

THE CO-EVOLUTION OF HUMMINGBIRD BILL
MORPHOLOGY AND FLORAL STRUCTURES WITH
REGARD TO BOTH NATIVE AND NON-NATIVE FLOWER
SPECIES.

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ABSTRACT

Cusuco National Park in NW Honduras is home to half the country's total number of hummingbird species. A large body of research has been conducted upon the co-evolution of hummingbird bill morphology with the floral structures that they feed upon, yet there is a void of information on how the birds forage on non-native flower species in disturbed areas with regards to their bill morphology. The effect of disturbance upon hummingbirds, from low level urbanization found in the park buffer zone, was also investigated. Bird biometric data from mist netting and spot observations were combined with flower measurements to identify a relationship between the bill and the morphology of the flowers, and the utilisation of both native and non-native species by the bird. A suite of correlations and regression identify the importance of bill length and curvature in flower choice and the Shannon-Weaver Diversity Index illustrates how hummingbirds can adapt to and thrive in disturbed areas. A key finding was the sensitivity of the endemic Green throated mountain gem to deforestation, a result that highlights the requirement for a conservation strategy.

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1.0 INTRODUCTION

Introduction

Hummingbirds belong to the family Trochilidae (Howell and Webb, 1995) and have undergone an extraordinary evolutionary radiation with more than 330 species allocated into over 100 genera (Bleiweiss, 1997). Within the Trochilidae exist two monophyletic sub-families; the Hermits (Phaethomithinae) and the Non-hermits (Trochilinae) (Bleiweiss, 1997). Although hummingbirds are only found in the New World (Camfield, 2004) some species are more adept at colonisation than others and in general forest dwelling species are more specialised and have been attributed poor colonisation abilities particularly over water. These different species of hummingbirds can be characterised by their habitat preferences, for example the Hermits prefer the interior of lowland forest whereas the non-Hermits reside principally in the edge and the canopy (Bleiweiss, 1998).

Hummingbirds feed mostly on nectar and this makes up 90% of their diet with insects making up the remaining 10% (Camfield, 1994) and use their slender, proportionately lengthy bills in combination with their tubular, bifurcated tongues to probe flowers and use capillary action to draw the nectar along their tongue (Camfield, 1994, Howell and Webb, 1995). As hummingbirds have a very high basal metabolic rate they can consume their body mass in nectar in less than 24 hours and will utilise the sap from trees when nectar sources are scarce. Darwin (1876, as cited in Temeles, 1996) declared, “beaks of hummingbirds are specifically adapted to the various kinds of flowers they visit” and, in turn, there is a high diversity of hummingbird pollinated plants (Bleiweiss, 1998). There has been much research conducted upon the possible co-evolution of hummingbird bills with the flowers they prefer to utilise.

The majority of hummingbird species are polygynous and are sexually dimorphic with some male hummingbirds having elaborate ornamentation such as elongated tail feathers and iridescent crests. Male hermits display together in large groups called leks

while trochilines are mainly territorial with dramatic aerial courtship displays (Camfield, 2004).

Different species of hummingbird that are coexisting in the same habitat will specialise on certain flowers or subdivide the habitat. They will either defend their nectar resources on a territory or move between patches of flower-rich areas in a behaviour called traplining (Camfield, 1994).

Hummingbirds as pollinators

Birds have been shown to be effective pollinators, for example, Anderson (2003) demonstrated experimentally that the percentage fruit set was significantly higher in flowers exposed to birds than those from which birds were excluded. From the same study, endemic birds were shown to be most likely to meet the requirements for successful pollination.

Hummingbirds are considered to be effective pollinators as they do not collect pollen for themselves, but only groom it off their bills. Theory predicts that pollen from hummingbirds should therefore be presented less restrictively and in fewer, larger doses (Castallanos et al, 2003). However, hummingbirds often forage from a variety of plant species resulting in pollen being transferred among heterospecific flowers (Murcia and Feinsinger), the 'Sexual Architecture Hypothesis' predicts that the severity of interspecific pollen transfer should reflect the similarity in the architecture of the sexual structures (Murcia and Feinsinger, 1996). However, the theory has not been upheld experimentally as every species of intervening flower, regardless of sexual architecture, strongly reduced pollen transfer (Murcia and Feinsinger, 1996).

Pollination in montane habitats is conducted mainly by hummingbirds as the low temperatures, in contrast to lowland habitats, may have resulted in the displacement of bees (Bawa, 1990). Whereas birds can pollinate bee-syndrome flowers almost as well as bees do, bees pollinate bird-syndrome flowers very poorly as they are impeded by narrow

corollas (Castallanos et al, 2003). As birds are more efficient pollinators it may be in the plants interest to encourage them as pollinators and exclude the pollen feeding bees (Castallanos et al, 2003).

Plant-hummingbird associations

To encourage bird pollination, some species of flowers have evolved certain features that can be classed as an ornithophilous syndrome (Temeles and Rankin, 2000) or as a ‘hummingbird pollination syndrome’ These flowers tend to be characterised by red coloration, an absence of odour, a pendant, tubular shape and a dilute nectar source rich in sucrose (Tadey and Aizen, 2001).

Flowers can be arranged to allow easy access for flying pollinators. Plants from the genus *Erythrina* are well known for producing nectar rich, bird pollinated flowers and has evolved inflorescences that are held upright and arranged radially along the axis. This, combined with the narrow, standard petal is coduplicately folded into a pseudotube to target hummingbirds. The same plant targeting passerine species have a different structure (Ragusa-Netto, 2002)

Plants with flowers that are oriented downward are also common among hummingbird pollinated plants, for example, *Tristerix corymbosus*, a mistletoe pollinated by hummingbirds in the southern Andes, as they allow more contact with the head of the bird and the pollen producing anthers or the pollen receiving style due to the required upward hovering (Taday and Aizen, 2001). The presence of ‘lips’ on the flower of the perennial herb, *M. didyma*, enhanced pollen removal by slowing a hummingbird’s bill insertion, increasing the handling time so that the bird was positioned for longer under the anthers (Temeles and Rankin, 2000). Lab experiments also show that flowers having recurved nectar spurs deposit significantly more pollen grain on the hummingbird than perpendicular spurs. This is possibly conditional upon the environment where good conditions would allow for larger flowers and therefore longer spurs (Travers et al, 2003)

Lab experiments on female ruby throated hummingbirds showed that the bird's handling times increased with decreasing corolla widths and so plants may have evolved narrower corolla widths so as to maximise the time for pollen deposition (Temeles, 1996).

Hummingbird bill morphology

Smith et al (1995) illustrated how strong evolutionary pressures of flower shape are upon bill morphology: I'iwi birds found in the Hawaiian Islands were inhibited from feeding upon Ohias by the behaviourally dominant Hawaiian 'o'o. When the 'o'o became extinct in 1900, the I'iwi shifted its foraging emphasis resulting in new selective pressures on bill morph as they switched from utilising long, decurved flowers of the Lobeliolidae to the open, non-tubular Ohia. In this short period of evolutionary time, the upper mandible has become shorter and the bill is less decurved.

The morphology of the hummingbirds' bill can relate directly to its foraging efficiency at flowers of different shapes. Temeles (1996) found that longer-billed birds had greater maximum extraction depths and shorter handling times than shorter billed birds at all corolla diameters greater than the width of the bill. In contrast, it was found that shorter billed birds made fewer errors inserting their bills into narrow flowers. Temeles therefore argued that differences in bill lengths can be related to trade-offs in foraging ability, whereby long billed birds are able to feed more quickly at flowers with long corollas but may make more insertion errors than short billed hummingbirds which may be energetically expensive (Smith et al, 1996).

Temeles et al (2002) furthered the research on the effect of corolla width on hummingbird foraging strategy by demonstrating that Monteverde hummingbirds actively choose flowers that relate to their bill morph. Both short and long billed hummingbirds would include long, wide flower species in their diets, but that short billed hummingbirds would not include long, narrow species because nectar in these species may be beyond the reach of their bills.

It is also important to consider the morphological correlates of foraging for arthropods as well as nectar. Hermits have long, curved bills and are nearly exclusively understorey hover gleaners that take mostly spiders. Non-Hermits with shorter, straighter bills employ a greater range of foraging tactics, taking a wider variety of prey. Among La Selva hummingbirds, bill curvature is strongly correlated with the proportion of gleaning versus hawking and with the proportion of prey taken from the substrate as opposed to volant prey. Also, breeding females spend more time foraging for arthropod prey than do males in the same times and places (Stiles, 1995).

The effect of sexual dimorphism on foraging choice

Sexual dimorphism is prevalent among hummingbirds and female bills are proportionately longer than male bills as sexual dichromatism increases, whereas male bills are proportionately longer in both lekkeepers and clustered breeders (Bleiweiss, 1999).

The morphology of the bill has been experimentally shown to have a direct effect on foraging efficiency. Bills of the female *S.rufus* are approximately 10.5% longer than the bills of the males and this difference has been associated with differences in foraging ability. Female *S.rufus* have the potential to feed from longer flowers and do so more efficiently than males (Temeles and Roberts, 1992).

Female purple-throated carib have a 30% longer bill than males that is 100% more curved. Each sex prefers and feeds most efficiently from the *Heliconia* species that most matches its bill. The male prefers a red bracted morph, *H.caribaea*, but where this plant is absent *H.bihai* has evolved a red-green bracted morph that corresponds to both male and female bills. Males are most associated with these whereas females will use both (Temeles and Kress, 2003). The energetic rewards of the flower morphs correspond to the body sizes of the male and female hummingbirds. The males are bigger and so *H.caribaea* offers slightly more nectar and has more bracts than *H.bihai* (Altshuler and Clark, 2003).

Experiments on migrant rufous hummingbirds have shown that adult females surpassed immature males by some measure of territorial ability although mature males were always more dominant. This may be due to sexual differences in their ability to exploit resources as different age-sex classes use different resources as they differ in their net energy intake, generally as a result of differences in morphology and/or experience. Males with shorter bills have a lower efficiency of nectar intake whereas the longer billed females are more efficient as they can feed more quickly and so can increase the range of their habitat. Females also gained mass at the same rate as other age-sex classes, despite them utilising sparser habitats and non-territorial females lost mass less quickly than non-territorial males (Carpenter et al, 1993). Carpenter (1993) conducted further research that showed that males were more likely to expand their territory boundaries upon flower reduction than females thus maintaining a constant number of flowers defended.

In conclusion, the shorter bills and brighter plumage of males are associated with their dominance over females, who are therefore forced to feed on more dispersed nectar sources (Paton and Colins, 1989, as cited in Bleiweiss, 1999). A possible mechanism for the evolution of longer, more curved bills by females may be that have evolved bills that are capable of exploiting a wider range of resources more efficiently due to their forced exploitation of poorer habitats by males (Bleiweiss, 1999).

The effect of urbanisation on bird populations

Urbanisation can be described as homogenising the landscape and as it often produces a local gradient of disturbance one can often observe a gradient of this homogenisation. However many suburban and urban fringe habitats are occupied by native species that become regionally widespread. These species generally consist of early successional plants and “edge” animal species such as mesopredator mammals and ground foraging, omnivorous and frugivorous birds that can utilise gardens, forest fragments and many of the other habitats that are available in the suburbs. The importation of species that are adapted to the urban environment, combined with many food resources imported for human use, often produces local species diversity and

abundance that is often equal to or greater than the surrounding landscape (McKinney, 2006).

Species with small geographic ranges and species of terrestrial insectivores have particularly low tolerance to fragmentation (Renjifo, 2001). However, Renjifo (2001) demonstrated that forest fragments embedded in pastures or exotic tree plantations can be beneficial for hummingbird species. Renjifo (2001) also described studies in shade and sun coffee plantations that have found an increase in diversity and abundance of birds as the complexity and floristic diversity of the arboreal strata increases. Structurally complex anthropogenic matrices, such as shade coffee, have potential as management tools for bird conservation by supplementing habitat protection and restoration in fragmented forests

In contrast, habitat disturbance has been shown to have negative effects on forest bird species. Ming Lee et al (2005) examined the effects of local-scale habitat disturbance on mixed species flocks along an escalating gradient of anthropogenic modification in a sub-montane tropical rainforest in Peninsular Malaysia that is presently experiencing low intensity development. Mixed species flocks in the forest interior and forest edge habitats had a significantly higher number of species than those observed in the urban habitat. It was therefore concluded that sub-montane mixed flock species are affected by even small scale development and can be used as effective ecological indicators.

Watson et al (2004) examined how forest bird communities and different foraging guilds were affected by patch habitat quality and landscape context in the threatened littoral forests of SE Madagascar. The littoral forest core had significantly more bird species than forest edge and matrix habitats. 68% of forest dependent species were found to be edge sensitive and edge sites had fewer species and a higher representation of common species than forest interior sites. The majority of canopy insectivores including all six endemic species were edge sensitive and so deforestation in Madagascar is degrading bird communities with the expectation of further decline of many bird species.

Endemic species are important contributors to biological diversity because their restricted distributions make them globally rare and particularly vulnerable to population declines or extinctions. Species with small ranges are also less abundant at a local scale than large range species and so populations may be more sensitive to local factors such as human disturbance, predation and competition (Garcia et al, 1998).

Conservation of hummingbirds

Two species of hummingbird, Brace's emerald and Gould's emerald, are known to be extinct and 29 other species are listed as at least vulnerable by the IUCN. Major threats to hummingbirds are habitat loss, degradation and fragmentation although habitat destruction in the tropics does not threaten hummingbirds to the same extent as other neotropical species. Banana and coffee plantations as well as flowering plants that can exist in some cleared areas can support hummingbirds (Camfield, 2004) and an experiment conducted by Araujo and Sazima (2003) demonstrated how hummingbirds showed no preference between native and non-native flower species and so could support themselves in environments devoid of native flower species.

The National Park

The Cusuco National Park was founded in 1987 in the Merendon mountain range of NW Honduras. The 7 690 Ha core zone consists of a combination of secondary pine forest and mixed broadleaf forest with some dwarf forest at high altitudes. Surrounding this is a 15 750 Ha buffer zone containing semi urban areas and agricultural land. The Park has two main research camps; Base Camp that is found within the Core Zone at 1700m altitude with a forest consisting mainly of pines and large tree ferns; Buenos Aires, a mountain village positioned within the Buffer Zone at 1200m altitude where high concentrations of non-indigenous flower species are grown for ornamental purposes and the surrounding area consists of agricultural land including both sun and shade coffee and banana plantations

Figure 1.1



Figure 1.1 Map showing the position of the Cusuco National Park in the North West corner of Honduras near the Honduran-Guatamalan border.

Figure 1.2

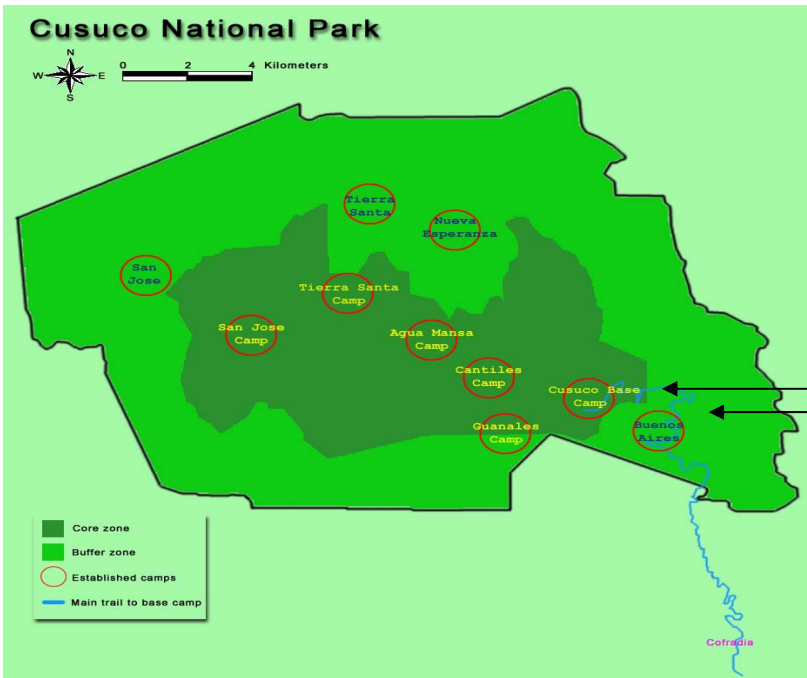


Figure 2.2 showing the core and buffer zones of the Park and the positions of Base Camp and Buenos Aires within these zones.

Cusuco National Park is rich in bird diversity, in particular hummingbird species, as half the total species of Honduras including the Green throated mountain gem hummingbird that is the only endemic species found within the park. However the Park is now under serious threat as the number of park guard patrolling the area has fallen from 12 to 1 since 2005 due to a collapse in funding. Consequently, this is having a major affect on the extent of illegal logging and hunting within the park.

Rationale for research

Cusuco National Park, Honduras, is a novel area for hummingbird research and as it has recently come under a greater degree of threat from deforestation it is vital to understand the affect of this on the hummingbirds in this area. As the park is also home to the endemic Green throated mountain gem it is important to understand the affect of disturbance on this species so a conservation strategy can be instigated if necessary.

The majority of studies have focussed on the co-evolution of the hummingbird bill with the native flower species that they have evolved with and how they actively choose these species during foraging. Little research has been performed on the hummingbirds' relationship with non-native species that have been planted in disturbed areas including if they are actively choosing flowers on the same principle. If bird species are choosing, this may have important consequences for conservation strategies if plants useful for hummingbirds could be planted in disturbed areas.

1.1 Aims of Investigation

The aims of this study are four fold:

1. To investigate correlations between hummingbird bill morphology and floral structures and to find if these correlations are conserved across both native and non-native species.
2. To find if bill morphology affects hummingbird foraging behaviour, i.e. do they specialise or generalise?
3. To compare species composition of hummingbirds in the core zone with the disturbed buffer zone.
4. To identify the effects of disturbance on the endemic Green throated mountain gem.

2.0 METHODS AND MATERIALS

2.1 Mist Netting

Mist netting was undertaken by Mr. Robin Cosgrove, a field ornithologist and licensed bird ringer with more than 30 years ringing experience mainly within forest habitats. Nets of various lengths were used to catch birds and were placed in three main sites that were deemed suitable for bird capture covering different habitat types:

Site 1-Base Camp

7 nets were used (5 x 12m, 1 x 9m, 1 x 18m) to capture birds over a period of 10 days in July, 2005. The area consists of closed canopy, broad leaved forest and is occupied by a static and characteristic hummingbird population. Although previously an area of logging in the 1930's and 40's, in recent years it has remained relatively undisturbed and now serves as a quiet visitors centre for tourists.

Site 2-Las Minas

7 nets were used (4 x 18m, 2 x 12m, 1 x 9m) over a period of 13 days in July and August, 2005. The site consists of semi-open canopy, coniferous forest with a dynamic, slightly distorted bird population as it is a low ridge between two valleys and is used by birds as a corridor for movement.

Together Site 1 and Site 2 will be combined to represent the core zone of the park and then compared to:

Site 3-Buenos Aires

Various nets were used at various sites in and around the semi-urban village of Buenos Aires over a period of 16 days in July and August, 2005. An agricultural area consisting of plantations surround a small village with many non-native flowering species grown in the gardens of the inhabitants. A disturbed hummingbird population is therefore in existence.

2.2 Bird Biometrics

For each hummingbird that was captured in the mist nets the following data was recorded. Due to the subjectivity of these measurements they were all taken by Mr. Robin Cosgrove for consistency.

Wing length

A millimetre ruler was used to measure the wing chord. Data could not be used if the longest primary feather was undergoing moult.

Figure 2.1



Figure 2.1 showing the technique for measuring the wing chord. Photograph is courtesy of Mary-Anne Collis.

Total Length

A millimetre ruler was used to measure the distance from tip of bill to the end of the tail feathers. Data could not be used if the tail is undergoing moult and depends on the degree of flattening of the bird so cannot be used as absolute values (see Figure 2.2).

Figure 2.2



Figure 2.2 showing the measurement of the hummingbirds total body length using a millimetre ruler. Photograph is courtesy of Dr. Robin Brace.

Weight

Weight of bird was taken using a digital scale that was tared to zero when used in combination with a cone to restrict the bird's movements. The data cannot be analysed due to temporal weight changes during the day.

Bill Length

Distance from tip of bill to the start of the feathering near the head, a technique commonly used in Britain, was recorded to the nearest 0.1mm using dial callipers.

Figure 2.3



Figure 2.3 showing the measurement of the bill length from the bill tip to feathering. Photograph is courtesy of Mary-Anne Collis

Bill Curvature

We developed a novel technique where the bill was placed on 2mm graph paper so that the straight part of the bill nearest the head was in line with the first 6mm. The deflection of the tip of the bill from the line was then measured to the nearest 0.5mm.

Figure 2.4



Figure 2.4 showing the top of the bill being lined up with the first 6mm (3 graph squares) and the deflection of the bill tip from this original line. Photograph is courtesy of Mary-Anne Collis.

With the bill length and size of deflection known, simple trigonometry was used to find the angle of deflection by dividing the size of deflection (a) by the bill length and then finding angle A using the Sine rule (see figure 2.7). The larger the angle A , the more curved the hummingbird's bill will be.

Figure 2.5

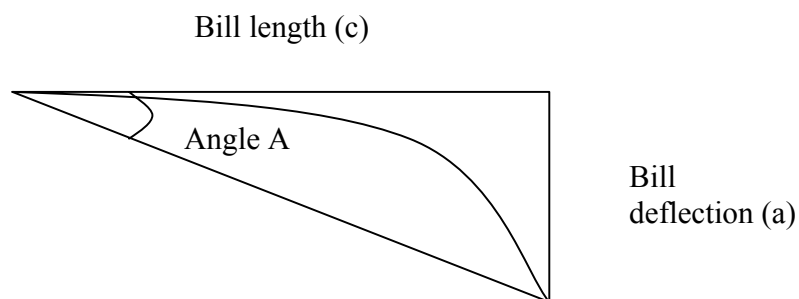


Figure 2.5 showing the principles of trigonometry used to find the angle of the bill deflection (angle A).

Other measurements

All identification was conducted based upon the Howell and Webb text. The aging criterion used was the Standard Aging Code that was set in the UK by the British Trust for Ornithology (BTO) which is also used through out Europe. Aging of hummingbirds can be a complex process due to the absence of well defined breeding seasons. Examining the stage of a hummingbird's moult, as well as considering the level of bleaching the feathers have undergone and the amount of wear and tear they have suffered can all contribute to determining age.

Birds were sexed by polymorphic plumage where possible or by standard techniques concerning the presence of a brood patch. There are errors in these techniques as little is known about hummingbird incubation, i.e. males may incubate or appear to have a brood patch through moulting. Unfortunately many species could not be identified with respect to sex due to these errors and monomorphic plumage.

A small notch was made in the outer tail feather using a pair of small scissors to ensure a previously caught bird was not processed twice (see Figure 2.8). This was a suitable method of identification as data was collected over a short time period and so the permanence of such a marker was not of importance.

Figure 2.6



Figure 2.6 showing the small tail notch cut into the bird's tail feathers to allow identification of a previously processed bird.

2.3 Site Observations

Spot observations were undertaken at twelve sites, six surrounding Base Camp in the core zone and six surrounding Buenos Aires in the buffer zone. Due to the ephemeral nature of flowering plants in the forest, sites for spot observations were chosen randomly in patches of high flower concentrations. Each site was tested for a period of two hours to identify if the area was being utilised by hummingbirds and if the site proved successful then a further ten hours of observations were conducted at Base Camp. Due to the collection of large amounts of repeated data, the length of these observations was reduced

to six hours in total at each of the Buenos Aires sites. Observations took place at different times of day and were prevented by heavy rainfall.

At each site the following data was recorded:

1. Species of bird
2. Sex of bird (where possible)
3. Time of arrival at flower
4. Species of the flower
5. Height of flower in the canopy
6. Weather conditions including temperature, cloud cover, wind speed and precipitation.

Originally the number of flowers visited and the average length of time at each flower was recorded. However, this was deemed unreliable due to the obscurity of flowers on trees, large numbers of hummingbirds etc. and so this information was removed from the dataset.

2.4 Site Descriptions

A comprehensive description of each site was taken. The size of each site was estimated by physically pacing out the edges of the site and then estimating the area within. In some of the larger sites it was impossible to pace all the edges due to the danger of snakes in long grass and so some distances were judged by eye. Due to this problem the larger sites will suffer greater inaccuracies than the smaller ones.

Panoramic site photographs were taken at each site and labelled according to compass direction to illustrate the differences in habitat composition.

Table 2.1 summarises the area of each of the sites used at Base Camp and gives a brief description of the type of habitat that was present. Table 2.2 is the Buenos Aires equivalent.

Table 2.1

Base Camp Site Descriptions			
Site Number	Area (m ²)	Qualitative Description	Flower Species Present
1	144	Large patch of small pink hibiscus next to river edge	Small Pink Hibiscus
2	1700	Overgrown clearing from logging activity	<i>Liana</i> , Red Trumpet
3	1438	Clearing surrounding dwelling. Dwelling contains garden of non-indigenous species.	Banana, <i>Bromeliad</i> , <i>Crocosmia</i>
4	1250	Patch of <i>Crocosmia</i> opposite above dwelling on slightly elevated land next to garden	Banana, <i>Bromeliad</i> , <i>Crocosmia</i>
5	169	Dense forested area surrounding trail	Small Pink Hib, <i>Heliconia</i> , Spike
6	169	Dense forest area surrounding trail.	Small Pink Hib, <i>Heliconia</i> , Spike

Table 2.2

Buenos Aires Site Descriptions			
Site Number	Area (m ²)	Qualitative Description	Flower Species Present
1	9	On side of valley, viewing point looked at top of trees next to tomato plantation and agricultural land	Purple Tree
2	28.8	On side of valley, viewing point looked at top of trees next to tomato plantation and agricultural land	Purple Tree
3	15.84	Small clearing along road adjacent to disused shed	Small Red Hib, Spikey Pink
4	7.2	Flowers surrounding old field station from adjacent garden and road	Big Red Hib, Spikey Trumpet
5	43.2	Flowers along side of road and within garden parameters	Big Red Hib, Nice Pink, Fluffy, Peach (NA)
6	6.48	Flowering plants within garden	Nice Pink, Bromeliad2, Pink Leaved

Preliminary habitat analysis was performed using the Domin Scale (Kent and Coker, 1992) to estimate the percentage cover occupied by the flowering plants that were utilised by the hummingbirds. Figure 2.9 and 2.10 show the Domin values for each of the

flowering plants found at each of the six sites at Base Camp and Buenos Aires respectively.

Figure 2.7

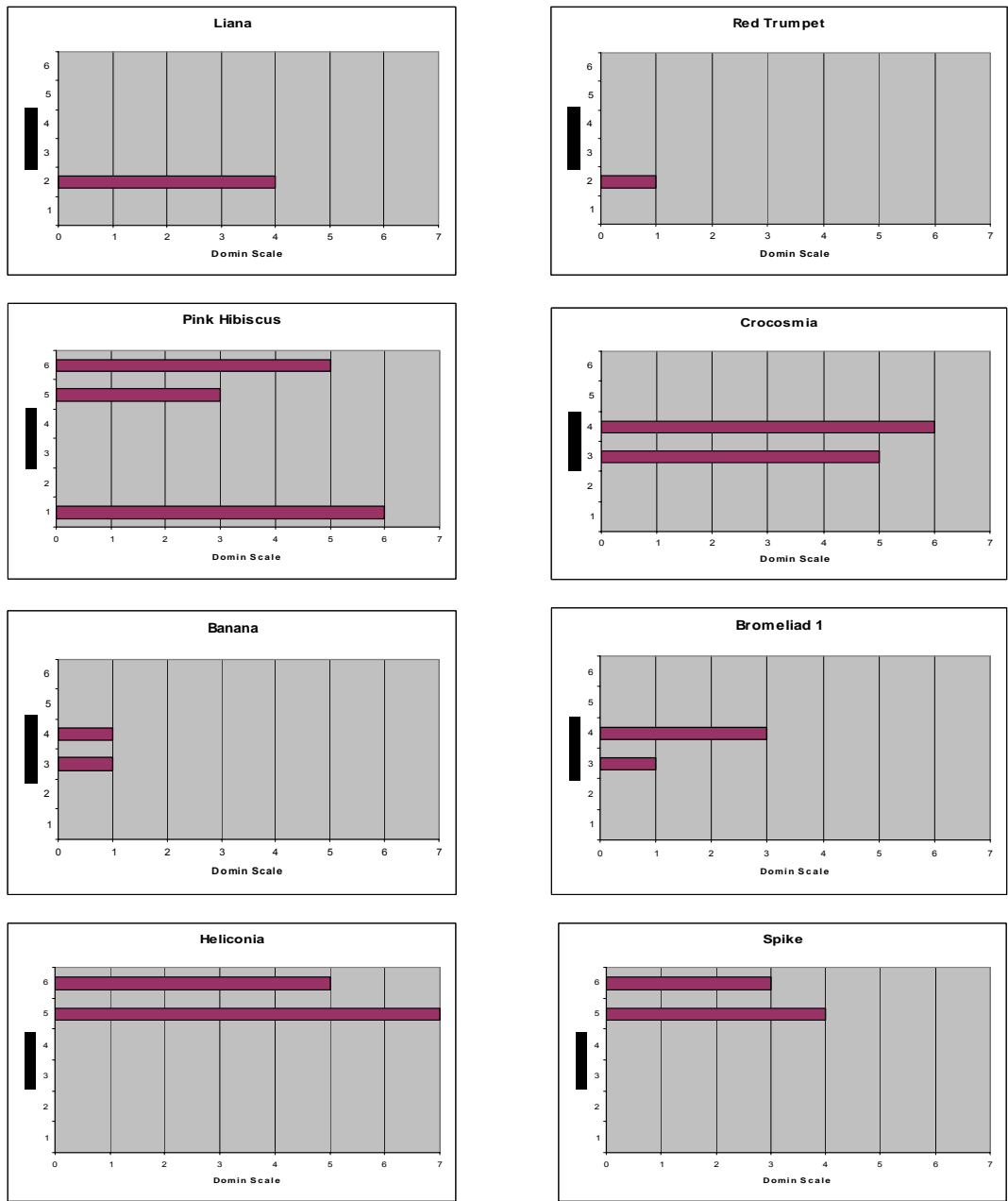
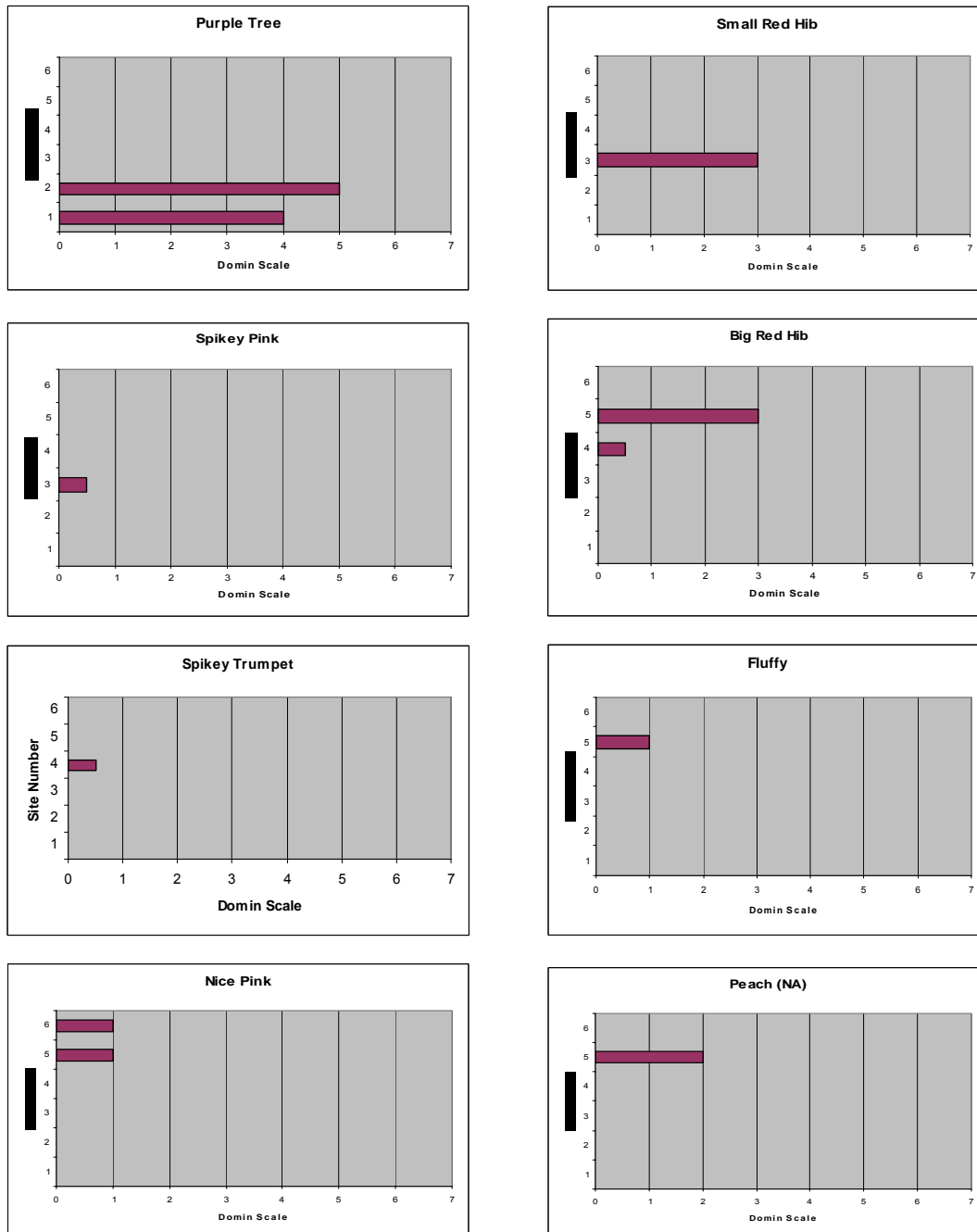


Figure 2.7 shows the Domin values for each of the flowering plants found in each of the six sites in Base Camp.

Figure 2.8



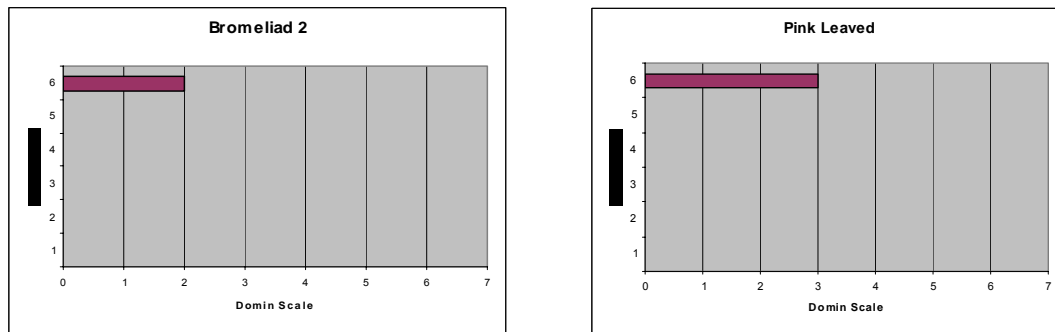


Figure 2.8 shows the Domin values for each of the flowering plants found in each of the six sites in Buenos Aires.

2.5 Flower Morphology

At least 10 flowers from each of the plants the hummingbirds were seen to be utilising were collected and the following measurements were taken for each individual flower using dial callipers to the nearest 0.1mm:

1. Width of aperture leading to the nectaries
2. Height of aperture leading to the nectaries
3. Length from aperture to the nectaries

The flower was then placed on a scale background and digital photographs were taken with a view to calculate the curvature of the flower.

Figure 2.9



Figure 2.9 shows a digital photograph of a Heliconia flower placed upon a scaled background.

Flower curvature was calculated by loading the digital photographs into the SigmaScanTM/Image computer software. The length of the base of the flower to the tip, as well as the length of the midline of the flower was calculated using the cumulative distance tool. These distances were then calibrated to the centimetre scale on the photograph. The length of the flower was then divided by the length of the midline resulting in a ratio value that corresponds to the curvature of the flower. It was originally planned to deduce the flower curvature using the same method as that used on the hummingbird bills. However, as the flowers do not have the same straight starting point to line up against an original line like the bills do, the angle of deflection can not be accurately found.

Figure 2.10

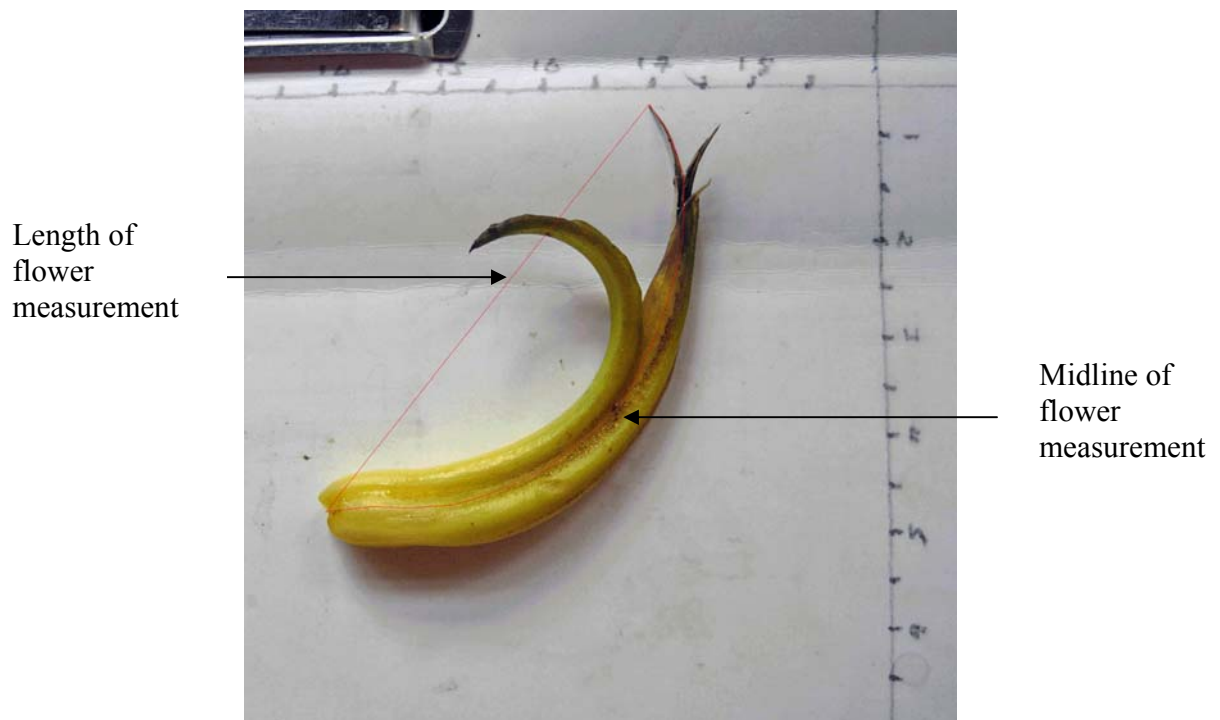


Figure 2.10 shows a *Heliconia* flower with the overlays of the SigmaScanTM/Image software superimposed upon it. These distances were then calibrated to the cm scale present in the photograph.

3.0 RESULTS

3.1 Notes on results

To maintain reliability the bird species that were used in the analysis have at least eight datasets from the mist net catches. From the field observations, only data from birds that were repeatedly observed were included in the analysis. When these two parameters were brought together the analyses was restricted to six hummingbird species, two of which were identifiable as sexually dimorphic:

Azure Crowned, *Amazilia cyanocephala*

Green throated mountain gem, *Lampornis v. viridipallens*

Green violet ear, *Colibri t. thalassinus*

Magnificent (male and female), *Eugenes fulgens*

Violet sabrewing (male and female), *Campylopterus h. hemileucurus*

White bellied emerald, *Amazilia candida*

3.2 Correlations between bird and flower morphology

Product moment correlations were conducted upon bill length and curvature against flower length, diameter and curvature. Native species of flower were split from non-native species for comparison.

Bill curvatures were correlated against native flower diameters which resulted in a weak, positive, non-significant correlation r value:

Table 3.1

	<i>Bill curvature</i>	<i>Flower diameter</i>
Bill curvature	1	
Flower diameter	0.2171128	1

Bill curvatures were then correlated against non-native flower diameters again with a weak, positive, non significant r value that is very similar to the native value:

Table 3.2

	<i>Bill curvature</i>	<i>flower diameter</i>
Bill curvature	1	
flower diameter	0.27636391	1

Hummingbird bill lengths were correlated against native flower diameters with a weak, positive, insignificant r value:

Table 3.3

	<i>Bill length</i>	<i>Flower diameter</i>
Bill length	1	
Flower diameter	0.320620132	1

Bill lengths were then correlated against non-native flower diameters with a weak, positive, insignificant r value that is again very similar to the native value:

Table 3.4

	<i>Bill length</i>	<i>flower diameter</i>
Bill length	1	
flower diameter	0.368703676	1

Bill lengths were correlated against native flower lengths which gave a positive, significant r value at the $p \leq 0.05$ level (see Table 3.5)

Table 3.5

	<i>Bill length</i>	<i>Flower length</i>
Bill length	1	
Flower length	0.611875678	1

However when bill lengths were correlated against non-native flower lengths it resulted in a very weak, positive, insignificant correlation:

Table 3.6

	<i>Bill length</i>	<i>flower length</i>
Bill length	1	
flower length	0.1793497	1

Finally, bill curvature was correlated against native flower curvature and a very weak, negative, insignificant correlation was found:

Table 3.7

	<i>Flower curvature</i>	<i>Curvature</i>
Flower curvature	1	
Curvature	-0.154530861	1

A slightly stronger, negative correlation was found when bill curvature was correlated against non-native flower curvature but the r value was still insignificant:

Table 3.8

	<i>Flower Curvature</i>	<i>Curvature</i>
Flower Curvature	1	
Curvature	-0.444456173	1

3.3 Flower choice based on bill morphology

3.3.1 Base Camp

The proportion of the total plants available at the Base Camp sites that are being utilised by the hummingbirds were found as percentage values. These values were then correlated against the birds' bill curvatures (Table 3.9 and Figure 3.1) and the birds' bill lengths (Table 3.10 and Figure 3.2). Both tests yielded insignificant r values:

Table 3.9

	<i>Proportion of available plants utilized</i>	<i>Bill Curvature</i>
Proportion of available plants utilized	1	
Bill Curvature	-0.590083208	1

Table 3.9 showing bill curvature correlated against the proportion of plants the birds utilised.

Figure 3.1

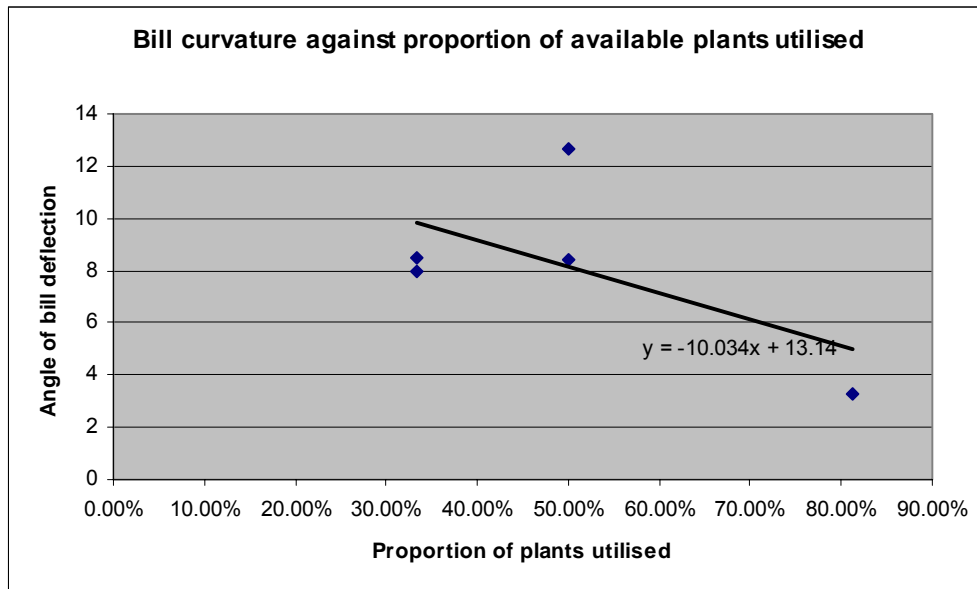


Figure 3.1 showing the insignificant, modest, negative correlation between the bill curvatures and the proportion of available plants utilized.

Table 3.10

	<i>Bill Length</i>	<i>Proportion of available plants utilized</i>
Bill Length	1	
Proportion of available plants utilized	0.171959896	1

Table 3.10 showing the very weak, positive insignificant correlation between bill lengths and the proportion of available plants utilised by the hummingbirds.

Figure 3.2

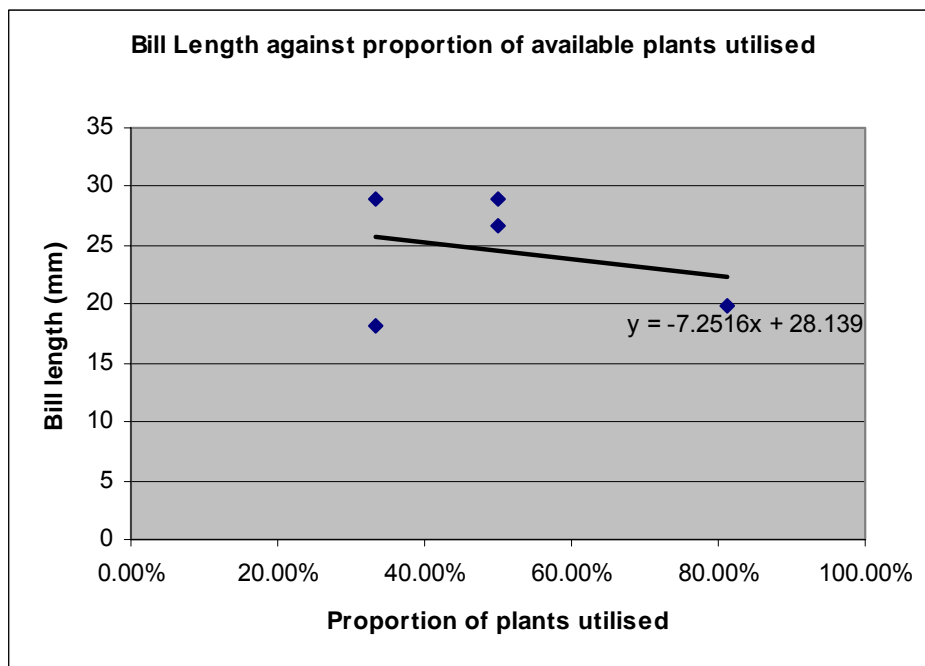


Figure 3.2 showing the weak, insignificant correlation between bill length and the proportion of available plants utilized.

3.3.2 Buenos Aires

Parallel tests to those in 3.3.1 were conducted on the bird species and the proportion of plants utilised in the village of Buenos Aires. Strong correlations were found for both bill curvatures and bill lengths but due to the small sample size of three bird species only the bill length correlation is significant to $p \leq 0.05$.

Table 3.11

	<i>Proportion of available plants utilised</i>	<i>Bill Curvature</i>
Proportion of available plants utilized	1	
Bill Curvature	-0.938554586	1

Table 3.11 showing a very strong, negative correlation between bill curvatures and the number of plants utilised in Buenos Aires.

Figure 3.3

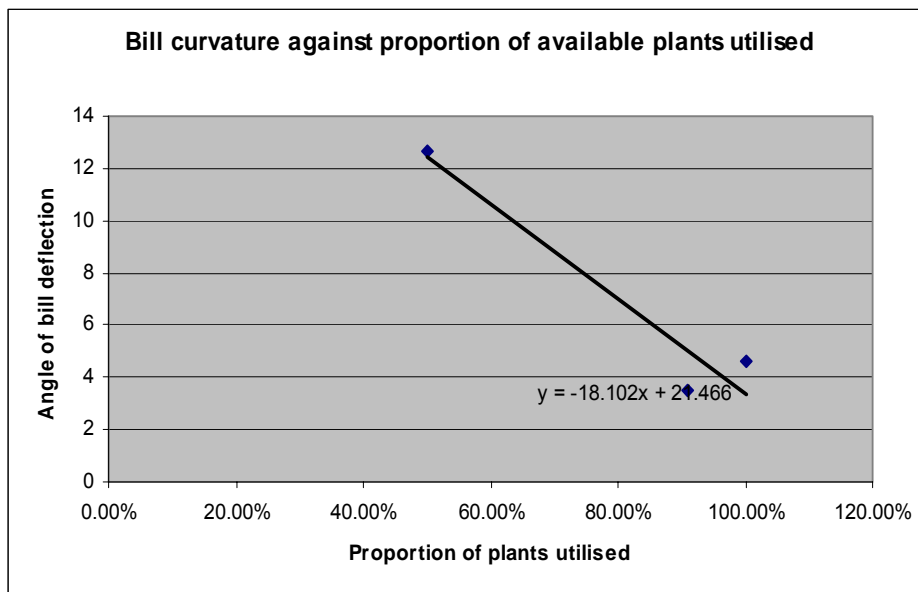


Figure 3.3 showing the strong, negative, insignificant correlation between bill curvatures and the proportion of plants utilised by the hummingbirds.

Table 3.12

	<i>Bill Length</i>	<i>Proportion of available plants utilized</i>
Bill Length	1	
Proportion of available plants utilized	-0.996569618	1

Table 3.12 showing the strong, negative, significant to $p \leq 0.05$ correlation between bill lengths and the proportion of plants utilised by the birds.

Figure 3.4

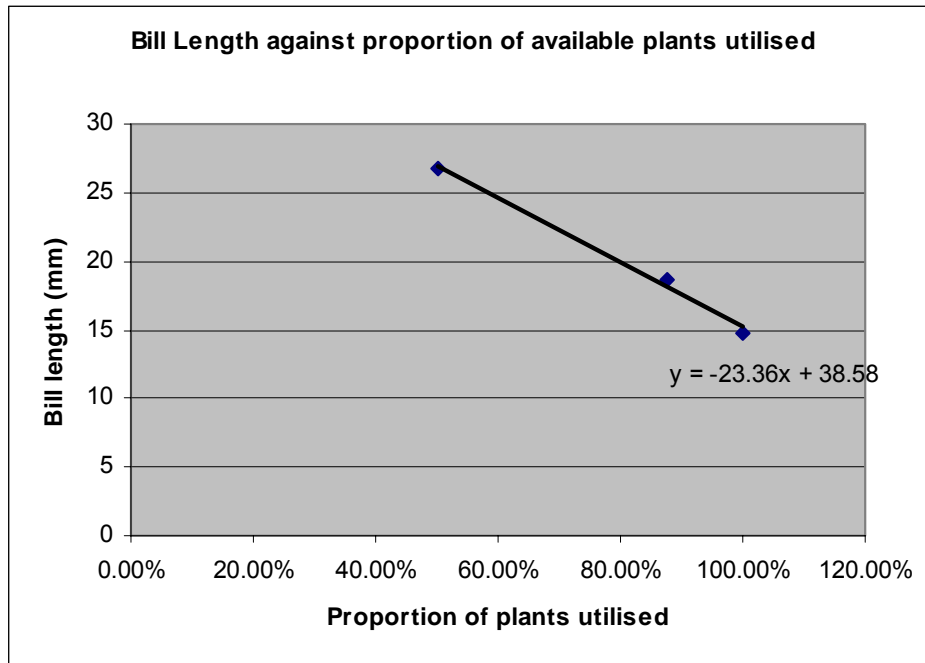


Figure 3.4 showing the strong, negative, significant correlation between bill lengths and the proportion of available plants utilised.

3.4 Selection of native and non-native species

From the initial graph (Figure 3.5) it would seem that hummingbird species may actually prefer non-native species to native species as non-native flower species have a higher number of different species visiting them.

A chi square test was conducted upon this data and it was found that the distribution of hummingbird species among flower species was due to random chance and not because the hummingbirds were selecting non-native flower species over native species (Table 3.13).

Figure 3.5

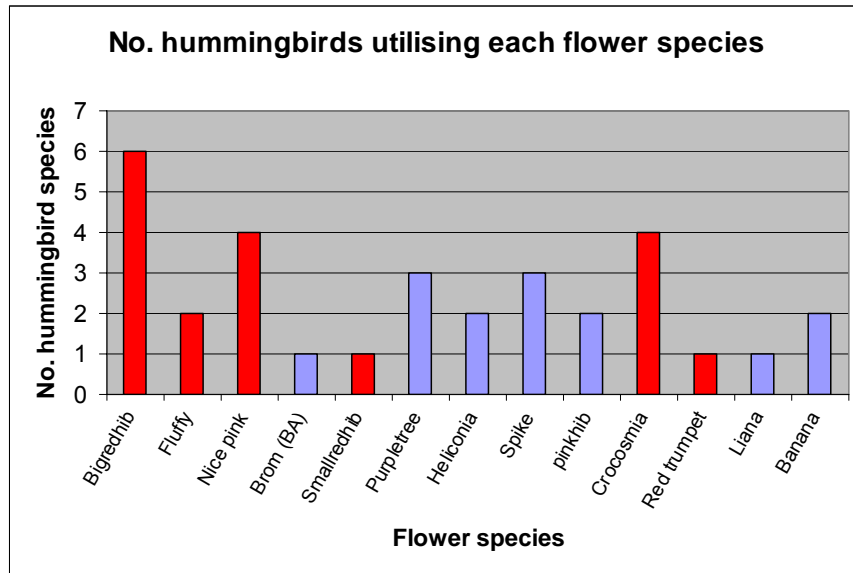


Figure 3.5 showing the number of hummingbird species utilising each species of flower. Non-native species are shown in red and native species are shown in blue.

Table 3.13

X2	df	critical value	
11.062	12	21.03	0.05
		26.22	0.01

Table 3.13 showing the chi square data for the above table. X2 does not exceed The critical values at the $p \leq 0.01$ or $p \leq 0.05$ levels and so the result is insignificant.

3.5 Specialisms with respect to bill curvature

An initial scatter plot regression of bird bill curvatures plotted against the number of flower species visited seems to show a trend that birds with straighter bills visit a greater number of flower species (Figure 3.6).

Figure 3.6

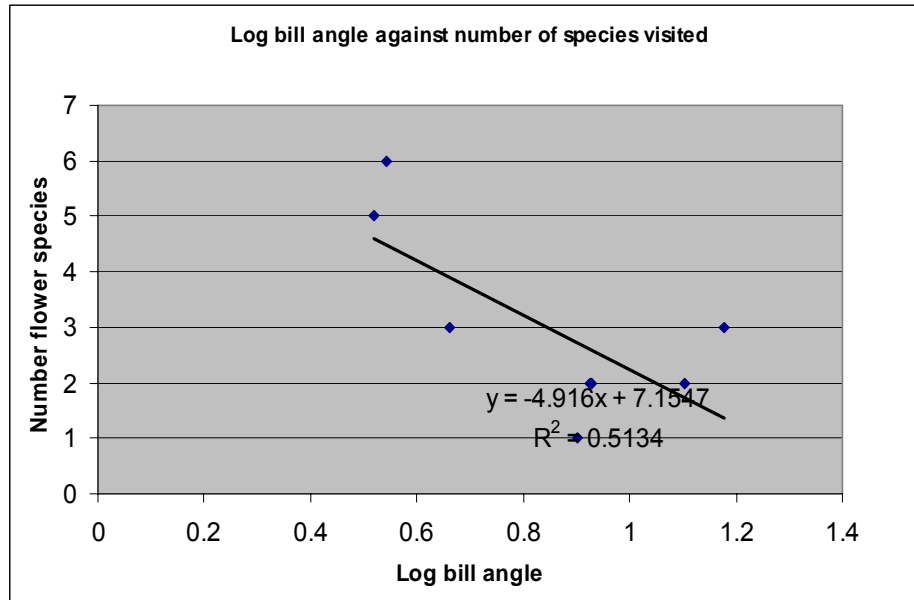


Figure 3.6 describing the significant regression where birds with straighter bills visit a larger number of flower species.

The regression performed between the number of flower species visited and the log angle of bill deflection was found to be significant to the $p \leq 0.05$ value:

Table 3.14

<i>F</i>	<i>Significance F</i>
6.330763489	0.04552629

3.6 The composition of hummingbird species in the core zone and the buffer zone

The composition of hummingbird species between the three mist net sites was compared. The most abundant species was given the value 100 and the data was transformed for the remaining species so that it represents a proportion of this value.

For each site a histogram of the data was constructed to show a graphical species comparison (See Figures 3.7, 3.8 and 3.9).

Figure 3.7

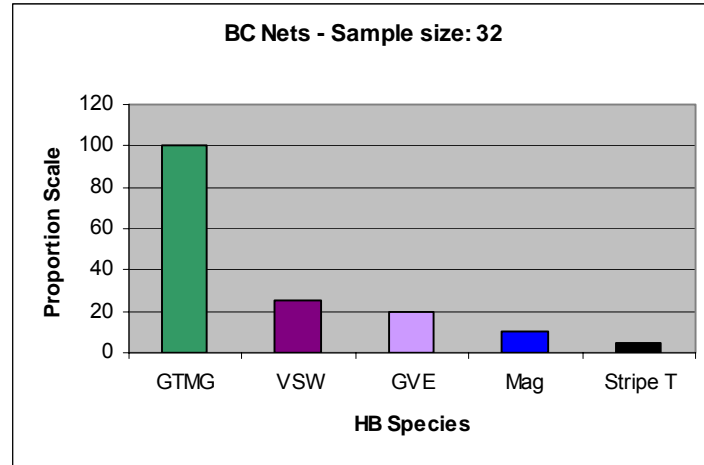


Figure 3.7 describing the species composition at the Base Camp mist net site.

Figure 3.8

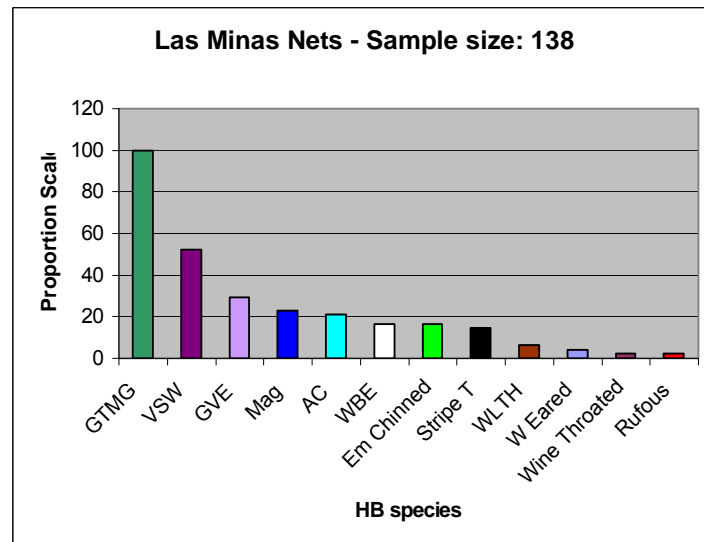


Figure 3.8 describing the species composition at the Las Minas mist net site.

Figure 3.9

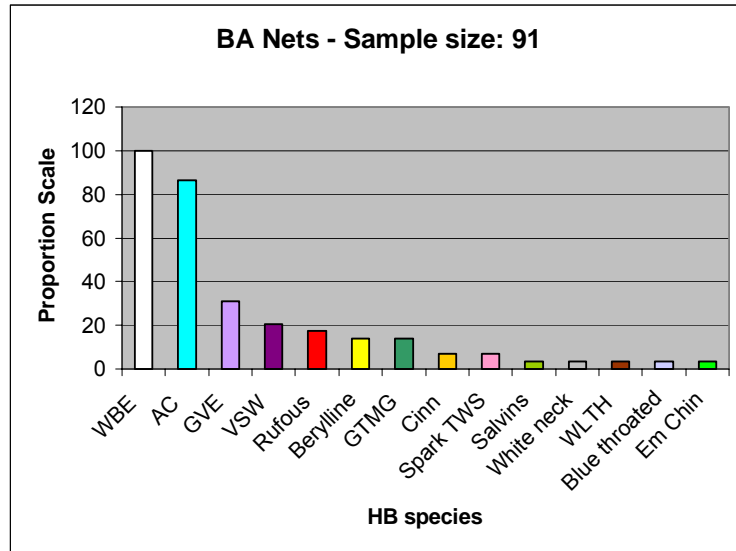


Figure 3.9 describing the species composition at the Buenos Aires mist net sites.

To compare the species diversity and evenness at each site statistically a Shannon-Weaver Diversity index was performed to give the species richness (H) and the evenness (J) of the species distribution separately for each site and then combining the Base Camp site and the Las Minas site to represent the core zone.

Table 3.15

Site	H	J
Base Camp	1.13	0.7021
Las Minas	2.00	0.8048
BC + LM	1.89	0.7606
Buenos Aires	2.05	0.7768

Table 3.15 giving the Shannon Weaver Diversity Index values of species richness (H) and equability (J)

Base Camp sites have a lower species richness than Las Minas sites and Buenos Aires sites however when Base Camp values were combined with Las Minas sites the core zone species richness, $H=2.00$, is very similar to the buffer zone species richness, $H=2.05$. Evenness was comparable across all three sites.

4.0 DISCUSSION

Correlations between bill morphology and floral structures

From the morphological correlations it can be concluded that there is no relationship between flower diameter, either native or non-native, and bill curvature (Tables 3.1 and 3.2) or bill length (Tables 3.3 and 3.4). Interestingly, this shows within Cusuco National Park shorter billed hummingbirds are not restricted to flower species with long, wide corollas as research by Temeles et al (2002) would suggest and they are able to utilise flowers with long, narrow corollas.

The correlation shown in Table 3.5 gives a significant result to the $p \leq 0.05$ value between bill length and corolla length of native flower species. The hummingbirds within this study have therefore been found to utilise native flowers which have a corolla length that corresponds to the bird's bill length. As this significance was found only in the correlation involving native flower species rather than non-native flowers (Table 3.6), which gave a particularly weak correlation, it may be evidence of a co-evolved relationship between the plant and the hummingbird. This finding is supported by Temeles (1996) who found that longer billed birds had maximum extraction depths and shorter handling times but made more insertion errors. This indicates that a trade off in foraging ability seems to exist as insertion errors made by the birds will be energetically expensive (Smith et al, 1996). The birds are therefore optimising their foraging ability by feeding on flowers that have a similar corolla length to their bill length.

Tables 3.7 and 3.8 show that there is no significant correlation between bill curvature and corolla curvature in either native or non-native flower species. As a co-evolutionary relationship seems to be absent between these variables it may be that differences in bill curvature may be due to some other factor, for example an adaptation for gleaning insects as seen in La Selva hummingbirds (Stiles 1995).

Bill morphology in relationship to bird generalisms and specialisms

At Base Camp, correlations between bill length and curvature with the proportion of available plants utilised by the hummingbird gave insignificant results (Tables 3.9 and 3.10), although a trend illustrating that birds with more decurved bills utilised a more limited range of species can be seen in Figure 3.1. It can therefore be concluded that bill morphology has no impact on the proportion of plants utilised in the core zone of the Park.

However, in Buenos Aires, much stronger trends were observed. The correlation between bill curvature and the proportion of plants utilised was insignificant (Table 3.11) but nevertheless describes a very strong correlation showing that birds with more decurved bills utilise much less of the flower species available than birds with straighter bills (Figure 3.3). $p \leq 0.05$ significance was found from the correlation between bill length and the proportion of available flower species utilised (Table 3.12) depicting the very strong trend that birds with shorter bills utilise a greater proportion of the flowers available (Figure 3.4).

Although a greater sample size would make these conclusions more significant ($n=3$) it does seem that bill morphology plays a significant role in flower utilisation in disturbed areas. Interestingly, the findings contrast with research concluding that birds with longer and more decurved bills can utilise a wider range of resources (Bleiweiss, 1999, Carpenter, 1993, Temeles and Roberts, 1992, Temeles and Kress, 2003) as birds with shorter, straighter bills appear to have the advantage, at least in the disturbed areas of Honduras.

Another unexpected finding was the results of the chi square test shown in Table 3.13. This shows that the hummingbirds are not choosing native flower species over non-native species or vice versa. From the principles of co-evolution, one may expect that hummingbirds would be more closely evolved with the native flower species

that have been present for a greater period of time and so an evolutionary relationship has had time to evolve. However, the birds utilise non-native species with just as high a frequency as they utilise native species and so seem to show no preference. This finding is supported by Araujo and Sazima's (2003) research on hummingbirds in the Brazilian capoes that showed no preference between ornithophilous and non-ornithophilous species of flower. A possible strategy to further these findings would be to observe the frequency of utilisation of each flower species to identify if the birds are visiting native flowers at a higher rate than non-native species.

The regression conducted on the log bill angle against number of flower species visited gave a significant result to the $p \leq 0.05$ value (Table 3.14) indicating that birds with straighter bills do show generalist behaviour when feeding on flower species and birds with more curved bills show specialist behaviour. This may be due to the composition of the morphology of the flower species within the park as birds with straighter bills may be at an advantage in an area where many of the flower species, both native and non-native, have particularly short and wide corollas. From the flower measurements taken, this appears to be the case in Cusuco National Park, and so the expected conclusion that birds with longer, more curved bills can be more generalist (Bleiweiss, 1999, Carpenter, 1993, Temeles and Roberts, 1992, Temeles and Kress, 2003) may be reversed in areas with this flower composition.

Comparison of species composition

From the preliminary species diversity analyses from the mist net catches (Figures 3.7, 3.8, 3.9) it can be seen that Base Camp and Las Minas sites are very similar in terms of composition and so can be representative of the core zone. Although the four main species at Base Camp (Green throated mountain gem, Violet sabrewing, Green violet ear and Magnificent hummingbirds) are identical, Las Minas is much richer in diversity with twelve species as opposed to the five found at Base Camp. This can be seen from the Shannon-Weaver Diversity Index (Table 3.15) as the H value for Base Camp is 1.13 as opposed to $H=2.00$ at Las Minas. This may be due to different habitat

vegetation in each of the valleys in Las Minas and so increasing the number of species of hummingbird moving across the ridge.

The data from Buenos Aires (Figure 3.9) portrays a completely difference composition of species than that of Base Camp and Las Minas. Here, the White bellied emerald and Azure crowned are the primary species with the Green throated mountain gem contributing very little to the proportion of the data. The number of species found in Buenos Aires (14 species) is comparable to that of Las Minas ($n=12$) although there is not a complete species overlap.

From the Shannon-Weaver Diversity Index (Table 3.15) the H values for the core zone (combining Base Camp and Las Minas sites) and the buffer zone (Buenos Aires) are 1.89 and 2.05 respectively with comparable evenness values of $J=0.76$ and 0.77. From this data it can be seen that the disturbed buffer zone actually supports higher species diversity with almost equivalent evenness to the protected core zone.

The type of urbanisation seen in Buenos Aires has produced a local species diversity and abundance that is greater than the surrounding landscape. Evidence supporting this effect of urbanisation can be found in McKinney (2006) who stated that urbanisation which forms urban fringe habitats can support species such as early successional plants and edge animal species such as mesopredator mammals and ground foraging, omnivorous and frugivorous birds. This study has provided data to extend this theory to include nectarivorous hummingbirds, which have been observed to utilise and thrive in gardens and forest fragments.

Some of the major plantations surrounding Buenos Aires consist of sun coffee, shade coffee and banana plantations and these plant species may contribute to the species diversity of hummingbirds found in Buenos Aires (Renjifo, 2001, Camfield, 2004). However, some general observations of the plantations have given the impression that competition for food is much higher with greater interactions between a greater number of individual hummingbirds and between many different hummingbird species

over the same food source (generally established, flowering trees that have been preserved within the plantation) an observation that was incredibly rare within the core zone. These observations have led me to speculate upon the stability of species composition in such areas, especially if further urbanisation begins to take place.

The effects of disturbance on the Green throated mountain gem

The Green throated mountain gem is the only endemic species to the park and the change in its distribution from being the most abundant species in the core zone (n=68) to being considerably rarer in the Buenos Aires (n=4) seems to be due to its sensitivity to the disturbance found in the buffer zone. Interestingly, the Green throated mountain gem was found to be the species that utilised the largest number of different flower species (n=9) and so its range cannot be restricted by its inability to utilise non-native flower species in disturbed areas. Its restricted range could therefore be a result of a closer evolutionary relationship between itself and the endemic plant species or other resources in the core zone leaving it more sensitive to forest (Renjifo, 2001) and human disturbance (Garcia et al, 1998, Watson et al, 2004).

This research has provided a case for the protection of the Green throated mountain gem as evidence has been provided to illustrate the drastic effect disturbance is having on the population's range. If the species distribution becomes even more restricted and isolated the Green throated mountain gem will be particularly vulnerable to further population declines or extinctions due to genetic isolation (Garcia et al, 1998).

Conclusions

Hummingbird bill lengths are significantly correlated to flower corolla lengths in native flower species ($r = 0.611875678$, $p \leq 0.05$) indicating some form of co-evolution has taken place.

In the disturbed buffer zone, bill length is significantly correlated to the proportion of plants available being utilised ($r = -0.996569618$, $p \leq 0.05$) whereas no such relationship is present in the core zone. This indicates that a shorter bill length is an important factor in determining success in disturbed areas as the ability to utilise a wider range of flower species will increase the stability of the hummingbird population as it will be more resistant to the removal some species that it feeds upon.

The significant regression (Significance $F = 0.04552629$) showed how decreased bill deflection allows hummingbirds to visit a wider number of flower species than those with curved bills and so straighter billed birds should be less sensitive to disturbance where their usual food sources are replaced by novel, non-indigenous flower species.

The findings from these correlations and regression contradict a large body of research that predicts that birds with longer, more curved bills will be able to utilise a wider range of resources. This could be due to the morphology of the floral structures being different in the Cusuco National Park to other research areas, involving more flower species with shorter, wider corollas, giving birds with long, curved bills no advantage over those with short bills. If this is the case then the reduction in insertion errors of birds with short bills will give them an energetic advantage over those with long bills and so may allow them to utilise a greater number of non-native species that have lower nectar content than native species.

The village of Buenos Aires provides a high concentration and diversity of flowers providing many niches for a variety of species to occupy. Hummingbirds seem generally resistant to such forms of forest fragmentation and can exploit a variety of

disturbed habitats. However, it is important to have high concentrations of flowers in such areas as populations of birds in the plantations seem to be in much more territorial conflict due to more ephemeral food sources. From the results of the chi square, villagers in the Cusuco National Park should therefore be encourage to grow flowers in their gardens regardless of whether the species is native or not, to help support hummingbird populations in these areas.

The Green throated mountain gem is endemic and, as predicted by the research, is particularly vulnerable to disturbance as it is almost absent from the hummingbird composition in Buenos Aires. I believe that this research warrants conservation measures be set in place to protect this species as further isolation through increased disturbance may lead to a severe population decline or even extinction.

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