Cue use affects resource subdivision among three coexisting hummingbird species

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Competition for food can influence the coexistence of species via habitat selection, and learned behavior can influence foraging decisions. I investigated whether learned behavior and competition act together to influence species interactions between three coexisting hummingbird species: black-chinned (*Archilochus alexandri*), blue-throated (*Lampornis clemenciae*), and magnificent (*Eugenes fulgens*) hummingbirds. I found that color cue use by individuals affects not only their foraging choices but also population-level responses to competition. I presented hummingbirds two types of habitats (rich and poor feeders). All birds shared a preference for the rich feeders, but shifted preference toward poor feeders in response to competition. I used color cues to manipulate the amount of information available to birds and examined the effects of two information states (complete or incomplete) on their foraging choices. I examined hummingbirds' preferences for the rich feeders when both competitor densities and information varied. To relate foraging choices to energetic intake, I also analyzed energy gained during a single foraging bout. Males of all species exhibited strong preferences for rich feeders when they foraged with complete information and low competitor densities. Without complete information, the two subordinate species (black-chinned and magnificent) shifted preference away from rich feeders in response to high densities of the dominant species (blue-throated). Each subordinate species shifted in a unique way: black-chinned hummingbirds reduced foraging efficiency, while magnificent hummingbirds reduced foraging time. Birds foraging with complete information remained selective on rich feeders even at high competitor densities. Thus, learned information affected competitive interactions (for rich feeders) among these species. *Key words: Archilochus alexandri,* color cues, competition, *Eugenes fulgens,* foraging, ideal free distribution, hummingbirds, isoleg theory, *Lampornis clemenciae,* learning. [Behav Ecol 11:550–559 (2000)]

Competing species may coexist because they subdivide similar resources. This subdivision should depend on individuals' abilities to assess those resources. In nature, color cues or other environmental cues can allow animals to use resources more efficiently (e.g., Mitchell, 1989; Weiss, 1997). For example, Weiss (1992) demonstrated that many flowers change color after pollination. Often, a plant retains pollinated flowers to increase the size of the display to attract pollinators from a distance (Lewis, 1993). However, when the pollinator gets closer to the display, it follows these different color cues to choose only those flowers that contain nectar (because they require pollination). Natural selection should favor an animal's ability to learn cues that help it exploit its environment better (see Stephens, 1993). Giraldeau (1997) provides a comprehensive review of the effects of information on ecology and behavior.

Hummingbirds readily use several types of environmental cues such as location (Bené, 1941; Goldsmith and Goldsmith, 1979; Hurly and Healy, 1996; Miller and Miller, 1971; Stiles, 1975), patterns (Healy and Hurly, 1995), and colors (Gass and Sutherland, 1985; Goldsmith and Goldsmith, 1979; Mitchell, 1989; Sandlin, 1999). Cues allow individual hummingbirds to predict resource quality so they may increase their foraging efficiency (Mitchell, 1989). Could cue use also affect resource subdivision among species?

The term "information state" refers to the ability of an animal to predict the quality of its environment (see Mitchell, 1989). An animal with complete information can use cues to predict the quality of its environment with no additional sampling. An animal with incomplete information can only pre-

dict the quality of its environment by sampling from it (Stephens, 1993; Stephens and Krebs, 1986) or by watching other foragers (Bednekoff and Balda, 1996; Fiorito and Scotto, 1992; Kodric-Brown and Nicoletto, 1993). I examined the effects of two information states (complete or incomplete) on hummingbird foraging choices to elucidate a possible mechanism by which learned information affects species coexistence.

Theoretical framework

Isoleg theory helps us understand how habitat preferences can evolve to facilitate stable coexistence among populations of competing species (Rosenzweig, 1979, 1981, 1986, 1987). This theory, based on ideal free distribution theory (IFD; Fretwell and Lucas, 1969), assumes that competition helps to determine foraging behavior and, thus, habitat selection. It assumes that the competitors use two habitats and that higher population densities depress resource availabilities to force alterations in habitat use for at least one of the species. Asymmetry in competitive abilities can force a subordinate species away from its primary (preferred) habitat and into a secondary one.

Although isoleg theory predicts behavioral shifts of entire populations, it necessarily depends on the behavior of the actual foragers (i.e., the individuals within each population). Classical optimal foraging theory (OFT; reviewed by Pyke et al., 1977) predicts that individuals should feed exclusively from the most profitable resource as long as that resource is in sufficient supply. Considerable empirical evidence confirms that individuals of most hummingbird species choose the richest sucrose solutions available from their environment (Mitchell, 1989; Montgomerie, 1984; Pimm, 1978; Pimm et al., 1985; Pyke, 1978; this study).

Mitchell (1989) showed that information state affects an individual hummingbird's selectivity for rich (versus poor) feeders, especially when travel costs are high. Mitchell defined

selectivity as "the proportion of the diet comprising rich resource items" (1989: 147). I adopt his definition here. Pimm et al. (1985) empirically tested isoleg theory using the same three hummingbird species treated herein. They discovered the predicted competitor-driven thresholds in selectivity for all three species. However, they did not vary information state.

Cue use and decision making

The word "choice" implies that individuals can discriminate between available alternatives. How important is this discriminating ability for habitat selectors, especially those that can learn cues from their environment? I reasoned that the abilities of foragers to choose among patches of habitat (e.g., rich and poor hummingbird feeders) should depend not only on competitor pressure but also on information state. Do individuals that can learn from their environment make better foraging (or habitat) choices in different competitive situations? Could the competitor density that causes population-level switches in selectivity (sensu Pimm et al., 1985; Rosenzweig, 1979) vary with respect to the individuals' information state? Using IFD, OFT, and isoleg theory, I predicted that: (1) Regardless of competitor density, foragers with an information deficit should use poor feeders more readily than those with complete information (i.e., incomplete information decreases selectivity). (2) At high competitor densities, thresholds of foraging selectivity should exist such that foragers switch from exclusive use of rich toward opportunistic use of rich and poor feeders (i.e., high competition decreases selectivity). (3) Individuals foraging at similar competitor densities, but with different information states, should sometimes exhibit different degrees of selectivity for rich feeders. (4) Subordinate species should exhibit a greater decrease in selectivity in response to information deficit and competitor pressures than the dominant species. Each of these predictions is based on theory; prediction 1 comes from OFT, prediction 2 comes from IFD, prediction 3 is a combination of OFT and IFD, and prediction 4 comes from isoleg theory.

METHODS

Study area

All research was conducted at the American Museum of Natural History's Southwestern Research Station (SWRS; 31°50′ N; 109°15′ W) in southeastern Arizona, USA. At an elevation of approximately 1650 m, the 36.4-ha SWRS is located along the Middle Fork of Cave Creek, one of the major drainages in the Chiricahua Mountains. At this elevation, the dominant plant communities are pine-oak-juniper scrub in xeric areas and sycamore-cottonwood-walnut forest along the mesic creek bottoms. My study site is a small (ca. 0.25 ha) meadow immediately south of Cave Creek on the SWRS property. Vegetation along the edges of the meadow provides shade and perching sites for hummingbirds. Dry grasses and some sedges cover the meadow during the dry season (March–July) when I conducted this study. Dry season conditions do not favor the growth of flowering plants normally visited by hummingbirds (e.g., *Penstemon, Mimulus,* and *Aquilegia*); I found none growing nearby. Arthropod resources (e.g., leafhoppers, flies, gnats, spiders) appropriate for hummingbirds were abundant throughout my study, as evidenced by the full crops of all specimens sacrificed for another study (Van Hook et al., manuscript in preparation). Even though hummingbirds were aggressive there, no single individual could defend this meadow, so all individuals foraged in it.

Overview of experimental design

I examined the effect of changes in information state on hummingbirds' foraging choices. I superimposed this examination onto changes in foraging choices generated by the competitive milieu. To manipulate information state, I provided either color cues that allowed birds to distinguish between rich and poor resources or color cues that did not allow such discrimination. While I watched focal birds forage in each of these two information states, my assistant counted and cataloged the numbers of birds, thus quantifying and characterizing the competitive milieu.

Description of species

I studied breeding males (only) of black-chinned (*Archilochus alexandri,* hereafter BC), blue-throated (*Lampornis clemenciae,* hereafter BT), and magnificent hummingbirds (*Eugenes fulgens,* hereafter MA). These birds migrate from Mexico and, possibly, Central America to breed in the Chiricahua Mountains in the spring (Johnsgard, 1997). Male BTs (ca. 8.3 g) behaviorally dominate the other two species and hold territories in rich riparian areas (Pimm, 1978; Powers and McKee, 1994). BC males (ca. 3.2 g) may hold territories, but only in relatively xeric sites (Powers and McKee, 1994). Rather than hold territories, male MAs (ca. 7.9 g) trapline [defined by Feinsinger and Colwell (1978) as following "a repeated foraging circuit among successive flowers or clumps"] throughout the canyon (Johnsgard, 1997; Lyon et al., 1977; Pimm, 1978; Powers, 1996).

Bird identification

To identify individual males, several assistants and I trapped and marked as many males of the three study species as possible (see Sandlin, 1999, for details). To distinguish between individuals, I painted (with Polly S nontoxic hobby paint) the backs of those males with a unique combination of three color bars between their shoulders. A bird foraging at a feeder board (see below) presents its dorsal side, usually allowing the observer to see these color bars.

Theoretical considerations

I presented patches of habitat (feeders) in such a way that I could easily watch individuals select among them. To efficiently observe numerous individuals as they made patch choices, I provided the birds with arrays of closely spaced feeders. Putting feeders in close proximity reduced travel costs for the birds, thus approximating an assumption of the simplest isoleg theories (e.g., no cost to switching between habitats; Rosenzweig, 1979).

Is a hummingbird feeder a patch or simply a modified prey item? I assert that feeders are patches in the truest sense of the word. According to Stephens and Krebs (1986: 14),

> A *prey* yields a fixed amount of energy and requires a fixed amount of time to handle: the forager can control neither the energy gained nor the time spent in attacking a prey item. However, the forager controls the time spent in, and hence the energy gained from, a *patch,* because there is a well-defined relationship between time spent and energy gained. Any predator that sucks the juices out of its prey might be thought of as preying upon patches.

A tight positive relationship exists between the time a hummingbird spends at a feeder and the energy it gains from that feeder (Montgomerie, 1984; see below). Therefore, I refer to hummingbird feeders in the text, but the reader should re-
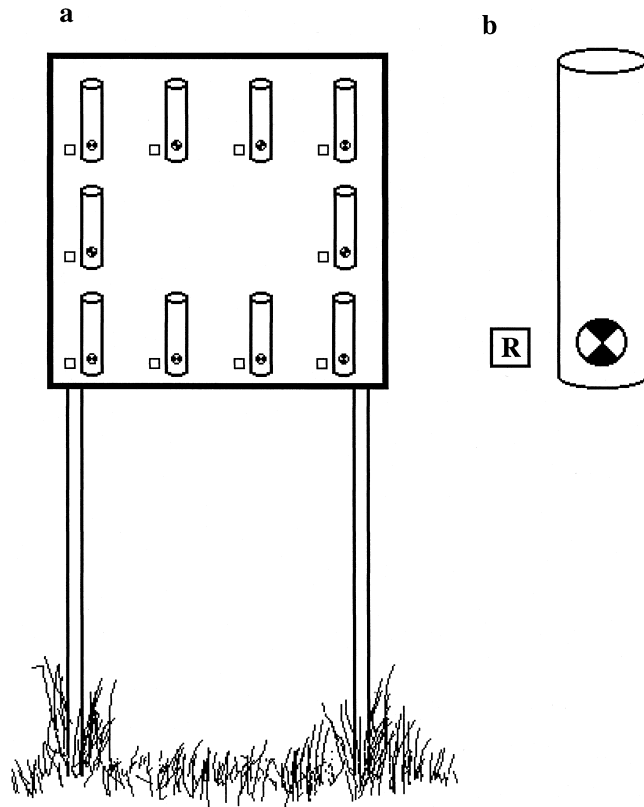
Figure 1
(a) A feeder board with ambiguous cues. The small squares to the left of each feeder show "R" for rich feeders and "P" for poor feeders. These squares mark feeder quality during data collection with ambiguous cues. (b) Enlargement of one feeder to show pie-shaped design of an ambiguous bee guard with dark quarters blue and open quarters yellow. Reliable bee guards (not shown) were either blue or yellow.

member that each feeder is a patch of habitat that can be selected by individual foragers.

Feeder boards

A feeder board is an array of 10 (5 rich and 5 poor) acrylic 88-ml feeders (Perky-Pet cat. no. 214) which each present one fountain covered by a detachable bee guard. I used Velcro to attach feeders 15–20 cm apart in a square pattern on a 0.61 m × 0.61 m pegboard (Figure 1a). The pegboard rested atop two PVC poles so that its bottom feeders were about 0.9 m above the ground. This distance above ground assured that vigilance for ground predators (e.g., roadrunners, *Geococcyx californianus*; Lima, 1991) should not influence a bird's decision to use feeders on the lower part of the board.

Information state

Manipulation of information state required that the birds first learn cues so they could predict the location of rich (30% = 0.86 M sucrose) and poor (15% = 0.43 M sucrose) feeders. All three species of hummingbird learned to associate a color cue (via blue or yellow bee guards) with feeder quality (Sandlin, 1999). Once birds learned to associate bee guard color with feeder quality, I could deprive them of these learned cues and the information that cues convey.

Reliable cues

Most individuals learned color cues in 3 days or less (unpublished data). I let blue = rich and yellow = poor because I discovered that naive birds (either juveniles or adults new to the area) may exhibit a bias for yellow (Sandlin, 1999). I call these blue or yellow bee guards "reliable cues." Birds can benefit from reduced search costs after they learn to associate cue color with feeder quality. With this knowledge, the bird enjoys complete information about feeder quality (Stephens and Krebs, 1986) so it can predict a priori the quality of every feeder it encounters.

Ambiguous cues

To deprive birds of information, I painted another set of bee guards with a four-quarter pie-slice design with two opposing quarters yellow, and the others blue (Figure 1b). I call these bee guards "ambiguous cues." To make the birds suffer an information deficit, I put ambiguous bee guards on both rich and poor feeders. Even though the birds still see blue and yellow, ambiguous cues contain no information about feeder quality because all feeders look the same. In this case, search costs should increase because birds cannot predict feeder quality without first sampling from the feeder. OFT predicts that selectivity, and thus foraging efficiency, should decrease if a forager incurs higher search costs (Pyke et al., 1977; Stephens and Krebs, 1986).

Even with ambiguous cues, birds can still learn feeder locations (Healy and Hurly, 1995; Miller et al., 1985; Sutherland and Gass, 1995). Therefore, I randomized the locations of the five rich and five poor feeders on feeder boards at least once a day, even on days that I did not collect data. I also randomized locations immediately before data collection, making location per se a relatively unreliable cue.

Data sessions

My assistant and I arranged three feeder boards facing inward from the corners of an equilateral triangle with 10.5-m sides. This presented birds with a constant supply of sugar water distributed among 30 feeders. On days we collected data, we watched each feeder board (A, B, C) twice—once with reliable cues and once with ambiguous cues—for a total of six 30-min data sessions per day. I never mixed cue types during a data session; in each session, all three boards provided the same type of cue. Over the course of the field season, I also varied the time of day for sessions so that the data sets include observations from just after dawn through dusk. However, I generally avoided the hottest part of the day (e.g., 1030–1530 h) when bird activities seemed lower. To avoid possible bias at certain times of day (e.g., always watching board A at sunrise or always beginning with reliable cues), I randomized the order in which these six data sessions occurred (e.g., 5 June: 0622 h, B reliable; 0657 h, A ambiguous; 0837 h, B ambiguous; 1635 h, A reliable; 1711 h, C ambiguous; 1848 h, C reliable). Immediately before data collection, my assistant and I put the feeders on the focal feeder board (e.g., C reliable) in new randomly determined locations.

With two stopwatches (one for rich feeders and one for poor), I measured the cumulative amount of time a focal male spent feeding from each feeder type during one visit to the board (a foraging bout). For 30 min, I recorded these data for as many foraging bouts as possible. Occasionally, I observed the same individual more than once during a data session. To avoid problems with nonindependent estimates of foraging preferences, I used the average amount of time that particular individual spent at rich and poor feeders during all

his visits within that data session. For each species, I treated all unpainted males as the same individual in subsequent analyses. I did not purposely bias sampling toward any particular species or attempt to get equal numbers of observations from each species. Therefore, my observations should reflect the relative activity densities (sensu Pimm et al., 1985; see below) of males of these three species.

My assistant's censuses also measured activity densities. While I watched a single feeder board for 30 min, my assistant watched all three feeder boards (in a randomly-determined order) for 10 min each. During a 10-min segment, each bird was counted and identified as it arrived at that board. These counts estimate bird activity densities because they reflect the degree and type of competitor pressure (see below) birds encountered as they foraged. Differences in bird densities can vary by an order of magnitude over the course of 30 min (see below). I relied on this natural variation in bird density to vary competitor pressures.

Measurement of species-specific nectar extraction rates

Species-specific constraints on extraction rate place limits on how efficiently birds may use their time. Therefore, I measured the average extraction rate of each species separately using wild-caught birds that I put into a large aviary (ca. 8 m $\times$ 4 m $\times$ 3 m). I placed one feeder with a known volume of one of the sucrose solutions (rich or poor) in the aviary and used a stopwatch to measure the cumulative amount of time all birds (7–16 individuals) spent drinking from the feeder. They almost always drank one at a time. Once the volume of solution in the feeder noticeably decreased, I measured the remaining volume. I then calculated the change in volume per time spent foraging to estimate extraction rate. Because I presented only one feeder to several birds, this estimate represents the average extraction rate for the population of each respective species. I followed this procedure for each species and for each sucrose concentration. I used these extraction rates to convert measurements of foraging time at feeder boards into energy gain (kJ) per foraging bout (see below).

Data analysis

The data come from the field and are, therefore, inherently noisy and non-normal. Because of the noisy nature of the data, I relaxed my requirements for statistical significance and rejected the null hypothesis if $p < 0.07$. I used JMP IN (SAS Institute, Inc., 1996) to perform standard analysis of variance (ANOVA) on these data because ANOVA is usually robust with respect to deviations from normality (Sokal and Rohlf, 1981). The basic analysis was a three-way factorial design to examine selectivity (proportion of total foraging time spent using rich feeders; sensu Mitchell, 1989) with the main treatment effects of information state, competitor density, and bird species. My predictions require this multifactorial analysis, and I expected complicated patterns to emerge from the data (e.g., predictions 3 and 4). Fortunately, most patterns in the data are clear.

RESULTS

Foraging behavior at feeder boards

Birds used feeder boards in the same way they would use an inflorescence of flowers: they hovered at the board, feeding or sampling from one, a few, or most of the feeders. Remember that, from a theoretical perspective, one feeder is a patch of undepletable resource. Thus, 1 feeder board contained 10 patches from which a hummingbird could forage. The birds need not switch between rich feeders, and they need not show

aggression toward other birds feeding at other feeders. However, hummingbirds did not seem to perceive feeders as undepletable patches. Almost all birds were aggressive at feeder boards, suggesting that they viewed the boards, or feeders therein, as depletable patches that were profitable enough to defend. This is probably because high visitation rates of competitors (as many as 194 female BC visits and 16 male BT visits in 10 min; up to 273 individuals in 30 min) made access to feeders the limiting factor. Pimm (1978) showed that competition for time at feeders affected niche width, so it seems reasonable to think that hummingbird aggression in my experiments reflected their perception of limited access to feeders. This is the usual way that competitor pressure manifested itself in these experiments.

Activity densities and estimates of competitor pressure

The estimates of activity density often contain counts of the same individuals during a 30-min session. The relevant measure of competitor pressure, activity density (sensu Pimm et al., 1985), estimates how many birds were active and how often. Activity density is not a count of population size; it is an estimate of the intensity of competition experienced by individuals while foraging. Here, activity density especially concerns the effects of male BTs, whose presence probably influenced foraging choices of other birds (others often aborted their visit; see Pimm et al., 1985). It makes no difference if this competitor pressure resulted from repeated activities from a few individuals or the same level of activity from many individuals. The resulting effects of competition on subordinate switches in feeder preference should be the same.

Objectively measuring competitor pressure proved difficult because this pressure was manifested in many ways. Interference competition from aggressive male BTs was particularly fierce. In addition, high densities of female BCs provided pressure via exploitative competition. On average, we counted more female BCs in 30 min than all other birds combined (number of female BCs = 93.16 ± 42.71, number of all others = 54.3 ± 21.22; $z = 6.81$; $p < .0001$). Often, a focal male would leave a feeder—or the entire board—not because of active aggression but because of passive displacement by another bird, usually a female BC. Therefore, I considered exploitative competition from female BCs an important component of the competitive milieu. MAs also tended to displace others, rather than exhibit overt aggression at feeder boards.

Before data analysis, I separated each data session into one of two categories. I considered competitor (activity) densities to be high if counts showed more than 40 female BCs or more than 10 male BTs during at least one 10-min surveys ($n = 27$ data sessions). All other data sessions ($n = 29$) represented low competitor densities. The total number of birds varied greatly between one data session and the next (range: 65–273; mean: 147.46 ± 44.71, coefficient of variation = 30.32). These bird counts were not correlated between one data session and the next (Sandlin, 2000). Therefore, I am confident I sampled foraging behavior under a wide variety of competitive regimes.

Estimates of selectivity

I calculated s, a measure of each individual's preference, or selectivity, for rich feeders, as

$$s = (\text{time spent feeding from rich feeders})$$
$$\div (\text{time spent feeding from rich feeders}$$
$$+ \text{ time spent feeding from poor feeders}).$$

This index ranges from 0 to 1; $s = 1$ indicates exclusive use of rich feeders, $s = 0.5$ indicates equal use of rich and poor
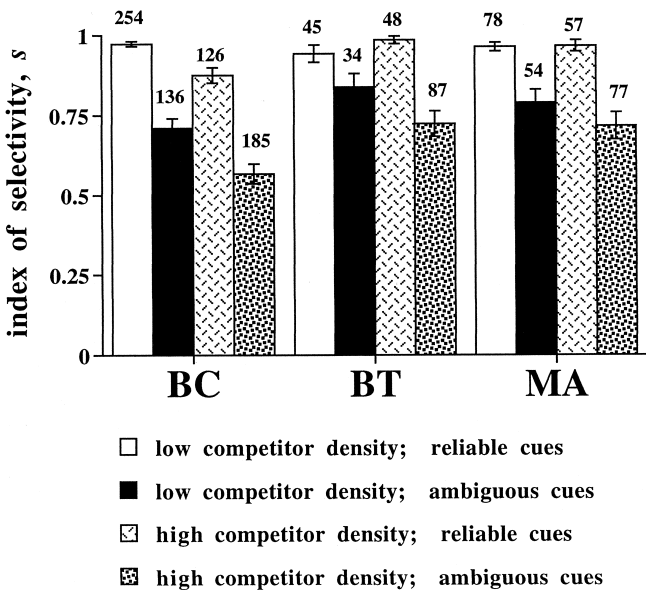
Figure 2
Mean values + SEs for *s*, the index of selectivity. Sample sizes are above each bar. Reliable cues allow the birds to predict the locations of rich feeders without sampling. Ambiguous cues do not. See text for criteria that separate data into low or high competitor density treatments. BC, black-chinned hummingbird; BT, blue-throated hummingbird; MA, magnificent hummingbird.

Table 1

Significance values from a three-way fixed factor ANOVA showing variation in the index of selectivity (*s*) and energy intake per gram per foraging bout (*e*/g)

Source	df	*s* (*p* > *F*)	*e*/g (*p* > *F*)
Competitor	1	.0061	.1647
Cue	1	< .0001	.0904
Species	2	< .0001	.0009
Competitor × cue	1	.0284	.0605
Cue × species	2	.0624	.0125
Competitor × species	2	.0260	.0037
Competitor × cue × species	2	.3887	.0023
Whole model	11	< .0001	< .0001
Total	1180		

Main treatment factors are species (black-chinned, blue-throated, or magnificent), cue type (reliable or ambiguous), and competitor density (high or low).

feeders, and *s* = 0 indicates exclusive use of poor feeders. In the context of isoleg theory, *s* measures a forager's preference for rich patches of habitat. Here, I am most concerned with population-level changes in *s* for the two subordinate species. A population's average *s* should equal 1.0 as long as foragers can withstand competitor pressures in the rich habitat. As competition forces the birds to accept trade-offs and follow an IFD, the average *s* should decrease to the point that it approximately equals 0.5. This value of *s* indicates that the subordinates have suffered sufficient costs from competition to switch to opportunistic use of both habitats. A positive relationship exists between *s* and the energy gained per unit of foraging effort (e.g., kJ/s). Therefore, *s* can also be interpreted as a measure of relative foraging efficiency. Because *s* is a proportion, I subjected it to a standard arcsine-square-root transformation before subsequent data analysis.

Predictions revisited

Prediction 1 requires *s* in all ambiguous cue treatments to be less than *s* in reliable cue treatments. Prediction 2 requires *s* at high competitor densities to be less than *s* at low densities, all other things being equal. It predicts that *s* should change from being indistinguishable from 1.0 to being indistinguishable from 0.5. Prediction 3 is an interaction of predictions 1 and 2, and says that, when competitor pressures are the same, *s* for foragers with an information deficit should be lower than that of foragers with complete information. Prediction 4 requires the two subordinate species to exhibit greater changes in *s* than the dominant species.

Figure 2 shows species-specific differences in *s* with respect to cue type and competitor density. Notice three patterns. First, birds of all species foraging with reliable cues and low competitor densities (LD) were most selective (Figure 2). The values for *s* in this case are 0.97 for BC, 0.94 for BT, and 0.96 for MA (and are indistinguishable from 1.0). All individuals foraged almost perfectly with reliable cues. This result is ex-

actly what OFT predicts for foragers with complete information, immediately renewing patches, and no travel costs between patches.

Second, in all cases, birds of each species were less selective with ambiguous cues than with reliable cues (Figure 2). This pattern of response to incomplete information is predicted by OFT. I outlined this expectation in predictions 1 and 3.

Third, for BC at high competitor densities with ambiguous cues, *s* = 0.571. This value is indistinguishable from *s* = 0.5 (H_o: *s* = 0.5: Wilcoxon signed-ranks test: *p* = .70) and shows the predicted shift in BC selectivity. This result, that competitively driven thresholds in selectivity exist, is expected from prediction 2 and corroborates those of Pimm et al. (1985). However, MAs exhibited no such shift to opportunistic foraging. Because the pattern exists for one subordinate species but not the other, prediction 4 is equally supported and refuted.

ANOVA results for individual preference

Patterns revealed in Figure 2 show that information state (cue type), competitor pressure, and the species of forager all affected selectivity. Predictions 3 and 4 lead us to expect a three-way interaction between these three treatment factors. Specifically, I expected all three species to reduce *s* in response to high competition and an information deficit, but not necessarily to the same degree. All birds should suffer from an information deficit; BCs and MAs should suffer from high competitor pressures more than BTs. Contrary to these expectations, the three-way interaction term was not significant (Table 1). However, all three two-way interactions and the three main treatment effects were significant, consistent with predictions 1 and 2.

I separated the data into smaller logical segments to more closely examine these patterns. First, to examine species-specific differences in response to competitor pressure and cue type, I analyzed *s* for each species separately. Each species responded differently to these two main factors (Table 2). Selectivity by BCs was negatively affected by both factors (Figure 2). Selectivity by BTs was affected by these main factors in combination and by cue type alone; Figure 2 shows the synergistic negative effect of both factors on *s* for male BTs. Selectivity by MAs was affected only by cue type and not by competitor pressure. This last result contradicts prediction 4 for a subordinate species and may reflect the transient nature of individual MAs (see below).

Second, I let competitor density remain constant. Two-way

Table 2

Significance values from two-way fixed factor ANOVAs for each species showing variation in the index of selectivity (s) and energy intake per gram per foraging bout (e/g)

Species	Factor	df	s (p > F)	e/g (p > F)
BC	Competitor	1	<.0001	.3806
	Cue	1	<.0001	.7095
	Competitor × cue	1	.4626	.8680
	Whole model	3	<.0001	.0042
	Total	700		
BT	Competitor	1	.4863	.6952
	Cue	1	<.0001	.9036
	Competitor × cue	1	.0405	.5964
	Whole model	3	<.0001	.5567
	Total	213		
MA	Competitor	1	.2972	.0027
	Cue	1	<.0001	.0354
	Competitor × cue	1	.8718	0.0080
	Whole model	3	<.0001	.0074
	Total	265		

Main treatment factors are cue type (reliable or ambiguous) and competitor density (high or low).

ANOVA of s in the low competitor density data revealed a cue type × species interaction ($p = .01$). This interaction indicates that, when competition is relatively low, the species responded to the information treatments in different ways. Inspection of Figure 2 reveals the source of the interaction term: with ambiguous cues, BCs suffered a greater decrease in s than the other two species. A two-way analysis of the high competitor density data revealed no significant interaction term ($p = .69$). Instead, both main treatment effects were significant (cue type: $p < .0001$; species: $p < .0001$). Therefore, when competitor densities were high, the species exhibited different selectivities (BC s was lower than BT and MA), and s depended on information state, just as prediction 4 requires.

Third, I examined s when information state remained constant. Analysis of the ambiguous selectivities with species and competitor density as treatment factors revealed no significant interaction term (species × competitor density: $p = .55$), but the main treatment effects were significant (competitor density: $p = .007$; species: $p = .001$). Analysis of the reliable-cued selectivities revealed that s differed, depending on competitor pressure and the bird species (species × competitor density: $p < .0001$). Thus, even when birds had complete information, the species responded differently to competition, a pattern expected from isoleg theory and prediction 4.

Taken together, these two-way ANOVA results strongly suggest a trade-off between competitor pressure and information. Specifically, low competitor pressures can compensate birds for the added cost of finding rich feeders in the ambiguous cue situation. Alternatively, reliable cues can compensate birds for the added cost of high competitor pressures. However, because of the drastic drop in s for BCs in the high density ambiguous situation, we also know that the species respond to these trade-offs in different ways (cf. prediction 4 above). These two-way ANOVA results also conform to the other three predictions and may offer better understanding of the complex patterns than the three-way ANOVA.

Relating selectivity to energetics

My analysis of s is based on theoretical predictions that arise from ecological and evolutionary arguments. However, analysis of selectivity per se may not provide a rigorous enough understanding of the constraints that animals actually endure.

Natural selection often acts on factors that affect survivorship. Furthermore, OFT arguments often assume the forager optimizes its rate of energy intake. I chose to study hummingbirds largely because they must meet their short-term (ca. 60 min) energy needs or they lose the ability to fly and may die (Sandlin, personal observation; see Diamond, 1990; Hixon et al., 1983; Tiebout, 1991; Wolf and Hainsworth, 1971). This energy demand closely ties a hummingbird's foraging choices to its survival and reproduction. Therefore, I converted s into a currency that might make the interpretation of such constraint-bounded behaviors easier.

Nectar extraction rates

My index of selectivity is based on the time that birds apportion to feeding at rich feeders. For hummingbirds, however, nectar extraction rate is a function of bill length (Montgomerie, 1984), and these species have different bill lengths (BC: 19.3 mm, BT: 22.6 mm, MA: 26.9 mm). Species-specific constraints on extraction rate place limits on how efficiently birds may use their time. My results (from the aviary) confirm Montgomerie's (1984) report that extraction rate is a function of bill length ($y = 3.441x - 53.609$, $R^2 = .77$, $p < .0001$). Furthermore, extraction rates differed between species (BC: 8.71 µl/s; BT: 30.37 µl/s; MA: 35.66 µl/s; one-way ANOVA: $n = 19$, df $= 2$, $F = 111.17$, $p < .0001$). This means that the time the different species spent feeding at rich feeders yielded different energetic rewards.

Montgomerie (1984) also showed that sucrose concentration can affect hummingbird extraction rate. However, I found no significant differences between extraction rates for my two sucrose concentrations (one-way ANOVA: BC: $p = 0.65$; BT: $p = 0.75$; MA: $p = 0.74$). For subsequent data analysis, I used the overall average extraction rate for each species.

Converting time into energy

How much energy does an average bird of each species acquire during an average foraging bout at a feeder board? I examined the amount of energy an individual gained during a single foraging bout by converting my time measurements (that contributed to s) into energy gain measurements. First, I determined that every milliliter of 30% sucrose contains 5.16 kJ (Weast et al., 1983). I used this equality to calculate the energy content of each microliter of rich and poor solutions (each aliquot of the rich solution contained twice the energy as the same volume of the poor solution). I then used these quantities to calculate energy gain. I know how much time each bird spent feeding from rich and poor feeders, so it was easy to convert time spent feeding into energy gain. The resulting measure, e, is simply the total energy (kJ) an individual ingested during a single foraging bout. The measure e accounts for species-specific differences in nectar extraction rates.

An individual also spends energy while it forages. Unfortunately, I could not directly calculate each bird's foraging costs because I do not know the total amount of time the birds spent hovering at a feeder board (they hover even when not feeding). Considerable variability existed in the proportion of time birds spent feeding while hovering at a feeder board (Sandlin, personal observation), so I cannot make an informed estimate of hovering cost. However, general metabolic costs scale with the mass of the individual (Calder, 1996; West et al., 1997), and flight costs relate to both mass and wing area (Calder, 1996; Carpenter et al., 1991; Feinsinger et al., 1979). BTs are significantly larger than MAs (BT: 8.28 ± 0.44 g; MA: 7.9 ± 0.49 g; $t = 8.06$, df $= 86$, $p < .0001$), and both species are considerably larger than BCs (3.18 ± 0.22 g) (mass
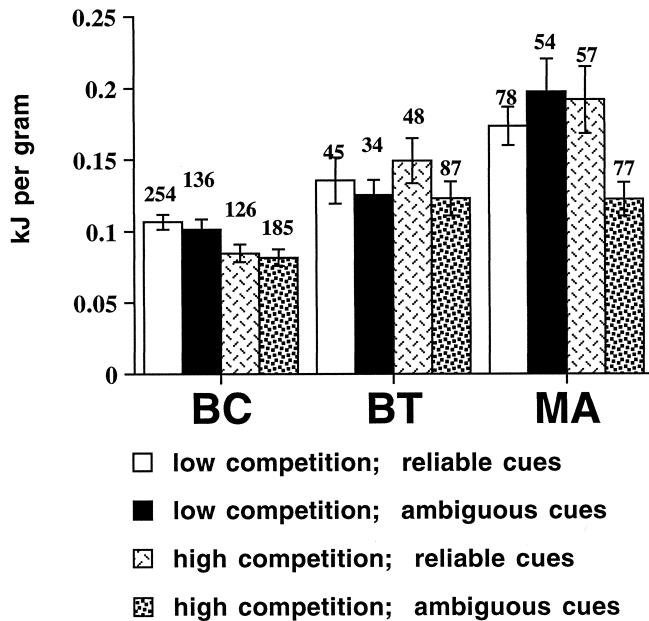
Figure 3
Mean values + SEs for total energy (kJ) intake per gram of bird (*e*/g) by individual male hummingbird during a single foraging bout. BC = black-chinned hummingbird; BT = blue-throated hummingbird; MA = magnificent hummingbird.

measurements from Powers DR, unpublished data). In addition, the species differ in wing morphologies. For example, BTs and MAs differ in wing chord length (BT > MA), but not wing depth (chord: $p < .0001$; depth: $p = .24$). We might be tempted to incorporate wing disc loadings here (see Epting and Casey, 1973; Feinsinger and Chaplin, 1975); however, power output can change while a bird hovers, as can its metabolic rate (see Feinsinger and Chaplin, 1975, and references therein), making the effect of wing disc loading on estimates of energy expenditure somewhat uncertain. Moreover, recent work on this problem by Wells (1993) showed that flight costs do not greatly differ between hummingbirds of similar body mass but dissimilar wing areas. Therefore, I assumed that a hummingbird's costs while foraging relate most closely to its body mass.

I adjusted each bird's calculated energy gain by dividing *e* by the average mass for males of its species. This new measure is the energy gain per gram of bird (kJ/g) during an average foraging bout (Figure 3). It reflects an estimate of the birds' flight costs as well as their immediate energy benefits from foraging. I use *e*/g as shorthand notation for this estimate.

ANOVA results for energy gain per gram

Three-way ANOVA (same design as for *s* above) of *e*/g revealed the predicted significant three-way interaction (Table 1). Therefore, in terms of *e*/g per foraging bout, each species responded to competition differently, depending on cue type. Two-way ANOVAs (as above) also showed different responses between the species (Table 2). In addition, each species' pattern of response to competitor density and cue type for *e*/g was different from its pattern of response for *s*. For BCs, *e*/g decreased only in response to high competitor densities and not cue type (one-way ANOVA for BC competitor density: $p = .0004$; Figure 3). There were no differences in BT energy intake per foraging bout, regardless of cue type or competitor density. MAs suffered reduced *e*/g only when they experi-

enced high competitor density coupled with an information deficit (Table 2, Figure 3).

DISCUSSION

Information and selectivity

Foraging information strongly influences an animal's foraging efficiency (Bateson and Kacelnik, 1996; Krebs and Inman, 1992; Mitchell, 1989; Valone, 1991, 1992). I have confirmed that competitor pressures also affect hummingbird foraging decisions (see Pimm et al., 1985; Rosenzweig, 1986). Competition must exert a strong force on hummingbird behaviors because, in the present study, their responses occurred at a short time scale (ca. 3–8 s) and a small spatial scale (ca. 10 cm). But competitor pressures were much more severe when these animals foraged with incomplete information (ambiguous cues).

Selectivity, the proportion of rich food in the diet, indicates an animal's degree of preference for rich food. Changes in selectivity (*s*) reflect trade-offs between foraging efficiency and other constraints. Hummingbirds that enjoyed low competitor densities (LD) used reliable cues to forage almost perfectly (Figure 2). Therefore, a decrease in *s* reflects, at least in part, the energetic price a bird paid to forage with either high competitor densities (HD), an information deficit, or a combination of these two factors. All three species showed a decrease in *s* with a decrease in their information state. Although they responded further to competitor pressures, only the BC exhibited the predicted (by isoleg theory) drastic switch in *s* in the HD ambiguous situation.

Information modulates density-dependent habitat selection in hummingbirds

The measure of energetic intake per gram per foraging bout, *e*/g (Figure 3), revealed different aspects of hummingbird decision making than did the measure of selectivity, *s* (Figure 2). To understand these differences, let us compare and contrast the two measures (see Table 2). BCs reduced their *e*/g in response to high competitor densities. However, at either competitor pressure, *e*/g was the same for both cue treatments (Figure 3). This result is predicted by IFD theory and usually assumed in experimental studies. We rarely see empirical confirmation that animals trade-off two currencies to gain the same fitness. In this case, male BCs gained the same total amount of energy during a single foraging bout, regardless of cue type (Figure 3, Table 2). This means that the birds compensated for their reduced foraging efficiency (because of an information deficit; Figure 2) by spending more time feeding at poor feeders than they did when they had complete information.

Spending additional time hovering at poor feeders caused birds to suffer proportionally higher flight costs than they would if feeding at rich feeders. The costs of spending more time at feeder boards are at least fourfold: (1) added flight cost for hovering longer at the feeder board, (2) missed opportunity costs for not feeding at rich feeders and not doing other activities, (3) predation risk (probably very low during the day), and (4) added risk of conflict with another hummingbird. This last cost must be real for BCs because they experienced reduced *e*/g in the HD situation relative to the LD situation (Figure 3). These results show the true nature of BCs' subordinate status in this guild. In other hummingbird guilds, small-bodied species sometimes show flexibility in their roles within the community (Feinsinger and Colwell, 1978). Perhaps BCs exhibited such flexibility by switching to opportunistic foraging.

BT males gained the same e/g regardless of cue type or competitor density (Figure 3). We know that BTs suffered reduced foraging efficiency in the ambiguous cue × HD situation (Table 2, Figure 2). But, just as BCs did, male BTs paid the extra costs associated with foraging longer (relative to other situations) at ambiguously cued poor feeders to obtain the same e/g (Figure 3). Notice that, even though BT s decreased, it stayed as high or higher than that for the other two species in every case (Figure 2). Therefore, via aggressive behavior, the BTs dominated the others and controlled distribution of the food resources (see Lyon et al., 1977; Pimm et al., 1985), or they controlled the amount of time available to use rich feeders (Pimm, 1978; Sandlin, 2000).

Like BTs and BCs with low competitor pressures, MAs compensated for an information deficit by feeding longer at poor feeders (than they did with reliable cues) to get the same amount of energy they would enjoy with complete information (Figure 3). Unlike the BCs and BTs, however, male MAs did not spend a greater proportion of their time feeding at poor feeders in the HD situation. They spent less time feeding and, therefore, got significantly less energy per foraging bout in that case.

Magnificent hummingbirds

Magnificent hummingbirds have puzzled many scientists because they do not seem to fit nicely into any given category in hummingbird communities (see Colwell, 1973; Feinsinger and Colwell, 1978; Mitchell, 1989; Pimm, 1978; Powers, 1996; Sandlin, 2000; Van Hook et al., in preparation; Wolf et al., 1976). Why might MAs respond differently to competitor pressures than the other two species? This species, called an ''interstitial species'' by Colwell (1973), behaves differently in different competitive situations. It holds territories in the highlands of central Mexico, although it remains subordinate to BTs there (Johnsgard, 1997; Lyon, 1976; Wolf et al., 1976). In the Chiricahua Mountains of southeastern Arizona, though, this species is a ''high-reward trapliner'' (Feinsinger and Colwell, 1978; Powers, 1996) and not a territorialist. This traplining strategy seems to allow MAs a degree of foraging flexibility not available to its competitors in southeastern Arizona (Van Hook et al., in preparation).

Lyon (1976) found high turnover among nonterritorial individuals (of several species) in Mexico. Examination of my focal observations of marked males suggests different trends in the visitation rates of individuals differ between the species. Individual MAs tended to be less likely than BCs or BTs to contribute multiple times to my data (mean number of visits per individual in entire data set: BC: 7.28 ± 8.75, BT: 4.08 ± 5.58, MA: 3.81 ± 4.83). In addition, more focal MAs were unmarked than the other two species (25.5% of MA observations were on unmarked birds, while 10.5% of BC and 13.8% of BT were unmarked birds). My results seem to punctuate the truly ephemeral nature of any individual MA's membership in the competitive milieu.

Because individual MAs probably range widely throughout the canyons, individuals suffering from high competitor pressures and incomplete information at feeder boards may have abandoned the area to continue along their trapline. However, during the dry season, my feeder boards were likely the major sources of quick carbohydrate energy. Therefore, I propose another interpretation of the observed MA response to high competitor densities and ambiguous cues.

Until now, I have restricted the discussion to behavioral switches between two alternatives (rich or poor feeders). Yet MAs may switch to another source of energy: arthropods (Powers, 1996; Van Hook et al., in preparation). In fact, I speculate that MAs might eat more arthropods than either of the other two hummingbird species (see Feinsinger and Colwell, 1978, for characteristics of high-reward trapliners; Powers, 1996, and references therein). The secondary habitat for MAs may contain patches of arthropods, rather than patches of low-reward sucrose. Results in Figures 2 and 3 are consistent with my assertion that MAs may switch to some other habitat. This scenario is similar to Rosenzweig and Abramsky's (1986) discovery that two gerbil species share a primary habitat, but each uses a unique secondary habitat. It also agrees with Feinsinger and Colwell's (1978) assertion that MAs (although in another multispecies assemblage) restrict themselves to the highest nectar concentrations available. Finally, if this species exhibits a differentially high use of arthropods, that difference may explain why it enjoys the freedom of a trapliner, rather than the confinement and energy demands of territorial defense of nectar resources (Lyon, 1976; Lyon et al., 1977; Stiles and Wolf, 1970; Wolf et al., 1976). I discuss this idea in more detail elsewhere (Sandlin, 2000).

Theory revisited

Ideal free distribution theory predicts that animals will trade-off various costs so they obtain the same fitness in two different habitats. Rich and poor feeders provide patches of different habitats (Stephens and Krebs, 1986). For hummingbirds, average energy gain seems to serve as an excellent surrogate for fitness. Results here confirm that hummingbirds follow ideal free distributions with respect to feeder quality (Figure 3).

Rosenzweig and Abramsky (1997) discuss shared-preference systems in which there is asymmetric competition between the species. In shared-preference systems, both species prefer one habitat but can profitably use another (Rosenzweig, 1979). One species, the dominant one, cannot tolerate energy losses (due to use of the second habitat) as well as the subordinate species can (see also Rosenzweig, 1987). Therefore, Rosenzweig and Abramsky (1997) call the dominant species the ''intolerant'' one, while the subordinate species is labeled the ''tolerant'' one. These labels apply especially well to hummingbirds. Dominant BTs reduced s in response to ambiguous cues and high competitor densities but never tolerated a reduction in e/g. Subordinate BCs tolerated a reduction in both s and e/g in response to high competition and incomplete information. Subordinate MAs reduced s only in response to incomplete information. The MAs tolerated reduced e/g (from nectar feeding) in response to a combination of ambiguous cues and high competitor densities. Each species' response reflects its place in the hummingbird guild. As discussed above, the results also suggest that the secondary habitat for MAs may differ from that for BCs and BTs (see Feinsinger and Colwell, 1978; Rosenzweig and Abramsky, 1996; Sandlin, 2000; Van Hook et al., in preparation).

In summary, the observed differences in hummingbird foraging responses to competition, cue type, and resource subdivision suggest that information may be important in regulating not only individual foraging efficiency and competitive interactions but also species coexistence for these three hummingbird species. Foraging behavior provides a good indicator of niche breadth because habitat selection usually reflects the animal's food requirements (see Perry and Pianka, 1997; Schmitz, 1997). An animal's experiences (e.g., via learning) can also strongly influence its foraging behavior (e.g., Mitchell, 1989; Sandlin, 1999; Valone, 1991, 1992). Until now, no one has attempted to carry out an integrative study that links learned behavior to interactive phenomena involving several species that coexist via density-dependent habitat selection. Complete information allowed hummingbirds to better withstand the negative effects of competition. This allowed the

subordinate species to forage more efficiently or gain more energy than they would without information. These results should be general for species that use information to choose among resources. Therefore, the ability to learn and use information from the environment may allow more species to coexist than could otherwise exploit a single type of resource.

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