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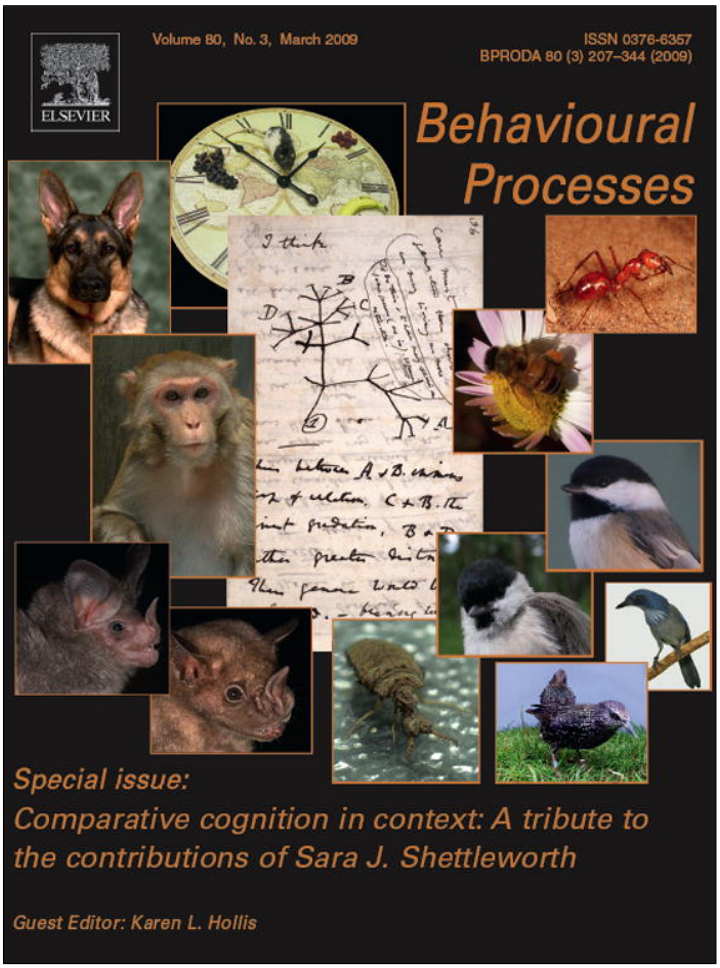

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Use of spatial and colour cues by foraging pine siskins (*Carduelis pinus*): A field study

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ABSTRACT

Pine siskins (*Carduelis pinus*) frequently forage at known high quality food supplies such as backyard feeders. In this field study, pine siskins visited backyard feeders of differing colour and spatial position. The three feeders contained varying amounts of food in a ratio of 3:2:1. The birds quickly distributed their visits in this ratio to the three feeders. During unbaited tests, two feeders on a given day had their positions swapped. The siskins appeared to primarily use both large-scale spatial or distal cues when foraging as well as local colour cues.

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1. Introduction

Most research on avian cue use during foraging has been performed either in lab enclosures using operant tests (e.g. Brodbeck and Shettleworth, 1995) or in larger enclosures, such as aviaries, where captured birds are free to fly around (e.g. Brodbeck, 1994). These experimental designs allow control and manipulation of specific visual cues available to birds and are generally the most productive conditions under which to study avian learning and memory (Healy and Hurly, 2004). Nevertheless, research within enclosures may not illustrate how such cues might function for naturally foraging birds in 'real-life', field situations.

Exceptions to this lack of field data are recent studies performed on free-ranging rufous hummingbirds (*Selasphorus rufus*) feeding on nectar-containing artificial flowers (e.g. Healy and Hurly, 1995) and similar research by Irwin (2000) on rufous and broad-tailed (*S. platycercus*) hummingbirds. These studies revealed that individuals remembered and avoided visiting flowers that they had recently emptied (Healy and Hurly, 1995), remembered the locations of nectar-containing and empty flowers after a single brief visit (Hurly, 1996), and may have relied more on distal cues than proximal cues when returning to rewarding flowers (Hurly and Healy, 1996); but may be able to use nectar volume itself as an additional proximate cue in the absence of both large-scale spatial and other simple proximal cues (Irwin, 2000).

In food-storing birds, returning to a cache location for retrieval may require attention to at least two types of visual cues which may be used sequentially or concurrently (Brodbeck, 1994; Brodbeck and Shettleworth, 1995). The bird may remember proximal characteristics which are closely associated with the food source, such as colour, pattern, or shape of the immediate surroundings. Alternatively, the animal may use more distal or spatial cues, and thus return to the site using memory of the site position with respect to large-scale landmarks.

Herz et al. (1994) investigated the use of visual cues by food-storing black-capped chickadees (*Poecile atricapilla*) to re-locate scattered caches in a laboratory enclosure. In the presence of proximal ('local') cues at cache sites and distal ('global') cues on the walls of the enclosure, the chickadees stored sunflower seeds in the artificial trees provided. Removal of distal cues prior to cache recovery significantly reduced the chickadees' recovery accuracy, whereas removal of proximal cues did not affect recovery accuracy. In other tests with the proximal cues removed entirely and distal cues rotated around the walls of the enclosure, the birds tended to search for food in artificial tree positions relative to the distal cues. Similar studies suggest that birds which store and recover food primarily use distal spatial cues observed during caching rather than colour or pattern cues (e.g. Vander Wall, 1982; Brodbeck, 1994).

Why might food-storing birds selectively use larger-scale spatial cues when non-spatial cues are also available and potentially relevant for remembering storage locations? Preferential use of distal rather than proximal cues most likely reflects the relative permanency of spatial cues and the potential superiority of spatial memory during cache relocation (Shettleworth, 2003). Larger-scale landmarks are generally more temporally stable than are local cues:

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the colours of leaves change with the seasons, snow cover comes and goes, and animal inhabitants make adjustments to their immediate surroundings. However, the position of the cache relative to nearby hills and streams does not change. Thus, a preference for proximal over local cues may be a general characteristic of many species that need to rely heavily on spatial memory in the wild (Healy and Hurly, 1998).

Differences in cue use have been found between storing and non-storing birds such that storers preferentially use distal cues over local cues whereas non-storers use both sets of cues equally (Brodbeck, 1994; Brodbeck and Shettleworth, 1995; Clayton and Krebs, 1994). This pattern of differences has been attributed to the necessity for food-storing birds to accurately remember cache locations. However, other tests of cue use by non-storers such as pigeons (e.g. Brodbeck et al., 1997; Wilkie et al., 1985) have found that spatial cues overshadow local cues such as colour.

Pine siskins (*Carduelis pinus*) are common in mountainous regions of northern North America such as British Columbia (Herbers et al., 2004) and western Newfoundland. These birds seem to migrate based on food supply (Dawson, 1997; Herbers et al., 2004). Siskins then ought to be quite sensitive to food density and there may have been selective pressure on them to accurately remember food locations as there has been on food storers. However, research on pine siskin memory is non-existent. In this paper we observed the use of distal spatial and proximal colour cues by wild, free-ranging pine siskins feeding at backyard feeders.

2. Methods

2.1. Study species and site

Pine siskins are found in open coniferous and mixed wood regions throughout North America, and reside most years in the boreal forests of insular Newfoundland (Dawson, 1997). They feed, often in large flocks, primarily on buds and seeds of birches (*Betula* spp.), alders (*Alnus* spp.), pines (*Pinus* spp.), and other trees, but will readily come to backyard feeders (Dawson, 1997). We conducted this research from late May through early August, 2003 in a small residential garden (approximately 750 m^2) located at the edge of a large forested area in the town of Pasadena, Newfoundland and Labrador, Canada. Three gazebo-type feeders with clear plastic sides (approximately 1000 ml volume) were mounted on top of three separate 1.75 m high wooden poles and positioned 2 m apart in a line in the garden. The feeders (but not the clear plastic sides) were painted one of three colours: green, red or yellow. The positions of the feeders were fixed in the initial training phase such that, when viewed by the observer, the left feeder was green, the middle feeder was red and the right feeder was yellow. Distinctive large-scale spatial cues or prominent 'landmarks' within the garden included the house, a shed, a diagonal clothesline, several trees and a flower garden.

2.2. Experimental procedures

2.2.1. Training and testing of training

To test whether pine siskins would modify their foraging behaviour in response to differing amounts of food in each feeder, black oil sunflower seeds were supplied and maintained throughout the summer at a 3:2:1 ratio in the green, red, and yellow (left, middle and right) feeders, respectively. During data collection, the feeders were monitored for 90 min at a time, for 3 h total daily, in the morning and afternoon. The number of pine siskins visiting each feeder during this time period was recorded with a visit defined as a pine siskin landing on the perch which encircled the gazebo-shaped feeder. Individuals frequently landed on the feeders multiple times

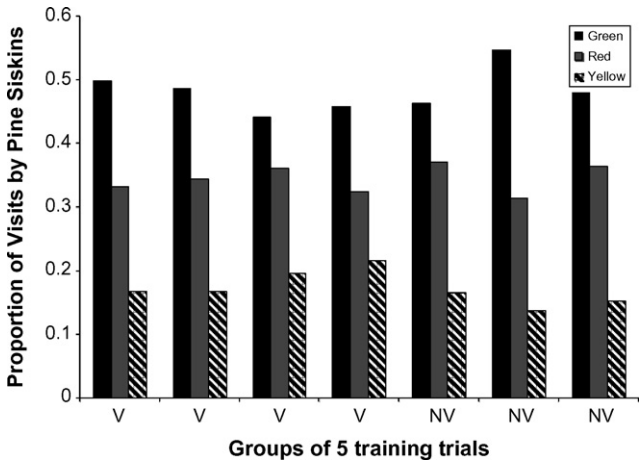

Fig. 1. Proportion of pine siskin visits to the green (left), red (middle), and yellow (right) feeder, summarized in groups of five 90 min training trials. The 3:2:1 ratio of black oil sunflower seeds in the green (left), red (middle), and yellow (right) feeders, respectively, were visible to the pine siskins in first four groups of trials (V) but not visible in the last three groups of trials (NV).

throughout the observation period, but no birds were individually marked so each visit was counted separately. All behavioural observations were collected by the first author and took place through a nearby house window (about 7.5 m distant) so as to minimize disturbance to the foraging songbirds.

Training of the birds to the amount of food available at each feeder was achieved very quickly. Although none of the feeders were significantly depleted of food during any 90 min observation period, the proportion of pine siskins visiting each of the feeders was directly related to the quantity of seed available at the start of each session (Fig. 1). This response apparently reflected the pine siskins' ability to view the quantity of seed in each feeder and was consistently maintained from almost immediately after the training experiment began until the initial training phase was completed (22 May through 2 June).

We next tested whether pine siskins would continue to distribute feeding visits in this approximate 3:2:1 ratio when the amount of seed in each feeder was no longer visible. From 3 to 9 June we provided seed to the feeders in a 3:2:1 ratio but blocked the view of the contents of the feeders with opaque panels which matched the colour of the feeder. Birds continued to visit the feeders at an approximate 3:2:1 ratio (Fig. 1) showing that the siskins had learned which feeder contained the most abundant supply of food and continued to favour the feeders as before.

2.3. Examining the use of spatial versus visual cues

By switching the position of each coloured feeder, we then tested whether the pine siskins associated relative food supply with the *location* of the feeder or the *colour* of the feeder. For example, the green and red feeders were switched so the (from left to right) green, red, yellow (GRY) array became (from left to right) red, green, yellow (RGY). In this example, if the pine siskins had associated the largest food supply with the *position* it had been in they might feed mostly at the red feeder, but if they associated the largest food supply with the *colour* (green) of the feeder which had contained the most seed, the birds would theoretically follow the green feeder to the center of the array and attempt to feed mostly in that position. All six possible combinations of the three colours were tested twice each; however the YRG array was tested an additional four times at the end of the experiment for reasons presented in Section 3. All tests were unbaited and so the feeders were empty during the entire 90 min test of each array. Feeders were switched from the

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original training configuration (from left to right, GRY) and emptied of seed only immediately before testing began. After each 90 min test phase, the feeders were immediately returned to the original (from left to right GRY) configuration and seed was replaced and maintained in the original 3:2:1 ratio. Between test sessions the food density was returned to the 3:2:1 ratio and no other testing was done until feeder visits returned to the 3:2:1 ratio observed in training for at least two consecutive 90 min observation periods to ensure they continued to respond to the original distribution. Aside from the initial testing, at no time were the coloured panels ever removed to reveal the quantity of seed in each feeder.

2.4. Statistical analyses

The null hypothesis (H_o) was that the pine siskins would not follow the moving colours but instead continue to forage at the feeders in the same ratio created by training. Therefore, the alternative hypothesis (H_1) was that the pine siskins would follow the colours, and thus the visitation rate would change from the expected near 3:2:1 ratio based on training. Chi square goodness-of-fit analyses were performed on all data with an alpha level of 0.05.

3. Results

During training, when seed was not visible (3–9 June), the distribution of pine siskin visits among baited feeders in the original, from left to right GRY array was 50.0% at green, 35.2% at red, and 14.8% at yellow (Fig. 2). Because the feeders remained covered with panels to block the view of any contained seed (none) for the entirety of testing, only the observational data collected during these training sessions where the feeders were covered were used in calculating expected values.

For four of the six different combinations of feeder colour locations there was no significant difference between observed visitation rates and those expected based on training (Table 1). Thus, location rather than colour cue appeared to be most important for determining visitation rates to the three feeders (Fig. 3). However, in both the YRG and RYG arrays, the distribution of pine siskin visits was significantly different from our expected values and it appeared that colour cues may have offset the information available to siskins from locational cues. Further testing of the YRG array confirmed a significant difference in the response of birds from that expected based on training (Table 1).

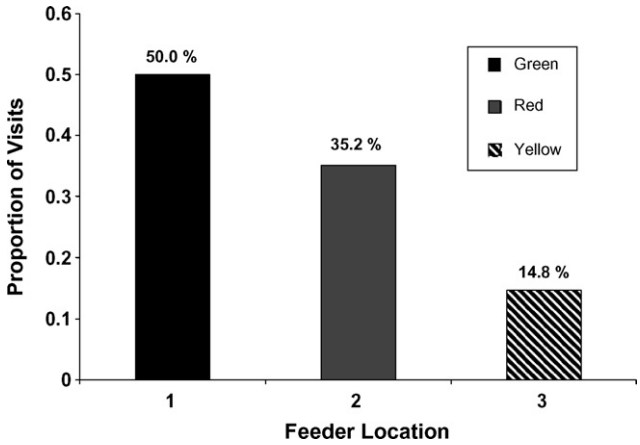

Fig. 2. Summary of the proportion of visits by pine siskins at each of the feeder colours in the original green, red, yellow feeder array containing 3:2:1 ratio of black oil sunflower seed, respectively. Seed in each feeder is not visible.

4. Discussion

While pine siskins seem to preferentially use large-scale spatial cues to locate desirable food supplies, they will also incorporate use of local colour cues. When the green feeder, which was the

Table 1
Observed number of visits per trial, and in total, by pine siskins at each feeder location during each 90 min test run. Expected values at each spatial position were derived from the observed distribution of pine siskin visits among feeders when seed was in a 3:2:1 ratio but not visible. Also presented are associated chi square and *P*-values (df = 2) based on testing the sums from the two trials.

Colour array	Trial	Observed			Expected values			X^2	*P*
		Visits to spatial position			Spatial position				
		1	2	3	1	2	3		
GRY	1	38	21	26					
	2	24	25	3	68.50	48.22	20.27	4.473	>0.100
	Sum	62	46	29					
GYR	1	33	11	7					
	2	9	15	12	43.50	30.62	12.87	3.663	>0.100
	Sum	42	26	19					
RGY	1	30	20	8					
	2	44	41	24	83.50	58.78	24.71	3.311	>0.100
	Sum	74	61	32					
YGR	1	20	17	9					
	2	21	13	9	44.50	31.32	13.17	2.101	>0.100
	Sum	41	30	18					
RYG	1	40	30	28					
	2	37	27	30	96.00	67.58	28.41	36.218	<0.001
	Sum	77	57	58					
YRG	1	14	21	28					
	2	21	18	5	53.50	37.66	15.83	25.048	<0.001
	Sum	35	39	33					
YRG (testing mirror)	1	20	15	3					
	2	16	20	34					
	3	20	25	23	137.00	96.44	40.55	48.725	<0.001
	4	40	33	25					
	Sum	96	93	85					

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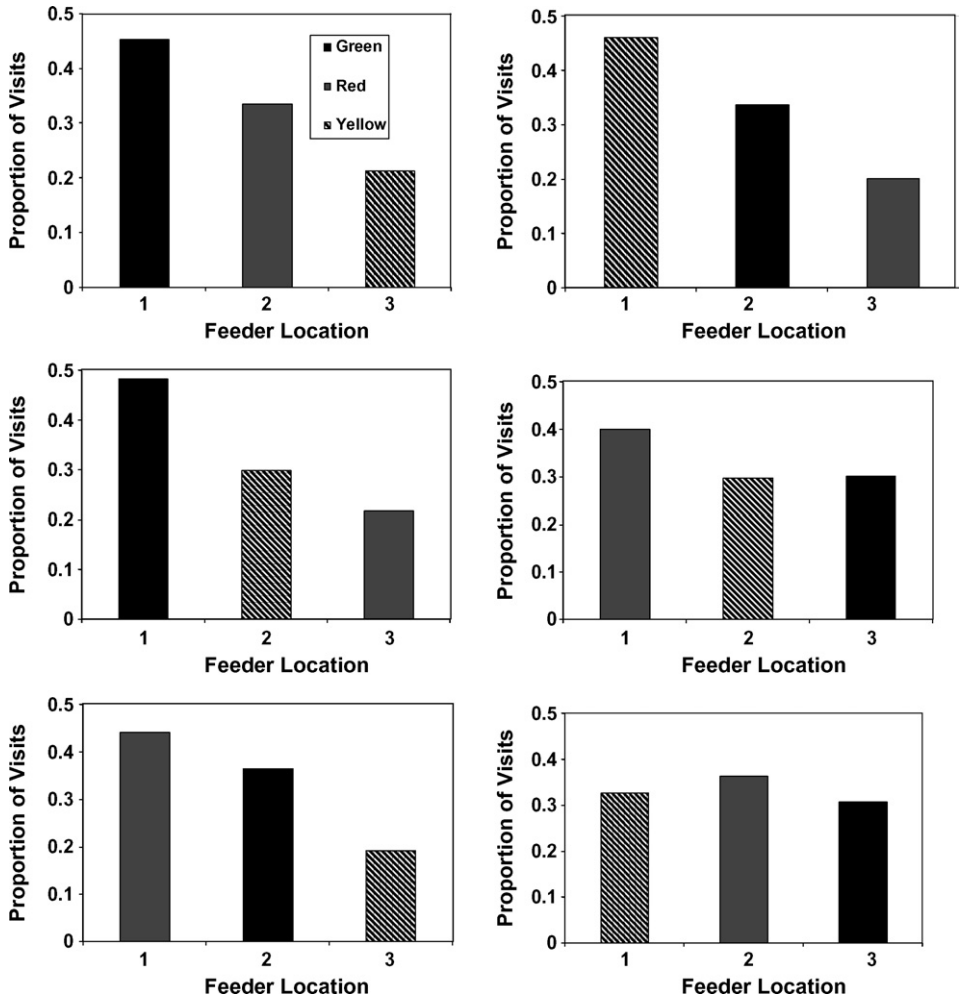

Fig. 3. Proportion of pine siskin visits at each unbaited feeder location for a 90-min observation period in which feeder colours have been switched; each colour array graph summarizes two individual test sessions. Left to right feeder positions in the array are as follows, column 1: GRY, GYR, RGY, column 2 YGR, RYG YRG.

feeder with the most food during training, was either in the leftmost (GRY or GYR) or middle position ((RGY or YGR), the birds visited the left, middle and right feeders in a ration of 3:2:1 just as they had done in training. These results agree with previous laboratory and field studies (see Section 1) which emphasize the reliance of various bird species on spatial cues during re-location of food supplies. However for both the (left to right) RYG and YRG feeder arrays, the siskins distributed themselves among the feeders in a ratio which was significantly different from the familiar 3:2:1 ratio.

In the (left to right) RYG array, birds continued to visit the position that during training had the most food (left) most frequently, but visited the spatial position that during training had the least food (right) much more frequently than in training trials. With dozens of pine siskins often present at any one time, perhaps some of the birds continued to rely on spatial cues while others followed the green colour to the poor spatial position; variation in response to cues may have existed among individuals, and some were observed visiting the leftmost feeder first then proceeding to another of the two feeders. This varying cue use between individuals would lead to the roughly equal visitation rate in the (left to right) YRG test. However, response to the (left to right) YRG colour array reveals an additional consideration: this array was simply a mirror of the GRY array to which the birds were trained. Thus, birds may have received conflicting cues and ignored the large-scale spatial cue, using instead the local colour cue to guide their foraging activity. It seems that pine siskins incorporate the use of both large-scale spatial and local colour cues while locating food in birdfeeders.

Pine siskins often forage in urban and suburban environments, where bird feeders are common. Such feeders could be considered as a renewable food resource that replenishes with moderate consistency. The dependability and predictability of such feeders might be likened to stored food to which pine siskins may repeatedly return to exploit. Studies have shown that food storers (e.g. black-capped chickadee; marsh tit, *Parus palustris*; European jay, *Garrulus glandarius*) prefer to use larger-scale spatial rather than local cues such as colour and shape to return to food locations, whereas non-storers (e.g. dark-eyed junco, *Junco hyemalis*; blue tit, *Parus caeruleus*; jackdaw, *Corvus monedula*) divide their preferences between these two cue types (e.g. Brodbeck, 1994; Clayton and Krebs, 1994; Brodbeck and Shettleworth, 1995; Shettleworth and Westwood, 2002). Thus, although pine siskins do not store food, selection might have favoured those individuals that developed the ability to remember and re-locate these dispersed but predictable food sources using stable large-scale spatial cues, as are preferred by food-storing birds.

Because pine siskins are typically nomadic and travel from place to place in association with food availability (Dawson, 1997; Herbers et al., 2004), it follows that there may have been selective pressure to remember as many cues when visiting food sites. Ours is the first study of memory in this species. While a field study is not

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an ideal preparation for studying cue use, the data presented here suggest that pine siskins warrant further study in the laboratory.

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