance. The ultimate goal of this paper is to facilitate the conservation of biodiversity in an ever-changing Monteverde.

Resumen

Se ha reportado recientemente que el clima en Monteverde, Cordillera de Tilarán, Costa Rica, está cambiando rápidamente, y que estos cambios han comenzado a afectar a las poblaciones de fauna en la región. Evidencias anecdóticas indican que las distribuciones y la abundancia de especies de colibrí están cambiando. Es posible que estos cambios estén relacionados con el clima. Este estudio investiga un posible vínculo, examinando cómo el clima afecta directamente a las especies de colibrí, y cómo afecta a sus recursos, específicamente el néctar producido por las plantas. Los colibríes producen efectos complejos sobre las comunidades de plantas por medio del mecanismo de polinización. Por otro lado, la producción de néctar y de flores afecta el comportamiento, el tamaño poblacional y el ciclo de vida de los colibríes. Las variables climáticas, incluyendo la precipitación, la temperatura y la cobertura nubosa afectan a la producción del néctar. Las investigaciones demuestran que la precipitación también afecta directamente a los colibríes. En Monteverde, donde la tendencia climática es hacia la disminución de la precipitación, el aumento de la temperatura, y el incremento en la cobertura nubosa, los efectos potenciales sobre poblaciones de colibríes y poblaciones de plantas que los sostienen son complejos. Es posible que se dé un cambio en las distribuciones espaciales y temporales de las especies de colibríes y plantas, así como un cambio en la abundancia relativa de especies. Un decline de los recursos del néctar con la consecuencia de una reducción de la diversidad de colibríes es posible. Debido a la complejidad de los posibles efectos, es crucial ejecutar un programa de monitoreo y realizar experimentos para profundizar nuestra comprensión de la relación entre el cambio de clima y la biología de la fauna silvestre. El Capítulo 2 describe un plan para emprender esta investigación en la Reserva Biológica del Bosque Nuboso de Monteverde. Esto incluye la determinación de los tamaños de la población y de la abundancia relativa de colibríes en la región, la identificación de especies de plantas florecientes importantes, la delineación de su fenología, y la observación de la frecuencia de visitación de los colibríes a estas plantas. Se describen técnicas para medir el néctar. Se delinean experimentos para comprobar los efectos de la precipitación, de la temperatura, y de la cobertura de nubes sobre la producción de néctar. Los datos de la línea de base de estudios anteriores en la región se podrían comparar con los nuevos datos, con el fin de determinar el grado en el cual el cambio de clima ha comenzado a afectar los colibríes de Monteverde. El Capítulo 3 discute las ventajas y desventajas en la utilización de comederos de colibríes como herramienta de la investigación, y recomienda que los comederos solamente sean utilizados en forma limitada y en áreas de alta abundancia de flores. El objetivo último de este informe es facilitar la conservación de la biodiversidad en un Monteverde siempre cambiante.

Climate Change and the Hummingbirds of Monteverde

Chapter 1
Hummingbird Ecology and Climate Change

HUMMINGBIRDS OF MONTEVERDE

Background
It is well known that the global climate is changing rapidly, and that these changes influence the ecology of many wildlife species. However, the specific nature of these biological changes is often unknown. Many wildlife populations and species throughout the world are threatened by climate change, and some have undergone dramatic declines. In Monteverde several species of amphibians have already declined, and a few have gone extinct. The data show that in the last three decades the regional climatic patterns have tended towards warmer temperatures, and have been characterized by a marked reduction in the rains and mist produced by the trade winds during the dry season (Pounds *et al.*1999). This cloud forest system, dependent on low lying clouds carrying moisture into the forest, is likely to suffer changes that will adversely affect plants and the species that depend on them in many ways.

Several recent biological changes have been statistically correlated with climate change at both local and large scales (Pounds *et al.* 1999, Pounds *et al.* 2006). A recent study demonstrates that the growth rates of trees in the forests of Central America and Asia have declined over the last twenty years, most likely as a result of increased temperatures and increased cloud cover (Feely *et al.* 2007). This trend is likely to have negative impacts for Monteverde's cloud forest and the species it supports both in the short and long term. Not only might this decreased growth rate reduce the available forest habitat for species, but it also reduces the ability of the forest to take up carbon, thereby leaving more carbon in the atmosphere and exacerbating the effects of climate change (Feely *et al.* 2007).

Climate and ecology are inextricably linked in Monteverde, and global warming combined with other forms of environmental degradation presents a considerable threat to the biodiversity of the area. Although previous studies have focused on the impacts on amphibians, reptiles, and orchids, many groups of organisms could be in danger. The published data show that the distributions of many species of birds that reproduce in the area are changing (Pounds *et al.* 1999). However, little knowledge of the mechanisms of these changes or their consequences exists. No detailed study of any group of birds has been conducted that would allow us to evaluate their survival prospects as the climate continues to change. The purpose of this study is to determine possible pathways through which the changing climate could impact one important avian family, hummingbirds, and then design a program to evaluate their future conservation status in Monteverde.

Recent Changes in Avian Populations

It has been reported that bird species in Costa Rica have already begun to respond to a changing climate. Avian studies conducted in Monteverde comparing data from the 1970s with that collected in the late 1990s report that several species have moved upwards in elevation, and that others, which previously occurred at higher elevations, have declined in abundance (Powell & Hamilton DeRosier 1999). These high elevation species are possibly at the greatest risk of population collapse since they cannot move any higher and may be displaced by lower elevation species. Ecologists link these trends to changes in climate (Powell & Hamilton DeRosier 1999, Pounds *et al.* 1999). While these studies lack baseline data for hummingbirds, the observed trend mirrors that of other avian species. Biologists have recently noted that in Monteverde, as in other parts of Costa Rica, hummingbirds are moving to higher ground. Steely-vented Hummingbirds, Fiery-throated Hummingbirds, Purple-throated Mountain-gems, and Magenta-throated Woodstars have all shifted their distributions upwards (Fogden & Fogden 2005, p. 68). Additionally the relative abundances of Purple-throated Mountain-gems and Green-crowned Brilliants appear to be changing (Fogden & Fogden 2005). If these changes are indeed related to climate, they are likely to continue and intensify.

Biologically, Monteverde has cause for celebration and cause for alarm. In general, middle elevations (between 1800 and 2500m in the tropics) support the greatest diversity of hummingbird species (Wethington *et al.* 2005). Likewise, neotropical mid elevation forests, ranging from 1800-2100m, host the greatest diversity of epiphytes of any habitat in the world (Nadkarni & Matelson 1989). Monteverde ranges in elevation from 700m to 1850m, thus occurring geographically at the lower edge of this center of biodiversity (Haber 2000, p. 39). It is well known that the effects of climate change are amplified in highland areas (Nadkarni & Solano 2002). Thus, Monteverde lies in an area of significant threat. As climatic conditions change and its impacts become more severe, it is likely that this biological center will shift upward in elevation. This means that Monteverde could easily lose some of the diversity it currently boasts, even as species from lower areas move into the zone.

PLANTS AND HUMMINGBIRDS

Co-evolution

In most cases, hummingbirds and the plants they pollinate have a mutually beneficial relationship. Hummingbirds obtain nectar, their main source of energy, from plants, and in turn pollinate them, thereby facilitating plant reproduction. It is believed that certain groups of plants and hummingbirds present an example of a co-evolved mutualism (Stiles 1985). Stiles (1985) uses the following criteria to define co-evolution: the occurrence of "repeated, reciprocal evolutionary responses of each partner to selective pressures generated by the other". Therefore, hummingbird characteristics affect the process of evolution by natural selection in plants and *vice versa*. As such, both groups have developed traits that suit the needs of the other.

Hummingbird Effects on Plants

The behavior, preferences, and needs of nectarivorous species affect the flowering biology of the plants they pollinate (Young & McDonald 2000, p. 201). Consequently, hummingbird plants differ from those pollinated by insects and bats in the characteristics of their floral displays. Often their flowers are brightly colored and tubular, and produce high volumes of relatively dilute nectar (Baker 1975, Bolten & Feinsinger 1978, Briscoe *et al.* 1983, Fenster *et al.* 2006, Nicolson 1995, Nicolson & Fleming 2003, Stiles & Freeman 1993, Wyatt *et al.* 1992). Hummingbirds prefer sucrose based (rather than fructose or glucose based) nectar, and not surprisingly, hummingbird pollinated flowers are indeed sucrose rich (Boose 1997, Murray *et al.* 2000, p. 250, Nicolson & Fleming 2003).

It remains unclear what exactly drives selection for the dilute nectar characteristic of hummingbird-pollinated plants. While it has been shown that hummingbirds cannot consume nectar that is too concentrated they may prefer nectar that is actually more concentrated than those they visit. Hummingbird flowers produce nectar that ranges from 20-25% in its sugar concentration (Baker 1975, Roberts 1996), but experimental studies show that hummingbirds actually prefer concentrations greater than 45% (Roberts 1996). This suggests that it is not the preference of hummingbirds that encourages the production of dilute nectar (Roberts 1996). However, this concentration is clearly not accidental. Flowers actively employ different mechanisms, including the secretion and reabsorption of sugars, to maintain this dilute concentration of their nectars (Corbet & Wilmer 1981, Nicolson 1995). A species of *Columnea* in Monteverde has been shown to use compass orientation to prevent excessive exposure to sunlight and therefore evaporation of water, which would lead to more concentrated nectar (Corbet & Wilmer 1981). This regulation of nectar concentration suggests that the specific concentration could be an adaptation to the needs of their pollinators by maintaining a low enough nectar concentrations for birds to consume in the face of constant evaporation (Corbet & Wilmer 1981, Nicolson 1995). Other theories explaining why hummingbird flowers produce secrete such dilute nectars include maintaining low viscosity for better assimilation by hummingbirds, deterring nectar robbing bees, meeting the hydration requirements of birds, preventing hummingbird satiation (thereby increasing visitation rates), and encouraging genetic outcrossing through pollination (Baker 1975, Nicolson & Fleming 2003).

Some argue that hummingbirds and other pollinators fail to have a significant influence on the quantity of nectar yield and the rate at which it is produced because they respond to overall nectar availability in the field, or standing crop, rather than the nectar production rate of individual flowers (McDade & Weeks 2004b, Zimmerman 1988). While it may seem counterintuitive, studies reveal that the relationship between nectar production rate and standing crop is weak (Zimmerman 1988) or nonexistent (McDade & Weeks 2004b). This is because not only is standing crop a factor of nectar production rate but also of all causes of nectar removal including legitimate visitation, nectar robbing, and evaporation. Because the standing crop of all species at a given time is so variable, pollinators find a wide range of nectar volumes regardless of which species they visit (Zimmerman 1988). This suggests that the difference in nectar availability among species is negligible and does not allow hummingbirds to discern among species on the basis of nectar production rate, thereby limiting their ability to exert selection pressure on this characteristic.

While animal visitation of nectar producing plants obviously reduces the standing crop, its influence on the rate of nectar production is highly variable. Investigators have found that for certain species, nectar removal suppresses nectar production (Corbet & Wilmer 1997, McDade & Weeks 2004b), while for other species visitation actually stimulates nectar and sugar production (Gill 1988, Torres & Galetto 1998), and in yet others it has no apparent affect (McDade & Weeks 2004b).

Certain groups of plants are adapted to serve the needs of particular hummingbird species. Morphologically, there are roughly two main groups of hummingbirds and two corresponding groups of plants. The length of the flower corolla corresponds to the length of the principal pollinator´s bill. Hermit hummingbirds with long, curved bills visit flowers with long corollas that produce copious volumes of nectar, while shorter billed hummingbirds can only access the less abundant nectar in flowers with short corollas (Feinsinger *et al.* 1979).

Through their nectar consumption and pollen transport, hummingbirds influence individual plant success (Hodges 1993). However, the effects are varied and confounding. Nectar encourages pollination by hummingbirds, but if the plant is not pollen limited, the energetic cost of producing nectar may lead to a decreased energetic resources for producing seeds, and reproductive output can actually decline (Pyke 1991). Likewise the quantity of nectar that a plant yields leads to complex outcomes in terms of plant fitness. For example, some hummingbirds visit more flowers on plants that provide more nectar, thereby conferring greater pollination success (Mitchell 1993). However, producing large volumes of nectar or many flowers may also cause hummingbirds to remain at each flower for a longer period of time, reducing pollen transfer and genetic outcrossing, with the end result being that the plant produces fewer seeds per inflorescence (Mitchell & Waser 1992, Schemske 1980). However, these large, high-yield plants may still have the advantage because their overall seed set may be larger due to the presence of more flowers (Schemske 1980). The effects also depend on which types of hummingbirds use a certain plant. It has been demonstrated that hermits, which are more likely to visit dispersed flowers cause more outcrossing among plants while pollination by species tending to remain close to one clump of flowers results in self pollination (Stiles 1975).

Hummingbird interactions in response to changing nectar supplies also have implications for plant fitness. When faced with intense competition for nectar, hummingbirds increase their foraging effort and visit more flowers (Garrison & Gass 1999). Because pollination success increases with frequency of hummingbird visits (Mitchell & Waser 1992), plants in nectar limited systems may receive more hummingbird visits and experience greater fitness. Taken together this portrays a complex balance between nectar and pollen transfer. Therefore, a plant must carefully balance its energy output according to the reproductive benefit derived from its nectar reward and the associated reproductive costs.

The combined effects of hummingbirds on plant fitness define the plant community composition. Hummingbirds help to structure the plant community by creating competition among plants for pollinators (Feinsinger 1978). When multiple species of plants flower contemporaneously, hummingbirds can choose to visit only the species that provide the greatest reward. Therefore, plant competition for pollinators may be lower when plants stagger their flowering peaks in time (Feinsinger 1978). This may also reduce the likelihood of hybridization among closely related species (Stiles 1975). In Monteverde, the competition is not intense enough to select for a divergent flowering phenology (Feinsinger & Tiebout 1991, Murray *et al.* 2000, p. 253, Young & McDonald 2000, p. 201). Although the reproduction of many plant species does not depend entirely on pollinators, which plants get pollinated does play a role in influencing the community structure. Only plant species that successfully reproduce will persist in the area. Therefore the interactions between plants and hummingbirds shape the community in dynamic ways (Feinsinger 1978).

Foraging Behavior

While hummingbirds are all related in one phylogenetic family, they have evolved varied morphologies to maximize their resource use. Ecologists have attempted to categorize hummingbirds in terms of correlations between their morphological characteristics, their foraging behavior, and their preferred plant species. Feinsinger and Colwell (1978) described six different behavioral roles played by different types of hummingbirds: high reward trapliners, low reward trapliners, territorialists, marauders, filchers, and generalists. However, because the groups are not fixed at the species level (behavior varies daily, seasonally, and with sex and individual characteristics) Stiles (1985) finds limited utility in the delimitation of these ecological roles and describes instead subcommunities consisting of several species of hummingbirds with similarly adapted morphologies that depend on similar resources (Stiles 1985). Regardless of the best way to classify hummingbirds, the six foraging strategies described by Feinsinger and Colwell (1978) shed light on the many ways hummingbirds use the landscape to meet their energetic needs. Their foraging behaviors vary according to levels of competition, resource availability (Feinsinger & Colwell 1978), and elevation due to the increased energetic costs of living at higher realms (Feinsinger *et al.* 1979). Different hummingbirds exhibit unique responses to changing ecological conditions. Territorial birds, which defend small but productive clumps of flowers are more affected by changes in the resource base than trapliners, which visit dispersed flowers on a fixed route in the forest (Feinsinger 1976). The territorial behavior of hummingbird species is not necessarily fixed, but rather shifts as different species of plants come into flower (Wolf 1970). Certain hummingbirds may only exhibit territorial behavior in periods of plant abundance, when the resource is rich enough to be worth the cost of defense (Wolf *et al.* 1976).

Hummingbirds rely on a diversity of plant species and forms. They are not restricted to terrestrial flowering species, but also forage high in the canopy on several species of epiphytic plants. The *Bromeliaceae, Ericacacea, and Marcgraviaceae* families are three of the most important groups of epiphytes to hummingbirds, which take advantage of their nectar resources (Nadkarni & Matelson 1989). A study in Monteverde revealed that Mountain Gems, *Lampornis castaneoventris*, use epiphytic species for a significant portion of their foraging needs (Nadkarni & Matelson 1989). In addition, the Striped-tailed Hummingbird, the Fork-tailed Emerald, the Coppery-headed Emerald, the Green-crowned Brilliant, and the Violet Sabrewing use epiphytes to varying degrees (Nadkarni & Matelson 1989).

Species behavior and competitive interactions impact the entire community. Certain species have a greater influence over the community dynamics than others. Dominant, aggressive, and territorial species affect the behavior of the more subordinate species. A flight cage experiment in Monteverde shows that traplining species increase their foraging visits during the times of day when the territorial species are least aggressive (Tiebout 1992). Similarly at Cerro de la Muerte where four hummingbird species coexist, the dominant species, the Fiery-throated Hummingbird (*Panterpe insignis*) affects the behavior of the other species. Its population size, along with nectar availability, determines the other species' places in the guild (Wolf *et al.* 1976). Likewise, in Monteverde, Feinsinger (1976) found that *Amazilia saucerottei* (Steely-vented Hummingbird) affects the other species' foraging patterns via its aggressive territoriality, while *Chlorstilbon canivetii* (Fork-tailed Emerald) organizes the non-territorial species (Feinsinger 1976).

How species fare when competing for scarce resources affects the community composition. Because species under pressure from competitors require increased energy they often cannot maintain adequate energy reserves. When species operate at an energy deficit their local abundance may decline (Tiebout 1993). This suggests that what happens to one species may have far reaching consequences for the ecological community at large.

Nectar Effects on Hummingbird Behavior

Just as hummingbirds affect plant biology, plants, through nectar, its presence, quantity, and concentration, influence hummingbird behavior (Hodges 1993, Murray *et al.* 2000, p. 250, Wolff 2006). Pollinator visitation is mostly driven by nectar volume (Wolff 2006), both in terms of how much is produced by a single flower and in terms of how many nectar-producing flowers are in bloom in an area at a given time. In general, hummingbirds avoid flowers that lack nectar, although it is unclear what cues they rely on to distinguish which flowers on a plant contain nectar (Irwin 2000). Hummingbirds prefer plant species that produce flowers with larger petal areas and corolla opening diameters, most likely because flower size is positively correlated with overall nectar reward (Fenster *et al.* 2006). Likewise, one study showed that hummingbirds visit flowers in their first day of bloom three times as often as flowers in other stages because they produce significantly more nectar (Schemske 1980). In addition, large plants with more flowers, and therefore greater quantities of nectar, receive more visits per plant and per inflorescence than small plants with few flowers (Schemske 1980).

In Monteverde, hummingbird visitation of short flowered *Ericaceae* species is affected mainly by the size of the floral display (Murray *et al.* 2000, p. 268, Busby). This indicates that the more flowers a plant produces, the more likely it is to receive hummingbird visitors. When a plant offers a greater nectar volume, hummingbirds visit more flowers and spend more time probing each flower (Mitchell 1993, Mitchell & Waser 1992). Under experimental conditions, traplining species such as the Long-tailed Hermit, change their rates of flower visitation as the resource base fluctuates (Garrison & Gass 1999). However, the correlation is not always positive; a patch that yields excess nectar leads to hummingbird satiation and reduced flower visitation (Garrison & Gass 1999).

As the abundance of flowers and nectar varies seasonally and annually, so does the population size of hummingbirds (Feinsinger 1976, Young & McDonald 2000, p. 198). Years with a lower nectar crop support fewer hummingbirds (Young & McDonald 2000, p. 201). Annual variation in population size is believed to be due largely to changes in immigration and emigration rather than in birth and death rates (Young & McDonald 2000, p. 198). This signifies that within normal ranges, nectar production affects hummingbird behavior by attracting or repelling visitors, but that it does not directly change fecundity or mortality. The number and diversity of hummingbirds increases more with number of open flowers than with diversity of plant species (Feinsinger 1976), suggesting that nectar presence and quantity is more important than the particular nectar characteristics of each plant in sustaining suites of hummingbirds.

In terms of the concentration of sugars, the observed effects on hummingbird behavior are contrasting. One study reports that varying the nectar concentration within natural ranges does not affect visitation rates of hummingbirds (Irwin 2000). Another study shows that an increase in sucrose leads to increased bird visitation, but only in the morning (Garrison & Gass 1999). Other studies report that concentrations do indeed affect visitation rates (Lopez-Calleja *et al.* 1997, Schemske 1980). Researchers contend that as nectar sucrose concentration increases, hummingbirds forage less frequently (Lopez-Calleja *et al.* 1997). When hummingbirds consume nectar of very low concentrations they must rely more frequently on nighttime torpor to conserve energy, and in some cases they suffer an energy deficit (Lopez-Calleja *et al.* 1997). A slightly higher concentration of nectar may provide another important benefit. When adults consume more concentrated nectar they increase their level of parental care towards their young (Nicolson & Fleming 2003). However, if nectar is too concentrated hummingbirds simply cannot consume it (Boose 1997, Nicolson 1995).

Life Cycle & Timing

The life cycle of a hummingbird consists of several important stages: nesting, molting, and migrating. The timing of hummingbird behavior in Monteverde differs from that of species found in other regions of the country, and is tied mainly to nectar availability (Fogden & Fogden 2005, p. 59). Because hummingbirds are so dependent on flowering plants, the exact timing of their life stages varies yearly in accordance with environmental conditions, abundance of nectar, and competitive dynamics (Young & McDonald 2000, p. 201). In the higher elevations of Costa Rica the breeding of the tiny volcano hummingbird coincides with the blooming of a plant species whose narrow corolla precludes its use by other species, thus ensuring that the volcano hummingbird has an ample food source during this important period (Hainsworth & Wolf 1972). Likewise, a resident species at *Cerro de la Muerte*, the Fiery-throated Hummingbird, breeds when a particular plant is in flower before the migratory hummingbirds arrive from other areas of Costa Rica (Wolf *et al.* 1976). At this site the greatest diversity and density of hummingbirds occurs during the period of peak blooming (Wolf *et al.* 1976).

Likewise, in Monteverde hummingbirds mostly nest during the last few months of the year when preferred plants are flowering (Fogden & Fogden 2005, p. 59). It has been proposed that they time their breeding effort to preempt the major flowering peak so their young will have sufficient food resources (Stiles 1985). Others suggest that it is the timing of their molt, which follows breeding and occurs from December to April, which coincides with the maximum abundance of flowers (Young & McDonald 2000, p. 195). Both breeding and molting require enormous energy expenditures, and nectar consumption during these periods increases significantly (Fogden & Fogden 2005, p. 59, Stiles 1985). Migration also depends on nectar production, although most of the species found in Monteverde migrate only short distances from other areas of Costa Rica (Fogden & Fogden 2005, p. 59, Young & McDonald 2000, p. 201). In Monteverde certain species including the Magenta-throated Woodstar, the Blue-throated Goldentail, and the Plain-capped Starthroat time their seasonal migrations in accordance with the flowering of one or two specific plant species (Young & McDonald 2000, p. 184). Because species migrate, conditions in all areas of their ranges affect their behavior, diversity, and abundance (Wethington *et al.* 2005).

CLIMATE & PLANTS

Environmental conditions impact many aspects of a plant´s life. Because of plants' sensitivity to the ever-changing environment, researchers have observed a great deal of annual variation in nectar production (Boose 1997). Below are several avenues through which climate influences the production of flowers and nectar, thus having significant consequences for all nectarivorous species including hummingbirds.

Hydrology: Water & Humidity

It is well known that in dry years plants generally produce less nectar, and that years with higher levels of precipitation yield greater nectar volumes (Boose 1997, Feinsinger 1978, McDade & Weeks 2004a, Petanidou & Smets 1996, Stiles 1978 Wethington *et al.* 2005, Wyatt *et al.* 1992). One study demonstrated that after a dry period, providing plants with supplemental water resources doubled their nectar production (Wyatt *et al.* 1992). In another experiment plants receiving less water produced 26% less nectar volume than those with sufficient water supplies (Boose 1997). A drought that occurred during one year of an investigation conducted at *La Selva* delayed, abbreviated, or eliminated the flowering peaks of several species. These effects lasted from several months to a year (Stiles 1978). In an extremely wet year in the same study several species of *Bromeliads* experienced much larger than average flowering peaks (Stiles 1978). Another investigation reports that severe drought during one season prevented 95% of the plants in the population from flowering (Hodges 1993). However, it cannot be assumed that more rainfall always leads to greater flower abundances. At *La Selva* a pronounced flower shortage occurs regularly during the wettest season (Stiles 1978).

In addition to the effects moisture may have on nectar in the form of rainfall, atmospheric moisture also plays an important role. The relative humidity of the air influences a plant´s nectar production, specifically its concentration of sugars (Boose 1997, Pleasants 1983). A single plant therefore can display significant variance in nectar concentration from one day to the next depending on humidity. Likewise, soil moisture may have significant effects (Boose 1997, Feinsinger 1978, Wolff 2006). One study found that in a clonal *Heliconia* species, the ramets occurring on the wettest soil produced flowers with high nectar volumes, while ramets on dryer soils produced "blanks", or flowers with minimal nectar yields (Feinsinger 1983). This may also be linked to the availability of nutrients in the soil (Boose 1997, Feinsinger 1978, Wolff 2006). These factors are at play at both the very local and the very broad scale. When soil moisture is limited in a restricted area, a single plant, or a single part of a plant, may be affected. However, if the general trend is one of reduced moisture over a broad geographic area, entire communities of plants may feel the impacts.

Temperature

Nectar production varies with temperature. Various studies report that low nectar production is related to low temperature (Jakobsen & Kristjansson 1994, McDade & Weeks 2004a, Nicolson 1995, Petanidou & Smets 1996, Wolff 2006). However, this is only true until a threshold is reached as nectar production increases with temperature until a maximum and then declines (Nicolson 1995, Petanidou & Smets 1996). Nighttime temperatures in particular may affect nectar production and may alter the relative sugar composition of nectar. Increased night temperatures have been shown to reduce the amount of sucrose relative to glucose and fructose (Jakobsen & Kristjansson 1994). Abiotic factors may interact in complex ways. For example, in certain species nectar volume along with sugar production and concentration increase with temperature, provided that the plant is not suffering water stress (Petanidou & Smets 1996).

Clouds & Light

It is also documented that solar irradiance and cloud cover affect nectar production because nectar production depends on photosynthesis, which is directly controlled by the intensity of sunshine (Stiles 1978). Studies show that low light conditions lead to a reduction in nectar crops and lowered sugar concentrations (Boose 1997, McDade & Weeks 2004a, Petanidou & Smets 1996, Pleasants 1983). One investigation found that ramets grown with 70% less light produced 27% less nectar than ramets under ambient light (Boose 1997). This may result in daily variance in nectar production of a single plant (Pleasants 1983). However, this may be true only for certain species, or at the very least, the effect may be stronger in plant species adapted to brighter conditions (Petanidou & Smets 1996).

Elevation

The elevation at which a plant grows affects its nectar attributes. In general nectar volume as well as sugar concentrations decrease with elevation (Baker 1975, Hainsworth & Wolf 1972, Murray *et al.* 2000 p. 250, Stiles & Freeman 1993). Viscosity increases both with elevation and with concentration, which may explain why nectars are often found at lower concentrations at higher elevations. The same concentration consumed at lower elevations may be too viscous for hummingbirds to consume at higher elevations. Therefore if plants are producing nectar for hummingbirds they must produce nectar that is less viscous, and therefore less concentrated (Baker 1975). Sugar compositions differ across elevational gradients. At higher elevations nectars contain higher percentages of fructose relative to sucrose than in lower regions (Stiles & Freeman 1993).

Plant genetics and variability

While plants respond in a variety of ways to environmental conditions, they are also constrained by their own genetic makeup. In general, the size of the flowers that a plant produces is positively correlated with nectar volume and concentration, or overall nectar reward (Bolten & Feinsinger 1978, Fenster 2006, Stiles 1985). In Monteverde, it has been reported that there are relatively few long-flowered plant species (Murray *et al.* 2000, p. 268, Busby, Stiles 1985). Much more abundant in the zone are flowers with shorter corollas and lower nectar rewards.

It has been widely observed that in spite of the many aforementioned correlations between environmental factors and nectar production, nectar yields are highly variable (Hodges

1993). In fact, there is a great deal of variation in nectar production among plants of the same species (Zimmerman 1988), plants within the same population, and even among flowers on same plant (Boose 1997). Different genets of a single plant also respond differently to environmental factors suggesting that some are more sensitive to abiotic factors while others are more fixed in their nectar production (Boose 1997). It has been suggested that within plant variation may have adapted to encourage outcrossing, rather than enticing pollinators to remain at a single plant (Boose 1997). It has also been shown that both the number of open flowers and the variance in nectar production are positively correlated with the mean nectar volume per flower (Torres & Galetto 1998). Therefore plants that are more variable in their nectar production actually produce more nectar per flower on average than those with more consistent nectar production.

Timing

Seasonality also influences nectar production. It has been shown that certain species of plants display a reduced nectar output as the flowering season progresses (McDade & Weeks 2004a, Pleasants 1983, Torres & Galetto 1998). This could be due to changes in abiotic conditions, plant and flower age (McDade & Weeks 2004a, Schemske 1980, Torres & Galetto 1998), or to the changing energetic demands on plants throughout their lifecycles. For example, certain species may produce less nectar later in the season when they are allocating their resources to seed production (Pleasants 1983). Another proposed hypothesis purports that attracting pollinators requires less nectar later in the season because by then hummingbirds have acquired knowledge of the nectar source and can rely on their spatial memory to locate nectar (McDade & Weeks 2004a).

Several factors affect the timing and duration of flowering peaks, thereby controlling nectar output and availability. The growth form of the species and its habitat type at both the large and small scale affect when the species flowers (Stiles 1978). For example, epiphytes have different phenologies than shrubs, species occurring in light gaps flower at different times than those under closed canopy cover, and those of the dry forest have a different flowering rhythm than those of the wet forests (Nadkarni & Matelson 1989, Stiles 1978). In the dry forests, where the water acts as a limiting resource, the flowering peaks among species are generally more synchronized than those areas that receive ample precipitation year round (Wolf 1970). In addition there may be a relationship between the duration and timing of flowering. It has been shown that plants that flower very briefly are more likely to have their period of maximum flowering during the dry season (Wolf *et al.* 1976). In the Caribbean lowlands of Costa Rica at *La Selva*, two annual flowering peaks of equal magnitude occur, first during the late dry season and later during the early wet season (Stiles 1978). In contrast the late dry and early wet seasons are the periods of lowest flowering at *Cerro de la Muerte*, a high elevation habitat in Costa Rica (Wolf *et al.* 1976). Seasonality affects flowering, but each habitat responds differently to the seasons.

Spatial Position

How and where species grow also plays a part in their sensitivity to climate. Epiphytes, because of their position at the interface between the terrestrial world and the atmosphere and their complete dependence on nutrients deposited by clouds and mist are among the most responsive to environmental factors governed by climate (Nadkarni & Solano 2002). They play an important role in the cloud forest by capturing essential inputs that might otherwise pass over the system completely (Nadkarni & Solano 2002). It has been shown that in the case of epiphytes, climate affects not only nectar production but also their very growth and survival (Nadkarni & Solano 2002). Obviously with the reduction or loss of epiphytes comes a decline in overall nectar resources.

CLIMATE & HUMMINGBIRDS

While very few studies have taken the next step and investigated the links between climate and hummingbird populations, an important correlation is evident. Precipitation patterns have dramatic effects on hummingbird populations at all spatial scales. Throughout their range in the New World, hummingbirds are most diverse in forested areas that receive high levels precipitation (Wethington *et al.* 2005). Areas of Central and South America with the highest annual rainfall support the greatest hummingbird species richness (Wethington *et al.* 2005). At more local scales and in shorter time frames hummingbird population size is also correlated with precipitation. During especially dry years hummingbird populations at various sites are markedly reduced (Wethington *et al.* 2005). Faaborg (1982) notes that drought, depending on its timing and severity, has negative impacts on hummingbird populations. A detailed study of long tailed hermits during a drought at *La Selva* on the Caribbean slope of Costa Rica corroborated this conclusion. The timing of the drought led to an interruption in molt, reduced fecundity, and lowered survivorship (Stiles 1992). In addition it took several years for the population to recover from this single drought event (Stiles 1992). Even at the smallest scales precipitation affects hummingbirds. On a daily basis foraging behavior changes with climatic conditions. In Monteverde Striped-tailed Hummingbirds display more active territoriality during rainy days when butterflies are inactive (Young & McDonald 2000, p. 195). Dry conditions, therefore, can affect virtually all periods of a hummingbird´s life cycle, and can reduce all aspects of fitness.

POTENTIAL IMPACTS OF CLIMATE CHANGE

Climate change is not a new phenomenon, and species have been adapting to an ever-changing world for eons, so one could argue that the plants and hummingbirds of Monteverde will simply adjust to the new conditions. However, the current period of climate change is believed to be significantly different from anything that has occurred in geologic history in terms of the rate of change. While over long time periods selection pressure from environmental factors will result in adaptation and genetic changes, the climate is currently changing more quickly than adaptation by natural selection can occur. Therefore, in the short term the ability of each species to respond is limited by its current genetic composition and its resultant morphological characteristics. However, species distributions may change rapidly depending on species motility.

The relationship between climate change and the hummingbirds of Monteverde is extremely complex. The potential impacts are many as both plants and hummingbirds are vulnerable to countless environmental factors throughout their life histories. Several possible ways in which climate could impact the species of hummingbirds found in Monteverde are described below along with important questions raised by these possibilities.

One possible outcome of climate change is that species may shift their distributions to higher elevations or more northerly latitudes. This may occur because any given elevation may take on the environmental characteristics of a lower elevation (i.e. warmer temperatures). However, it is uncertain how long such a response would take, and it is most likely that each species would adjust in a unique time frame. Hummingbirds, being highly mobile, may be able to move upwards sooner than the plants that sustain them. As species shift in distribution Monteverde will likely host a different suite of nectar producing flowers and hummingbirds. If the cloud forests of Monteverde routinely experience the climate of lower elevations, some of its current diversity will be lost and the plant community composition is likely to change, yielding manifold effects. A different group of plant species could alter competitive dynamics among plants for pollinators, which could have long-term consequences for the plant community. Different floral characteristics could attract different types of pollinators, or exclude some of the most currently abundant species (Feinsinger *et al.* 1979). For example, an increase in the proportion of large flowered plants may have positive effects in terms of overall nectar availability. However, if they displace short flowered plants, hummingbirds with short bills, which physically cannot extract nectar from long, curved corollas, will suffer a decline in nectar resources even when net resources have increased.

In Monteverde, it has been reported that the climatic trend is one of drying, indicating a reduction in rainfall and a decline in relative humidity (Pounds *et al.* 2006), both of which affect nectar production and hummingbirds. In general water stress leads to reduced nectar supplies, thereby depriving hummingbirds of their main energy source, altering competitive interactions, and potentially limiting the population size. In addition, even a short-term drought can impair hummingbird populations for several subsequent years (Stiles 1992). In the event of a long-term drought occurring at a broad geographic scale, or simply a switch to a drier climate, the hummingbird populations of Monteverde might be unable to recover. The recorded reduction in precipitation due to global climate change could be responsible for a concomitant decline in hummingbird populations.

However, the scenario is not necessarily so simple. Because the relationship between temperature and nectar production is positive, certain species of plants in Monteverde may increase their nectar output as the temperatures in the region rise. This could benefit the hummingbird populations by providing them with supplemental food resources. However, this can only occur if the temperatures do not exceed the threshold for any given plant, and that the increase in temperature is not coupled with a reduction in precipitation so severe that the plants are water stressed. Another important component of the temperature equation is the average nighttime temperature relative to the average daytime temperature. In Monteverde, the difference between the two has decreased (Pounds *et al.* 1999). The change in nighttime temperature could affect the sugar composition of nectar, changing its appeal to hummingbirds and other pollinators and affecting competition.

Confounding matters further, the climate in Monteverde shows a trend towards increased cloud cover. Because reduced light limits the ability of plants to photosynthesize and is associated with hampered nectar production for certain species, the new cloudier clime could result in diminished nectar production among Monteverde plants, which has potentially negative impacts for plants and nectarivorous species.

It is difficult to predict what will happen to high elevation hummingbird species in the face of a changing climate. In general, small species living at high elevations have the greatest difficulty meeting their energetic demands (Wolf *et al.* 1975). The Volcano Hummingbird (which does not occur in Monteverde) relies on two species of plants that produce small volumes of highly concentrated nectar. If these plants cannot tolerate the new conditions and the hummingbirds are forced to rely on other species that produce nectar in lower concentrations it is unclear whether they will still be able to meet their energetic demands. It is possible that their energetic demands will decrease if the climate is warmer, but if other species of hummingbirds move up in elevation into the range of the Volcano Hummingbird they will be forced to compete with larger, unfamiliar species for nectar.

A major unknown is how climate change will alter hummingbird foraging behavior via a novel nectar production regime. The adoption of different foraging strategies could change the competitive dynamics among hummingbirds. This could impact the population structure and size, relative abundances, and species distributions of hummingbirds in Monteverde. These changes will have consequences for pollination, plant fitness, and plant community structure.

Seasonality is important with respect to climate change because the seasons themselves may shift in time or change in their defining characteristics. Either of these possibilities could alter plant phenology. The timing of peak flowering and nectar abundance may change, having implications for both the plant community and their pollinators. If plants flower during new time periods the flowering peaks of plants species that had never previously flowered concurrently may overlap, thus changing plant competition. Certain plants that were abundant may not receive sufficient pollinators to reproduce at prior levels. This portends a potentially significant change in community structure. Furthermore, if the phenologies of species upon which certain hummingbirds depend change appreciably, nectar availability may not coincide with “normal” pollinator timing. Many hummingbirds come from other regions of the country in search of blooming plants, some seeking a single particular species. How they react to these changes in seasonality and phenology should be investigated. If plant phenologies do not shift, but instead plants continue to flower and produce nectar and seeds at the normal times but under sub-optimal conditions, plant fitness could decline. All phases of a plant’s lifecycle are equally important (Galen 1999). If a plant produces ample nectar and successfully attracts pollinators, but then fails to produce viable seeds, its fitness is severely compromised. The environmental conditions during all time periods must facilitate survival and reproduction. Therefore, when considering the impacts of changes in seasonality it is crucial to investigate the effects of environmental conditions throughout the entire cycle, not merely during flowering.

The potential effects of climate change may be significant in the cloud forests of Monteverde where epiphytes, which are highly sensitive to environmental change, contribute greatly to forest productivity and resiliency and support biodiversity (Nadkarni & Solano 2002). So important are these plants to hummingbirds that certain species time their nesting to coincide with the peak flowering of epiphytic *Ericaceae* species (Fogden & Fogden 2005, p.

59). Nadkarni & Solano (2002) have proposed that epiphytes could serve as indicators of climate change as they will be among the first plants to suffer its effects. This suggests that species of epiphyte-dependent hummingbirds may respond to climate change more quickly than other species. Therefore, both epiphytes and the hummingbirds that pollinate them could serve as indicators of climate change. Likewise, the reduction of epiphytic plants could lead to a decline in hummingbird populations or a change in species composition as those species most reliant on epiphytes fail to find sufficient resources.

As the climate changes, plants and hummingbirds will be confronted with challenges across multiple scales. At a global level, changes in the climate have resulted in an altered hydrological cycle and changes in precipitation patterns (Pounds & Crump 1994, Pounds *et al.* 1999). Throughout hummingbirds' ranges these changes could begin to affect their distribution and abundances. The regional climate in Monteverde has felt the effects of the global trend and has become drier and warmer. The microclimate as well is changing. Changes in the climate at every scale are important for species, and all can have severe consequences. It has already been proposed that other groups of species in the zone have undergone catastrophic collapses as a result of an altered microclimate within a larger global trend of climatic change, for example the Monteverde Harlequin Frog (see Pounds *et al.* 2006). To understand fully how climate change is affecting hummingbirds, it will be important to conduct studies at a wide range of scales.

FURTHER CONSIDERATIONS & CONCLUSIONS

All of the studies outlined above raise interesting questions about the relationship between climate change and hummingbirds worldwide, and in Monteverde specifically. To understand the effects to date, some basic questions to be answered are:

1. Is there a clear and quantifiable link between the observed changes in hummingbird populations and the warmer, drier climate in Monteverde?
2. Has the phenology of hummingbird pollinated plants changed along with the climate?
3. Has the timing of overall peak flowering in Monteverde changed?
4. Have nectar availability and flower abundance changed?
5. Is the new climate regime limiting, or otherwise altering nectar production in Monteverde?
6. Has the species composition of hummingbird pollinated plants changed?
7. Are changes in local species abundances of hummingbirds related to changing distributions, competitive interactions, flowering phenology or some interplay of all of these factors?
8. Has the species composition of the forest canopy changed, and more specifically has the abundance of nectar producing epiphytes declined?
9. Have epiphyte dependent hummingbirds declined in local abundance in recent years?

Recently documented climatic trends indicate many potential avenues for adversely affecting the diverse and abundant hummingbirds of Monteverde. The synergistic effects among the many environmental and ecological factors are likely to be far more complex than reasoning alone can predict. A monitoring program and a series of carefully designed experiments are needed in order to collect meaningful data. Through these investigations we can increase our understanding of the current situation in Monteverde, clarify the relationship between climate change and hummingbirds specifically, and protect the biodiversity for which Monteverde is so famous.

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Appendix

Hummingbirds of Monteverde

Source: Fogden & Fogden 2005

Species Common Name	Latin Name
White-tipped Sicklebill	*Eutoxeres aquila*
Green Hermit	*Phaethornis guy*
Little Hermit	*Phaethornis longumareus*
Green-fronted Lancebill	*Doryfera ludoviciae*
Violet Sabrewing	*Campylopterus hemileucurus*
White-necked Jacobin	*Florisuga mellivora*
Brown Violet-ear	*Colibri delphinae*
Green Violet-ear	*Colibri thalassinus*
Black-crested Coquette	*Lophornis helenae*
Green Thorntail	*Discosura conversii*
Fork-tailed Emerald	*Chloristilbon canivetii*
Crowned Woodnymph	*Thalurania colombica*
Fiery-throated Hummingbird	*Panterpe insignis*
Blue-throated Goldentail	*Hylocharis eliciae*
Coppery-headed Emerald	*Elvira cupriceps*
White-bellied Mountain-gem	*Lampornis hemileucus*
Purple-throated Mountain-gem	*Lampornis calolaema*
Green-crowned Brilliant	*Heliodoxa jacula*
Purple-crowned Fairy	*Heliothryx barroti*
Plain-capped Starthroat	*Heliomaster constantii*
Magenta-throated Woodstar	*Calliophlox bryantae*
Scintillant Hummingbird	*Selasphorus scintilla*
Steely-vented Hummingbird	*Amazilia saucerrottei*
Rufous-tailed Hummingbird	*Amazilia tzacatl*
Striped-tailed Hummingbird	*Eupherusa eximia*

Climate Change and the Hummingbirds of Monteverde

Chapter 2
Monitoring and Experiments

In order to understand how the hummingbirds of Monteverde may be impacted by climate change, a series of experiments must be conducted. Below are several strategies gleaned from the literature to answer a variety of pertinent questions.

To gain insights into the ecology of the plants most vital to local populations of hummingbirds, we must first identify which groups of plants are most commonly used now, and which have been used historically. According to Fogden and Fogden (2005), the five most important plant families to hummingbirds are: *Heliconiaceae, Bromeliaceae, Ericaceae, Rubiaceae, Acanthaceae,* and *Gesneriaceae*. Nadkarni and Matelson (1989) add *Loranthaceae* and *Marcgraviaceae* to the list of important epiphytic plants. Feinsinger (1976) identifies *Hamelia patens, Inga brenesii,* and *Lobelia laxiflora* as three key hummingbird pollinated species in Monteverde. Feinsinger (1978) researched ten plant species, Feinsinger *et al.* (1987) investigated twenty-six, and Stiles and Freeman (1993) conducted a study of twenty-two species of hummingbird pollinated plants in Monteverde. These combined species lists, organized by plant family are provided in Appendix A. When conducting studies it would be beneficial to incorporate a variety of the species in the groups listed above. The basic outlines for the observational and experimental ideas are summarized in Appendix B.

Field Observations: Hummingbird Population Size

One of the first tasks is to estimate the population sizes and relative abundances of the hummingbirds of Monteverde. Many researchers make these estimates by mist-netting or trapping birds at feeders. However, these methods are invasive and stressful to the captured individuals. Less intrusive techniques based on observations in the field are preferable. The first step is to establish transects or study areas in a variety of habitats in the region and conduct monthly hummingbird censuses (Feinsinger 1976, Nadkarni & Matelson 1989, Stiles 1985). During the censuses researchers record the frequency with which they encounter different species of hummingbirds to garner an idea of the population size (Wolf *et al.* 1976). It is important to make regular observations in all study sites to ensure that all hummingbird species in the region are encountered. Likewise, seasonal and yearly trends are essential to understanding the effects of climate change. Therefore, the censuses must be conducted during every month of the year.

Another strategy is to take advantage of the many already established hummingbird feeders in the area. One or two days each month should be devoted to observations at these feeders where hummingbirds are known to congregate. It is also possible to set up feeders in new locations in order to attract hummingbirds and determine the population size based on recruitment rates.

Field Observations: Flowering Phenology

In order to determine which species of hummingbird pollinated plants are found in the region and when they come into flower, researchers should use the same transects or study areas used for the bird censuses. Censusing the flowering plant species by recording how many individuals of each species are found along each transect reveals which plants are available to pollinators (Feinsinger 1976, Nadkarni & Matelson 1989, Stiles 1985). In order to census epiphytic species observations need be made from a canopy platform (Nadkarni & Matelson 1989). In order to evaluate when peak flowering occurs for each species, censuses should be conducted at regular intervals throughout the year (Stiles 1985 recommends every 4-6 weeks). To quantify the data, researchers count the number of flowers of a random sample of individuals of each species. It is also helpful to note whether flowering is increasing or decreasing for each species. This is determined by noting the relative abundance of buds, flowers, and fruits on each plant (Stiles 1985). This information can later be used to ascertain the timing of the overall multiple species flowering peaks, by counting the number of species in “good bloom” (defined respectively by Feinsinger 1978 and Stiles 1985 as attaining 25% or 50% of their maximum flower count in a season). During the period of peak flowering for each plant species the abundances of all flowering hummingbird species should be ranked (Wolf *et al.* 1976).

Field Observations: Hummingbird Visitation

The literature yields many different observational techniques for understanding hummingbird visitation patterns. During the early morning when hummingbird activity is at its peak, observations are made in the designated study areas for a specified period of time adjusted for the size of the observation area (Feinsinger 1976). Observers record all hummingbird visits to flowers within a standardized distance, identifying the bird and plant species and recording the behavior of the hummingbirds (Stiles 1985). It is useful to know which foraging strategies each bird employs and how long it spends at a plant during each visit (Stiles 1975).

For more in depth understanding, trained observers spend several full days at each site recording all audible and visible hummingbird activity and counting the number of inflorescences and flowers each bird visits (Feinsinger 1976, Schemske 1980). Estimates of the numbers of all species visited by hummingbirds should be made in order to categorize the plants according to visitation frequency.

Within each study area, more precise observations should be made on randomly selected clumps of flowering plants each month. One possibility is to choose the three most abundant flowering species each month and dedicate three days of that month to focusing observations on individuals of each of those species (Feinsinger *et al.* 1986). All observations should be undertaken throughout the year as species of hummingbirds fluctuate in abundance and species of plants come into flower. Researchers should augment their documentation by photographing hummingbird visitation and collecting plant samples for unidentified species (Stiles 1985, Torres & Galetto 1998).

Experiments: Nectar Measurements

For inquiries into trends in nectar production, following established nectar collection protocol insures comparable and relevant data. The first step is to select species and individuals to sample. Obviously it is important to use a variety of species known to be visited by hummingbirds. One option is to follow the lead of McDade and Weeks (2004a) and choose hummingbird pollinated plants opportunistically based on abundance and availability. Another possibility is to use some or all of the species used by Feinsinger (1976), Feinsinger (1978), Feinsinger *et al.* (1986), Feinsinger *et al.* (1987), and Stiles and Freeman (1993) listed in Appendix A. Individuals of each species can be chosen randomly (Fenster *et al.* 2006), and it may be helpful to determine the number of plants to be sampled based on the population size in the area. For example Boose (1997) chose approximately one third of the clumps of a certain species in the study area and selected four flowers on each plant to sample. The chosen plants and flowers should be marked clearly.

In order to gather information on nectar production rates it is important to exclude pollinators before the flower opens or immediately after removing all nectar. The most commonly used mechanism is bagging flowers with very fine mesh (Boose 1997, McDade & Weeks 2004a, Pleasants 1983, Schemske 1980, Wyatt *et al.* 1992). However, the effectiveness of bagging is not always guaranteed. It has been reported that some ants, mites, and even hummingbirds can find ways to consume nectar even when flowers are protected with one millimeter bridal veil mesh (McDade & Weeks 2004a). If pollinators are observed taking nectar through mesh, one alternative is to encapsulate the buds (Zimmerman 1988), or to cage entire plants using wire and fiberglass as per Fenster *et al.* (2006). However, it has been shown that using other types of bags, particularly paper, plastic, and pellon can alter the microenvironment of the flower enough to change the nectar production rate and may preclude accurate analyses (Wyatt *et al.* 1992).

After bagging buds or flowers, nectar must be extracted and measured at time intervals appropriate to the precise research question. For example, if the daily nectar secretion is the desired measurement, then open flowers should be bagged the afternoon before anthesis or at dawn immediately after draining all nectar in the corolla, and then the nectar produced subsequently should be removed late in the day when nectar production has stopped or several times in a 24 hour period (Boose 1997, McDade & Weeks 2004b, Pleasants 1983, Schemske 1980, Stiles & Freeman 1993, Wolff 2006, Zimmerman 1988). To determine the hourly production rate of a single flower, the nectar must be drained, the flower bagged, and then the nectar measured exactly one hour later. Then the flower must be rebagged and the process repeated, sampling the nectar and rebagging the flower every hour. The seasonal trend in nectar production can be derived by calculating a cumulative nectar volume produced by the population, and by resampling multiple times throughout the season (McDade & Weeks 2004a, Pleasants 1983).

Depending on the flower morphology, nectar may have to be sampled destructively, meaning the flower itself must be removed from the plant, dissected, and the nectar extracted (McDade & Weeks 2004a, Pleasants 1983, Stiles 1975). This is often the case for flowers with long, curved corollas. Wherever possible, nectar should be removed nondestructively as long as it is clear that the process of extraction does not damage the nectaries or otherwise impair nectar production. The obvious advantage of this method is the ability to resample the same flower to yield a calculation of nectar production rate for a single flower (Pleasants 1983).

Researchers extract nectar by probing the bottom of the corolla with a microcapillary tube or microsyringe of an appropriate size for the flower and the quantity of nectar (frequently ranging from 5-50 μl). To calculate the volume of nectar removed, the distance that the nectar travels up the capillary tube must be measured (ml) and then converted to a volume (μl) (Boose 1997, Fenster *et al.* 2006, McDade & Weeks 2004a, Schemske 1980, Wyatt *et al.* 1992). Nectar production rate can then be calculated as the volume of nectar divided by the time elapsed since the previous collection period (Boose 1997, Wolf *et al.* 1976). Studies of nectar volume and production rate should be undertaken in the field as often as possible, as Boose (1997) observed that nectar production is greatly enhanced under greenhouse conditions. If the study addresses a question of genetics, it is even more important to maintain field conditions as the greenhouse amplifies the heritability of nectar traits by reducing environmental variation (Boose 1997).

If the objective of the study is to determine how much nectar is actually available to hummingbirds in the field, rather than how much nectar a particular plant is capable of producing, researchers should collect data on unbagged flowers (Feinsinger 1978, Hainsworth & Wolf 1972, McDade & Weeks 2004b, Schemske 1980, Torres & Galetto 1998, Wolff 2006, Zimmerman 1988). Exactly the same nectar extraction techniques can be applied to plants that have been exposed naturally to pollinators and nectar thieves (i.e. flowers that are not bagged). Both pieces of the pollination puzzle are relevant to the goal of understanding the impacts of climate change on hummingbirds.

The next important step in describing nectar characteristics is to measure the concentration of sugars. Most studies report using temperature controlled handheld refractometers calibrated for sucrose equivalents (Fenster *et al.* 2006, McDade & Weeks 2004a). The concentration is most commonly reported as a percent in weight of solute per total weight of solution (mg/mg) but can also be recorded as a weight per volume (mg/μl), which is useful if the goal is to determine the energy value of the nectar (McDade & Weeks 2004a, Pleasants 1983, Wolff 2006, Wyatt *et al.* 1992). For a detailed explanation of the benefits and pitfalls of each measurement technique and converting between them, see Bolten *et al.* (1979). Pleasants (1983) points out the importance of making all nectar measurements at various times of day and season, and under various environmental conditions.

Experiments: Temperature Effects on Nectar Secretion

To isolate the effects of temperature on nectar, experiments are conducted in climate controlled chambers (Jakobsen & Kristjansson 1994, Petanidou & Smets 1996). Cuttings of individual plants collected from the field are potted and after a period of adjustment in a greenhouse moved into the chambers. Each chamber mimics a different climatic scenario using heat lamps to regulate the temperature. Treatments should vary both daytime and nighttime temperatures as both are affected by climate change (Jakobsen & Kristjansson 1994). The control group is kept under the ambient temperature. All other factors (light, water, soil moisture, nutrients etc) are kept as constant as possible across treatment groups. Nectar is collected and measured (volume, production rate, and concentration) and the results compared among treatments to determine effects. It is important to conduct this study in various seasons as the effects of temperature on plant physiology may vary based on when the plant is exposed to the different temperature regimes. Pollinators are kept out of the chambers to ensure the accuracy of the measurements.

Experiments: Watering Effects on Nectar Production

To ascertain how a change in precipitation affects the nectar production of hummingbird pollinated plants in Monteverde, different strategies can be employed. One option is to set up a study plot in the field where nectar measurements can be taken at regular intervals for an established period of time on a variety of species. Then researchers water the soil with the equivalent of a certain quantity of rain. For example Wyatt *et al.* (1992) measured the nectar production of flowering plants in a 25 m^2 plot. Later, they dumped 950 liters of water on the plot and reported this to be the equivalent of 10 cm of rain. They allowed three days to elapse and measured nectar production following the same methods as prior to the watering. They compared the nectar production before and after watering.

An alternative to this “before and after” approach is to use multiple small plots in close proximity to one another hosting a similar assemblage of plant species. Half of the plots receive supplemental watering treatments while the others do not. The amount of water provided to the increase treatment should be calculated to mimic levels of precipitation experienced before the recent drying trend. Then the nectar production values for each treatment should be compared.

Watering experiments can also be conducted in the greenhouse, particularly if other conditions are to be controlled. Cuttings taken from field specimen are grown in the greenhouse. Nectar is sampled before starting the experiments to gather baseline data and to determine whether certain individuals are predisposed to producing nectar quantities or qualities that deviate significantly from the norm. For the experiments it is important to choose either individuals with similar patterns of nectar production or individuals representing a wide range of variability. Treatments are set up based on the quantity of water received, with the control group receiving approximately the amount of water equivalent to the average rainfall. Other groups receive slightly more or less water as predicted by different climatic models. Then nectar is sampled from all of the different treatment groups to obtain data on volume, production rate, and concentration. The positions within the greenhouse are randomized repeatedly throughout the study to control for effects of spatial location (Boose 1997). Data are compared across treatments.

Experiments: Light Effects on Nectar Production

As cloud cover is expected to increase in Monteverde, it is essential to test for the effects of reduced light availability. One strategy is to follow the basic outline for the greenhouse watering experiment described above. Instead of varying treatments based on the quantity of precipitation, plants are grouped according to the level of light to which they are exposed. The control groups receive the ambient light of the greenhouse, while those under low light conditions are grown under a shade tent (Boose 1997). All other factors are controlled. This same experiment can be conducted in an outdoor garden if a greenhouse is deemed too unnatural.

If field studies are desirable, it is important to take advantage of the climatic conditions naturally encountered. During routine nectar sampling in the study areas, researchers make notes of the weather. Later the data is sorted and compared on the basis of cloudy days versus sunny days to determine the effects of cloud cover (Pleasants 1983). For a more complex biological picture a factorial design can be implemented using treatments of both water and light in the same experiment (Boose 1997).

Data Presentation

The data presentation in several papers provides useful templates that can guide data collection efforts. It is helpful to list the plant species observed in study areas and create a table providing essential information such as a description of their morphological characteristics and which species of hummingbirds visit them as per Stiles (1985). Feinsinger (1976) created graphs of flower numbers and diversity of all hummingbird visited plants in the study plots over time. Feinsinger also graphed hummingbird diversity over time. All of these graphs are useful in portraying the ecological picture. Pleasants (1983) presents a table of nectar production during the early and late part of the flowering season. A similar graph for the species in Monteverde will clarify seasonal trends in nectar production. His graph of sugar concentration with time of day compares sunny days to cloudy days. While hourly sugar concentration may not be of interest to this study, the effect of cloud cover certainly is. Therefore it may be a useful idea to graph sunny and cloudy day trends separately in the graphs of nectar volume and concentration to see the effects more clearly. For presenting data on temperature experiments, we can follow the example of Petanidou and Smets (1996) and create a data table with the mean nectar volume and concentration per flower at various temperatures.

Data to Replicate

Feinsinger directed several projects investigating the hummingbirds and plants of Monteverde. In some of his publications, the data are presented in a way that could be easily replicated. Thus his original data provide an excellent baseline for comparative studies over the time period in which the climate has changed significantly. For example, his 1976 publication presents a data table on the flowering characteristics of sixteen plant species used by hummingbirds in Monteverde. It would be relatively simple to collect data on the same characteristics for the same group of plants and compare the two data sets. Likewise, the graphs of flower numbers, plant diversity, and hummingbird diversity over time described above are important to replicate for understanding what changes have occurred. In the same paper he published graphs of the flowering phenologies of the three most important hummingbird pollinated plants in the region. After determining if these species are still essential to the hummingbirds of Monteverde, we can monitor and graph their phenologies to determine if they have changed. This is an important piece of the climate change puzzle. If it is clear that these are no longer the three most important plants, we can identify which have replaced them in significance and graph their phenologies. Then we can identify if these new species flower at the time of year when the original plants flowered. This will help us to determine if what makes a species important to hummingbirds in Monteverde is the flower itself or the timing of flower and nectar production. Additional phenology data is presented by Feinsinger (1978). This paper provides a temporal depiction of the different flowering peaks for ten species in Monteverde (where a peak month is defined as having a flower count equal to at least 25% of the maximum flowers for the season). Monitoring the phenology and flowering peaks of these species will again help us gain insights into the changes that have taken place in recent decades.

Additionally, Feinsinger (1978) presents graphs of the nectar production rates of five different species. When conducting nectar measurements, it will be useful to include these species as they have the distinct advantage of allowing us to observe changes. Likewise, Stiles and Freeman (1993) present nectar values for twenty-two species of hummingbird pollinated plants in Monteverde. Collecting data on these species, or any subset of them, will reveal if and how nectar yields in the region have changed.

Of the forty-six hummingbird pollinated plant species in Monteverde listed in Appendix A, thirty three have published data that will serve as a basis for comparison. Five of the species only have published data on phenology, eighteen have data values only for nectar characters, and ten have both phenology and nectar data.

In terms of hummingbird data for the Monteverde region, the best bases for comparison are the records of Michael and Patricia Fogden spanning the last three decades. In addition, the personal accounts of local forest guides who have worked in the field consistently for the last twenty years may reveal interesting insights into how populations have changed.

Initiating this program of experimentation and monitoring will allow conservationists to identify the changes that have already occurred, elucidate current trends, and provide a glimpse into the ecological future of Monteverde. The information gathered will help prepare ecologists and inform more enlightened decision-making as Monteverde plans its conservation strategy. The insights that these studies yield will help conserve not only the hummingbirds and plants of the region, but will bolster efforts to maintain the broader ecological integrity of the Neotropics in the face of a changing world.

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Appendix A:

Previously Studied Hummingbird Pollinated Plants of Monteverde

Family	Genus	Species	Growth Form	Reference
Acanthaceae	Dicliptera	trifurca	Herb	Feinsinger *et al.* 1987
Acanthaceae	Dicliptera	iopus **	Shrub	Stiles & Freeman 1993
Acanthaceae	Hansteinia	blepharorachis *, **	Shrub	Feinsinger *et al.* 1986 & 1987, Stiles & Freeman 1993
Acanthaceae	Justicia	aurea *	Shrub	Feinsinger 1978, Feinsinger *et al.* 1987
Acanthaceae	Justicia	macrantha *, **		Feinsinger 1978, Stiles & Freeman 1993
Acanthaceae	Poikilacanthus	macranthus	Shrub	Feinsinger *et al.* 1987
Acanthaceae	Razisea	spicata *, **	Shrub	Feinsinger *et al.* 1986 & 1987, Stiles & Freeman 1993
Amaryllidaceae	Bomarea	costaricensis **	Herb	Stiles & Freeman 1993
Apocynaceae	Mandevilla	veraguasensis *	Vine	Feinsinger 1976 &1978
Bromeliaceae	Pitcairnia	brittoniana **	Epiphyte	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Ericaceae	Cavendishia	capitulata **	Shrub	Stiles & Freeman 1993
Ericaceae	Cavendishia	crassifolia **		Stiles & Freeman 1993
Ericaceae	Psammisia	ramiflora **	Epiphytic shrub	Stiles & Freeman 1993
Ericaceae	Satyria	warscewiczii **	Shrub	Stiles & Freeman 1993
Fabaceae	Inga	brenesii *, **	Tree	Feinsinger 1976 &1978
Gesneriaceae	Alloplectus	tetragonus **	Shrub	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Gesneriaceae	Besleria	formosa **	Shrub	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Gesneriaceae	Besleria	triflora *, **	Shrub	Feinsinger *et al.* 1986 & 1987
Gesneriaceae	Capanaea	grandiflora	Climber	Feinsinger *et al.* 1987
Gesneriaceae	Columnea	lepidocaula **		Stiles & Freeman 1993
Gesneriaceae	Columnea	magnifica	Epiphyte	Feinsinger *et al.* 1987
Gesneriaceae	Columnea	microcalyx **	Epiphyte	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Gesneriaceae	Drymonia	conchocalyx **	Climber	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Gesneriaceae	Drymonia	multiflora **		Stiles & Freeman 1993
Gesneriaceae	Drymonia	rubra *, **	Climber	Feinsinger *et al.* 1986 & 1987
Gesneriaceae	Kohleria	spicata *	Herb	Feinsinger 1976 &1978
Heliconiaceae	Heliconia	monteverdensis **	Herb	Stiles & Freeman 1993
Heliconiaceae	Heliconia	tortusa **	Herb	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Lobeliacaea	Burmeistera	cyclostigmata	Epiphyte	Feinsinger *et al.* 1987
Lobeliacaea	Burmeistera	tenuifolia	Epiphyte	Feinsinger *et al.* 1987
Lobeliacaea	Centropogon	solanifolius **	Herb	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Lobeliaceae	Lobelia	laxiflora *, **	Herb	Feinsinger 1976 & 1978, Stiles & Freeman 1993
Loranthaceae	Psittacanthus	lateriflorus *	Epiphyte	Feinsinger 1976 &1978, Nadkarni & Matelson 1989
Lythraceae	Cuphea	sp *, **	Small shrub	Feinsinger 1976 &1978
Malvaceae	Malvaviscus	palmanum **	Shrub	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Malvaceae	Malvaviscus	arboreus *, **	Shrub	Feinsinger 1976 &1978
Marcgraviaceae			Epiphyte	Nadkarni & Matelson 1989
Rubiaceae	Cephaelis	elata	Shrub	Feinsinger *et al.* 1987
Rubiaceae	Gonzalagunia	rosea **	Shrub	Feinsinger *et al.* 1987, Stiles & Freeman 1993
Rubiaceae	Hamelia	patens *, **	Shrub	Feinsinger 1976 & 1978
Rubiacea	Manettia	flexilis *	Vine	Feinsinger 1976, 1978
Rubiaceae	Palicourea	lasiorrachis	Shrub	Feinsinger *et al.* 1987
Rubiaceae	Palicourea	macrocalyx	Shrub	Feinsinger *et al.* 1987
Rubiaceae	Ravnia	triflora	Epiphyte	Feinsinger *et al.* 1987
Symplocaceae	Symplocos	sp	Subcanopy tree	Feinsinger *et al.* 1987
Zingiberaceae	Costus	barbatus	Herb	Feinsinger *et al.* 1987

***** Phenology data is available for this species in a published paper cited here.
****** Nectar data is available for this species in a published paper cited here.

Appendix B:

Summary of Suggested Observation Techniques & Experiments

Hummingbird Populations

1. Set up transects or study areas throughout the Monteverde region, covering all possible Life Zones.
2. Dedicate several days each month to conducting censuses along each transect. Walk all of the transects for a specified period of time, make visual and audio observations of hummingbirds and record all individuals encountered.
3. Spend several days each month observing hummingbirds at the already established feeders in the region and recording all encounters.

Plant Phenology

1. Use the same study areas as for the hummingbird censuses.
2. Visit the study areas and count the abundance of all flowering species monthly.
3. Choose a random sample of individuals of each species, and count the number of open flowers.
4. For each species try to determine whether flowering is increasing or decreasing based on the relative number of buds, flowers, and fruits.
5. Rank the abundances of all hummingbird pollinated plants in flower.

Hummingbird Visitation
Method 1

1. Use the same study areas as for the hummingbird and plant censuses.
2. Spend a designated period of time at each study site observing and recording all hummingbird visits to plants within the study area. Repeat this several times each month.
3. Record which species of hummingbirds visit which plants, and note hummingbird behavior.
4. Photograph hummingbird – plant interactions.
5. Collect plant specimens for identification as necessary.

Hummingbird Visitation
Method 2

1. Spend one full day each month at each study area recording all audible and visible hummingbird activity,
2. Count the number of flowers and inflorescences visited.
3. Rank the plants based on visitation frequency.
4. Photograph hummingbird – plant interactions.
5. Collect plant specimens for identification as necessary.

Hummingbird Visitation
Method 3

1. Each month select the three most abundant flowering hummingbird pollinated plant species at each site.
2. Choose three representative individuals and focus observations on them.
3. During two or three mornings of the month spend an hour recording all visits to these individuals.
6. Photograph hummingbird – plant interactions.
7. Collect plant specimens for identification as necessary.

Measuring Nectar
Nectar Volume & Production Rate: Pollinators Excluded

1. Choose the hummingbird pollinated plant species to include.
2. Select and mark individual plants and flowers to sample in pollinator exclusion studies.
3. Bag selected buds the day before anthesis, or if using open flowers, drain all nectar and bag the flowers. Record the exact time.
4. Collect nectar from bagged flowers after designated time interval has elapsed. If the same flowers are to be resampled later, re-bag the flowers immediately and record the time.
5. Calculate nectar volume and nectar production rate.
6. Measure nectar sugar concentrations from all nectar samples.

Measuring Nectar
Nectar Standing Crop

1. Select and mark individual plants and flowers to sample that will be exposed to pollinators.
2. Collect nectar from marked flowers at designated time intervals.
3. Calculate available nectar volumes.
4. Measure nectar sugar concentrations from all nectar samples.

Temperature Experiments
Greenhouse

1. Take cuttings of plants growing in the field, and transplant them to a greenhouse for growth and adjustment.
2. Collect and measure nectar from all plants.
3. After designated period move healthy plants to climate chambers from which nectarivarous species are excluded.
4. Assign each plant to its treatment group, varying the day and night temperatures.
5. Collect nectar at predetermined intervals.
6. Measure nectar volume, production rate, and sugar concentration.
7. Compare data across treatment groups.

Watering Experiments
Field: Before and After

1. Set up several study plots in field.
2. Measure nectar volume, production, standing crop, and concentration of the plants in each plot at scheduled intervals for several days.
3. Water plots with equivalent of a specified amount of rainfall.
4. After a few days have passed, measure nectar volume, production, standing crop, and concentration at same scheduled intervals for several days.
5. Compare the data from before watering and after.

Watering Experiments
Field: Side by Side

1. Set up several study plots in field with similar plant assemblages.
2. Water half of the plots with the equivalent of a specified amount of rainfall.

3. Measure nectar volume, production, standing crop, and concentration of the plants in each plot at scheduled intervals for several days.
4. Compare the data for the plots receiving water to the plots not being watered.

Watering Experiments
Greenhouse

1. Take cuttings from selected plants in the field, and transplant them into a greenhouse.
2. Collect and measure nectar from all plants after a period of adjustment.
3. Assign individuals to different treatment groups.
4. Water individuals according to their treatments.
5. Sample and measure nectar production, volume, and concentration from all plants at specified time intervals.
6. Compare data across treatment groups.

Light Experiment
Greenhouse or Outdoor Garden

1. Take cuttings from selected plants in the field, and transplant them into a greenhouse or an outdoor garden.
2. Collect and measure nectar from all plants after a period of adjustment.
3. Assign individuals to different treatment groups.
4. Expose individuals to various light treatments. Reduced light exposure can be accomplished by using shade tents.
5. Sample and measure nectar production, volume, and concentration from all plants at specified time intervals.
6. Compare data across treatment groups.

Light Experiment
Field

1. Use data collected in routine nectar measurement studies in the field.
2. Sort data on basis of field notes regarding weather patterns: separate sunny day data from cloudy day data.
3. Compare the nectar values of all species for sunny days versus cloudy days.

Climate Change and the Hummingbirds of Monteverde

Chapter 3
Hummingbird Feeders

The question of whether or not to feed hummingbirds is largely subjective. There is a noticeable paucity of published literature addressing this subject, and virtually no experiments have been conducted. As such, researchers and citizens are left to weighing the pros and cons and using their own judgment. While the large scale feeding of wildlife is generally viewed negatively for a variety of reasons, the majority of ornithologists and bird enthusiasts seem to believe that a few well placed and well cared for hummingbird feeders provide a supplement to the resource base and allow close viewing of hummingbirds for research purposes.

The main arguments against feeding hummingbirds stem from a series of concerns. Some argue that feeding may negatively affect species behavior. Some have suggested that hummingbirds may not migrate at the appropriate time because feeders provide an incentive to stay in area after the season has passed. Some argue that hummingbird feeders will attract hummingbirds as well as many opportunistic predators. Others argue that feeding hummingbirds may promote the spread of disease as birds and other organisms attracted by the nectar congregate. It has been proposed that a fungus, harmful to hummingbirds, grows in feeders, particularly those that are not regularly maintained. Still others feel that feeding hummingbirds or any other wild animal takes away from their nature and habituates them to humans and artificial conditions. Some are concerned with the ecology of a system, suggesting that if hummingbirds drink nectar from feeders they will visit fewer flowers and thus offer reduced pollination services. This could result in an altered plant species composition in an area. All of these potential risks must be weighed against the benefits provided by feeding.

In 2003 a three month study was conducted in the Monteverde Cloud Forest Preserve examining the effects of three different hummingbird feeding stations on hummingbird behavior (Moreno 2003). This study compared observations of hummingbird interactions at feeders to observations at flowers far away from feeders. The author noticed that hummingbirds at feeders interact with one another more frequently and behave more aggressively, and that more males use the feeders than females. Thus hummingbird feeders do influence the behavior of these species. In areas with more feeders the effects were more evident. However, in terms of plant visitation and pollinization, the presence of feeders produced no clear effect. Fruits produced by hummingbird pollinated plants were counted close to feeders and far away, and while a difference was observed, the author concedes that the variables were not isolated so it would be impossible to determine the source of this apparent difference.

The many researchers who use hummingbird feeders to attract birds and allow for close up observations feel strongly that the feeders cause little harm. Of course feeding requires a great deal of responsibility, and those who use them insist upon high levels of care. According to many experts, hummingbirds should be fed a solution of one part sugar to four parts boiled water. The solution should be cooled before it is offered in the feeders, and all note that the sugar must be pure white sugar as others types are known to be harmful. They also implore that to prevent any problems with fermentation or fungus the feeders must be cleaned meticulously every five days. In addition if feeders are brought inside or emptied at night to prevent raids by other species, it is essential that they are filled and re-hung by dawn the following morning when hummingbirds are looking for their first meal. Feeder sites should be chosen carefully in areas that host hummingbird pollinated plants, thus providing habitat. It is important not to attempt to force hummingbirds into inhospitable areas where the feeder acts as an oasis in the desert. Rather the feeder is a complement to an existent habitat in which hummingbirds can survive.

In addressing the “cons” listed above researchers have many answers. Researchers insist that large-scale migration patterns have not been negatively impacted by feeders. They maintain that nectar provided by feeders is an ancillary source of energy, but that hummingbirds still migrate when their flowers have stopped blooming and the insects they consume for protein are no longer abundant. They say that responsible feeder management mitigates disease risks. They also argue that species congregate at any food source, whether artificial or natural, so feeders are no more dangerous than a group of flowering or fruiting plants. Ecologists, including Fogden and Fogden (2005), also report that hummingbirds continue to visit plants even when they have access to feeders, and as such continue to pollinate the native species in the area. In fact many argue that the additional energy provided by the feeders gives hummingbirds a boost that allows more activity, increased fecundity, and ultimately a slightly larger population size in a given area. This then results in more visits to flowering plants and greater pollination.

In addition, feeders allow people the opportunity to watch hummingbirds for hours at a time, helping to collect valuable ecological data. In North America the FeederWatch program has provided scientists with a wealth of information on the distributions and abundances of avian species. This has helped to answer many important questions and aid in conservation efforts. Likewise the feeders engage non-scientists, helping people to cultivate a relationship with nature and an interest in wildlife conservation.

It is the recommendation of this study that hummingbird feeders be used responsibly and with caution. They should be used in a limited capacity and only in areas where natural hummingbird pollinated plants are abundant, and feeders should not be densely congregated. Likewise they must be well kept and cleaned and placed in a way that minimizes risks of predatory attacks. They should not be installed haphazardly, but carefully with the goal of bolstering a particular data collection effort. The potential negative effects should always be kept in mind and monitored. If they seem to be causing problems the plan should be reevaluated and the appropriate course of action determined.

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