

SEARCH-PATH CHARACTERISTICS OF FORAGING RUDDY DUCKS

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ABSTRACT.—I analyzed the search behavior of 6 Ruddy Ducks (*Oxyura jamaicensis*) foraging on patchily distributed prey in a large aquarium. When searching for randomly placed food patches, Ruddy Ducks sampled previously profitable sites before investigating other areas more frequently than would be expected by chance. Revisiting previously profitable foraging sites may be important when exploiting a patchy food resource with prey densities that are likely to be quickly replenished after having been exploited. I also analyzed search paths of birds before and after they encountered prey and in low- (50 prey) and high- (250 prey) density patches. Search paths in food patches were longer in length and duration, had a lower velocity, and were more sinuous than in areas devoid of food. These search-path characteristics enable predators to locate and exploit patchily distributed food more efficiently than random search. Search-path length was similar in low- and high-density patches, but search-path duration was shorter in low-density patches in 5 of 6 birds. Search-path velocity was faster in low-density patches in 4 of 6 birds. Search-path sinuosity did not differ between low- and high-density patches. The differences in search-path characteristics between patches with different prey densities may be related to handling time of the food items. *Received 22 January 1988, accepted 2 August 1988.*

MANY predators consume prey that occur in patches of variable quality. The search behavior a predator should use to exploit patchily distributed food has received much attention in the optimal foraging literature (for reviews, see Krebs and Cowie 1976, Pyke et al. 1977, Krebs 1978, Krebs et al. 1983, Pyke 1984). The rationale of optimal foraging theory is that foraging efficiency and fitness are positively correlated. Foraging behavior is "efficient" when a predator obtains a rate of net energy intake that is greater than that achieved by random foraging (Sih 1982); therefore, a predator maximizing its foraging efficiency also maximizes its fitness.

To forage efficiently, a predator searching for patchily distributed food should use behaviors that vary with the probability of locating prey. Until a prey item is located, a predator should search superficially through a potential feeding site and avoid expending potentially unprofitable effort in areas previously searched unsuccessfully. Once a prey item is located, more food is likely to be found nearby because of the patchy prey distribution. Then the predator should

concentrate its foraging effort in the general area that food was located originally. Thus, after finding a prey item, the search path should become "meandering" or sinuous. This behavior has been termed "area-restricted" or "area-concentrated" search (Tinbergen et al. 1967, Croze 1970, Curio 1976) and has been observed in studies over a wide taxonomic range (e.g. Zach and Falls 1976a, b; Bond 1980; Rabe et al. 1983; Kohler 1984).

Ruddy ducks (*Oxyura jamaicensis*) forage by diving beneath the water surface and consuming benthic invertebrates, primarily chironomid (Family: Chironomidae) larvae, but also amphipods (Order: Amphipoda) and snails (Order: Gastropoda) (Siegfried 1973, Tome 1981). These prey are patchily distributed in the wetland substrate or on clumps of subsurface aquatic vegetation (Flannagan 1970, Oliver 1971, Tome 1981). The foraging behavior of Ruddy Ducks suggests that they locate a patch of prey, forage within the patch until it is depleted, and then search for another food patch (Tome 1988). When used in this context, "depleted" refers to a predator reducing the density of prey in a patch below some acceptable threshold (see Krebs 1978).

Female Ruddy Ducks must consume 5,000-

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8,000 chironomid larvae per hour spent feeding (Tome 1981) to meet daily energy and nutritional requirements during reproduction. These birds forage in wetlands with high turbidity and consume prey that are frequently found below the substrate surface. Consequently, visual location of prey is not possible and observations of Ruddy Duck foraging behavior in aquariums indicate that prey detection is primarily tactile (Tome and Wrubleski 1988).

The search behavior of birds that forage beneath the water surface has not been studied. I performed 2 experiments designed to analyze the search behavior of Ruddy Ducks. The objectives of the experiments were to determine if the foraging Ruddy Ducks remembered the location of a food patch that had been profitable previously, to compare search-path characteristics before and after the birds located prey, and to determine if search-path characteristics differed between low- and high-density food patches.

METHODS

I conducted the experiments in a concrete and glass aquarium that was 5-m long, 2-m wide, and 2-m deep. Three 1-m² plate-glass windows were located on one side and a single 1-m² window was located on one end. The windows permitted observation and filming of birds underwater. The substrate consisted of a 4 × 4 array of 1.0-m long, 0.5-m wide, and 0.1-m deep wooden trays filled with 6 cm of sand. These trays could be removed from the aquarium and replaced with trays that had food items hidden in the sand. Depending on the experiment being conducted, I designated one or two of the trays as food patches which contained a specified density of prey. I will refer to trays that contained food as "food patches" and trays devoid of food as "empty patches." Also, I will always present the tray location in the form "tray 1-2" where "1" and "2" are the row and column number, respectively, in which the tray was positioned.

Six Ruddy Ducks (4 males, 2 females) were selected randomly from the 45 that were available for the experiments. They were hatched from eggs collected in the wild and reared in captivity at Delta Waterfowl and Wetlands Research Station, Portage la Prairie, Manitoba, Canada, following techniques described by Ward and Batt (1973). First generation hatchery birds were used to minimize experimental bias that could result from observing descendants of birds reared in captivity for many generations. Individuals were named after their leg-band colors and will subsequently be referred to as Al (female aluminum), Blue, Green, Fred (female red), Red, and Yellow. These birds were housed in the aquarium for several weeks before

the experiments started to become accustomed to the environment.

Although wild Ruddy Ducks feed primarily on chironomid larvae, I could not obtain adequate numbers of this prey for my experiments; consequently, I substituted wheat grains for prey. Experimental birds had fed on wheat because it was contained in their daily maintenance diet. Several times I observed the birds foraging on both chironomid larvae and wheat grains; they did not exhibit obvious behavioral differences when consuming the two food types. Between experiments, birds were fed an *ad libitum* ration of wheat, commercial duck food, grit, and vitamins. Food was withheld from the birds for approximately 10 h before each trial.

The procedure for placing wheat grains in food patches was the same in both experiments. First, I counted out the appropriate number to be placed in the extra trays that were used as food patches for all experiments on that day. Before I placed the grains in a tray, I removed the top 1 cm of sand. The wheat grains were scattered evenly on the surface of the remaining sand. Sand that had been removed was then replaced carefully over the "prey" items so that they were not disturbed.

Before the experiments began, I conducted 7 "conditioning trials" to train the birds to find food in the aquarium substrate (before my experiments, they had fed in trays floating on the water surface). The procedures followed in the conditioning and experimental trials were both the same to the extent that 1 bird foraged in the aquarium at a time, 1 trial per bird per day was conducted, and as soon as the bird left the food patch to forage elsewhere in the array of trays, the trial was ended and the bird removed from the aquarium. The food patch was always located in tray 1-2.

In experiment 1, a single food tray was placed randomly within the 4 × 4 array of trays each morning, with the restriction that the food tray could not be located in the same position on 2 consecutive days. I observed each bird's search behavior (see below) in empty patches and in food patches containing 150 items. I also recorded the sequence in which patches were visited to determine whether the birds searched first in the tray where they had found food on the previous day. I conducted 1 trial per bird per day for 5 consecutive days.

In experiment 2, I recorded search-path characteristics in patches of 50 and 250 items. In these trials, I always placed the food patches in trays 1-2 and 4-2; both patch types were present in the aquarium in each trial. Five trials per bird were conducted.

Before each trial, the Ruddy Ducks were moved into a holding area adjacent to the aquarium where they could not see the placement of the food tray. The empty tray in the location designated as a food patch was removed and replaced with one that contained food. One bird was allowed to forage in the

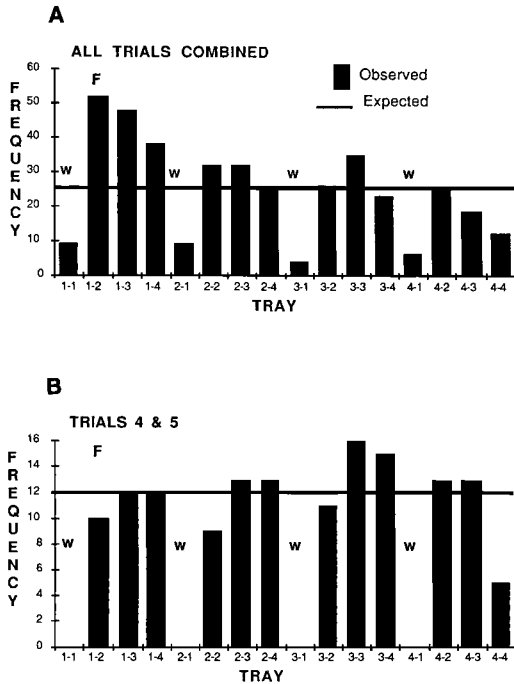


Fig. 1. Top: The observed (shaded bars) and expected (horizontal line) distribution of search effort in the foraging environment (395 patch visits). The expected distribution is based on the number of visits to a patch assuming uniform search effort in all trays. Bottom: The observed (shaded bars) and expected (horizontal line) distribution of search effort during trials 4 and 5 in the foraging environment excluding the trays immediately adjacent to the windows. The "F" is above the tray that contained food in the pre-trial acclimation period; the "w" is above the trays that were adjacent to the windows.

aquarium at a time. The order of the birds in the foraging trial was chosen randomly each day to avoid biases due to duration of pre-experiment food deprivation. Once a foraging trial began, I observed the bird while it searched for and foraged within a food patch. Typically, the bird would initially sample several trays over several dives before the food tray was found. The bird would then dive from one to several times to feed within the food tray. The trial ended when the bird abandoned the food patch(es) and began searching within the empty patches for more food. Occasionally, the foraging bird would start foraging in the food tray and would search into an adjacent empty tray; as long as the bird returned to the food tray during this foraging path, I allowed the bird to continue feeding. At the end of a trial the exploited food trays were removed and replaced with full food trays. I repeated this procedure until all birds had completed a trial each day. Each foraging trial

normally lasted several min; no trial lasted more than 15 min.

In both experiments, I observed the foraging behavior of the birds through the aquarium window that was nearest the location of the foraging bird. When the feeding trial began, an assistant recorded the number of each tray searched and mapped the search path by drawing on a scale (1 cm = 5 cm) map of a tray. A search path began when the bird's bill entered the substrate and continued until it left the substrate.

I used an engineer's plan measure to determine the search-path lengths to an accuracy of ± 0.5 cm on the map or ± 2.5 cm in terms of actual distance in the tray. The path length divided by the time spent in the path was used as an estimate of the average velocity in empty and food patches. Velocity varied within a search path, but it was not possible to measure the variation. I calculated the meander ratio (the ratio of the total path length to the straight line distance between the beginning and end of the path [Williamson and Gray 1975]) for search paths in empty patches and in each of the food patch densities. Using this ratio, a straight search path has a meander ratio of 1.0, whereas a sinuous path has a ratio of >1.0 .

I used a Chi-square or log-likelihood ratio test to detect differences in distribution of search effort among trays (Zar 1974). I used a two-tailed *t*-test (Zar 1974) to determine if each search-path characteristic differed between empty and food patches (experiment 1) and between low- and high-density patches (experiment 2) for each bird. Finally, I used paired two-tailed *t*-tests (Zar 1974) to determine if search-path characteristics averaged over all birds differed between each patch type within an experiment.

RESULTS

Search effort to find a food patch.—To determine whether the location of the food patch on the previous day influenced search effort, I compared the observed and predicted number of visits to the patch location that was searched first in each of the 30 trials of experiment 1. The birds dove first to the food-patch location of the previous day more frequently than would be expected by chance (12 observed visits, 1.88 expected visits; $G = 13.82$, $df = 1$, $P < 0.001$).

I next examined whether the birds searched randomly through the remaining trays after they determined that the tray which was the food patch on the previous day was empty and before they located the food patch. The distribution of visits to empty patches after the first visit in all 5 trials (Fig. 1a) indicated that search effort was not random within the array of trays ($\chi^2 = 127.42$, $df = 15$, $P < 0.001$). The birds avoided trays

TABLE 1. Search-path characteristics ($\bar{x} \pm SE$) of 6 Ruddy Ducks in empty patches and food patches containing 150 wheat grains.^a

Bird	Food density	<i>n</i>	Length (cm)	Time (s)	Rate (cm/s)	Meander
A1	0	84	43.6 ± 4.8 ***	2.0 ± 0.2 ***	22.8 ± 1.5 **	1.7 ± 0.3 ***
	150	29	273.6 ± 12.7	18.6 ± 1.0	15.4 ± 0.7	9.4 ± 1.3
Blue	0	107	24.1 ± 2.8 ***	1.3 ± 0.1 ***	18.9 ± 0.9 *	1.3 ± 0.1 ***
	150	18	215.8 ± 20.2	16.3 ± 1.4	13.4 ± 0.8	8.8 ± 2.3
Green	0	77	31.5 ± 3.1 ***	1.9 ± 0.2 ***	17.6 ± 0.8 ***	1.3 ± 0.1 ***
	150	28	187.5 ± 13.8	16.8 ± 1.0	11.2 ± 0.7	6.6 ± 0.9
Fred	0	81	26.8 ± 2.6 ***	1.7 ± 0.2 ***	18.4 ± 1.1 ***	1.2 ± 0.1 ***
	150	36	128.0 ± 9.8	14.1 ± 0.9	9.1 ± 0.5	6.6 ± 1.5
Red	0	106	28.3 ± 2.9 ***	1.4 ± 0.1 ***	21.4 ± 1.0 ***	1.2 ± 0.1 ***
	150	31	220.0 ± 18.3	19.1 ± 1.0	11.3 ± 0.5	6.7 ± 1.0
Yellow	0	58	43.5 ± 5.2 ***	2.1 ± 0.2 ***	23.8 ± 3.0 *	1.2 ± 0.1 ***
	150	28	195.4 ± 16.6	15.2 ± 1.1	13.6 ± 0.8	9.0 ± 2.5

* * indicates adjacent means within column differ significantly ($P \leq 0.05$); ** $P \leq 0.01$; *** $P \leq 0.001$.

located directly adjacent to the windows, possibly to avoid foraging close to the observer, and foraged most frequently in trays 1-2 and 1-3. This preference probably resulted because tray 1-2 (labeled "F" in Fig. 1a) was always the food patch in the conditioning trials conducted before the experiment. The bias of searching in tray 1-2 was not maintained, however, as search effort in trials 4 and 5 of this experiment (Fig. 1b) was distributed equally throughout the array of trays when the row of patches adjacent to the windows was excluded from the analysis ($\chi^2 = 6.90$; $df = 11$; $P = 0.8073$).

Search-path characteristics.—Each bird's search-path characteristics differed between empty patches and food patches containing 150 prey (Table 1). While in food patches, the search paths of each bird were longer in length and duration, had a lower rate of movement, and were more sinuous. These characteristics of the search paths differed significantly between empty patches and patches containing 150 prey when each path characteristic was averaged over all birds (Table 2).

Search-path lengths for 5 of the 6 birds did not vary between low- and high-density food patches (Table 3). Yellow's average search-path length was shorter in low-density patches than in the high-density patches ($P = 0.0487$). The

search paths of all birds except Red were shorter in duration ($P \leq 0.05$) in patches that contained 50 wheat grains than in patches that contained 250 items. The search-path velocity was lower ($P \leq 0.05$) in high-density patches than in low-density patches for all birds except Fred and Yellow. Meander ratios did not vary significantly ($P > 0.05$) between patch types for all birds.

I next compared search paths between the high- and low-density patch types when each characteristic was averaged over all birds (Table 4). Search-path length did not differ between low- and high-density patches, but search-path duration was shorter in low-density patches. Search-path velocity was faster in low-density patches; but, search-path sinuosity did not differ between low- and high-density patches.

TABLE 2. Comparison of search-path characteristics ($\bar{x} \pm SE$) of all birds combined ($n = 6$) in empty patches and patches containing 150 wheat grains.

Characteristic	Empty patches	<i>t</i> -test	150 prey
Length (cm)	33.0 ± 3.5	$P < 0.0001$	203.4 ± 19.5
Time (s)	1.7 ± 0.1	$P < 0.0001$	16.7 ± 0.8
Rate (cm/s)	20.5 ± 1.0	$P < 0.0001$	12.3 ± 0.9
Meander	1.3 ± 0.9	$P < 0.0001$	7.9 ± 0.6

TABLE 3. Search-path characteristics ($\bar{x} \pm SE$) of 6 ruddy ducks in patches containing 50 or 250 wheat grains.^a

Bird	Density	<i>n</i>	Length (cm)	Time (s)	Rate (cm/s)	Meander
Al	50	12	251.9 ± 16.0 NS	14.4 ± 0.8 *	17.6 ± 0.8 **	10.8 ± 2.5 NS
	250	19	255.7 ± 8.3	17.9 ± 0.7	14.5 ± 0.5	8.5 ± 2.1
Blue	50	15	223.6 ± 24.4 NS	11.8 ± 1.2 ***	19.1 ± 0.7 *	8.3 ± 1.3 NS
	250	29	258.9 ± 7.4	18.0 ± 0.4	14.5 ± 0.5	13.7 ± 2.4
Green	50	14	229.4 ± 25.4 NS	13.0 ± 1.2 **	16.4 ± 1.3 **	7.6 ± 1.2 NS
	250	27	210.2 ± 7.6	15.9 ± 0.4	13.3 ± 0.4	7.5 ± 0.9
Fred	50	15	240.4 ± 22.0 NS	13.1 ± 1.0 **	17.7 ± 1.0 NS	10.8 ± 3.7 NS
	250	44	259.9 ± 7.9	15.8 ± 0.3	16.4 ± 0.4	9.5 ± 1.0
Red	50	13	334.5 ± 17.3 NS	17.6 ± 0.7 NS	19.0 ± 0.5 ***	12.7 ± 5.8 NS
	250	31	293.7 ± 13.6	19.4 ± 0.7	15.0 ± 0.5	15.4 ± 2.9
Yellow	50	20	178.2 ± 18.0 *	12.6 ± 0.8 **	14.4 ± 1.1 NS	9.9 ± 2.5 NS
	250	50	219.7 ± 10.9	14.9 ± 0.4	14.5 ± 0.5	6.6 ± 0.9

^a NS indicates no significant difference ($P > 0.05$) between adjacent means within column; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

DISCUSSION

Foraging Ruddy Ducks exhibited area-restricted search behaviors that enabled them to exploit patchily distributed prey more efficiently than if they searched randomly. On the first dive of a foraging trial, the birds tended to visit first the tray that had been the previous day's food patch. Once the birds found that this tray was empty, they (for the first three trials of experiment 1) concentrated their search effort initially in an area that had contained food during the acclimation period. Search effort did not vary among the trays during the final 2 trials, possibly because the birds learned that the wheat found previously at that site had not been replenished. Revisiting previously profitable foraging sites may be important when exploiting a patchy food resource with prey densities that are likely to be replenished.

TABLE 4. Comparison of search-path characteristics ($\bar{x} \pm SE$) of all birds ($n = 6$) combined in patches containing 50 or 250 wheat grains.

Characteristic	50	<i>t</i> -test	250
Length (cm)	243.0 ± 21.0	$P = 0.6310$	249.7 ± 12.4
Time (s)	13.8 ± 0.8	$P = 0.0039$	17.0 ± 0.7
Rate (cm/s)	17.4 ± 0.7	$P = 0.0137$	14.7 ± 0.4
Meander	10.0 ± 0.8	$P = 0.8968$	10.2 ± 1.4

Chironomid larvae, the most common prey of breeding female Ruddy Ducks (Siegfried 1973, Tome 1981), would probably not exhibit patch renewal rates that are rapid enough to justify returning to previously exploited sites on a daily basis. Patch renewal would be dependent upon recolonization of the site by larvae hatching from eggs and from immigrations of larvae from other sites. The second most common foods consumed by Ruddy Ducks (gastropods and amphipods; Siegfried 1973, Tome 1981), however, are mobile enough to rapidly recolonize an area. These prey may continually immigrate to a site because it provides food or cover. Consequently, it may benefit the predator to remember that location as a likely area to find prey.

Other avian predators, including Great Tits (*Parus major*; Smith and Dawkins 1971, Smith and Sweatman 1974), Red-winged Blackbirds (*Agelaius phoeniceus*; Alcock 1973), European thrushes (*Turdus* spp.; Smith 1974a), Ovenbirds (*Seiurus aurocapillus*; Zach and Falls 1976a, b), Snowy (*Egretta thula*) and Great (*Casmerodius albus*) egrets (Erwin 1985), and hummingbirds (*Selasphorus rufus*; Gass and Sutherland 1985) have been observed to return to foraging sites that previously had been profitable. In addition, hummingbirds (Stiles 1975) and Canvasbacks (*Aythya valisineria*; Anderson 1984) may remember the location of profitable foraging sites from one year or season to the next. This has impli-

cations for birds that return to an area after an extended absence, e.g. a migratory species that returns to the breeding grounds from a distant wintering area. Individuals that are able to relocate feeding sites that were productive in the past may be able to obtain nutrients necessary for reproduction more rapidly than those that are unfamiliar with the local food resource distribution.

Numerous authors claim that predators that forage on patchily distributed prey should exhibit search behaviors that enable them to efficiently find and exploit food patches (e.g. Tinbergen et al. 1967; Smith 1974a, b; Curio 1976; Zach and Falls 1976b; Bond 1980). The search paths of the Ruddy Duck exhibit these characteristics. When Ruddy Ducks search for food items in areas devoid of prey, their search paths have a smaller meander ratio, shorter lengths, and a higher rate of movement than in areas with abundant prey. All of these characteristics enable the bird to search rapidly through an area until prey are located.

Once prey are located, the predator is likely to find more food in that area because of the patchy distribution. Its search-path characteristics should change to reflect the increased probability of finding more food. Relative to empty patches, Ruddy Duck search paths in food patches had larger meander ratios, longer path lengths and durations, and slower velocities: all characteristics that have been described for efficient within-food-patch search behavior.

I found that the rate of movement of the birds was slowest in the high-density patches. Presumably the birds searched more slowly through the substrate of high-density patches, either to decrease the probability of missing prey or because of time spent manipulating food items within the bill. Foraging Ruddy Ducks sieve through the substrate to locate prey and then manipulate prey within the bill while continuing to forage. In the empty and lowest-density patches, food items were absent or very rare; thus, the birds may have been able to search through these patches without slowing significantly to manipulate food items. Because of the handling time necessary in high-density patches, birds may slow the rate of movement through the patch so that other prey are not missed. Similar decreases in the rate of movement through food patches in comparison with velocities in areas that lack food have been observed in Wood Pigeons (*Columba palumbus*,

Murton et al. 1963). Goss-Custard (1970), however, found no relationship between rate of movement and patch density in Common Redshanks (*Tringa totanus*), but the rate of movement increased with patch density in thrushes (Smith 1974a) and ovenbirds (Zach and Falls 1976b).

The relationship between rate of movement in a patch and prey density also may depend partially on both how a predator locates prey and the handling time necessary to consume a food item. Predators that locate prey visually, such as ovenbirds and thrushes, may search slowly and intensely while trying to locate food items in areas where prey are absent or scarce. When prey are more abundant or conspicuous in a patch, the rate of movement may increase as the predator locates prey more quickly or develops a search image (Tinbergen 1960) for a particular food type. Also, some visual predators may continue to search while captured prey are manipulated in their bill. When prey detection is tactile, as in the Ruddy Duck, movement through a patch of food may decrease as prey density increases because of the increased amount of time spent handling prey before moving forward through the patch to locate and handle another food item. I was unable to observe handling times of natural prey consumed by Ruddy Ducks or of the wheat grains at the densities used in this study, so the hypothesis was not tested further.

Ruddy Ducks can remember the location of a previously profitable food site and exhibit search-path characteristics before and after locating a food item that are consistent with predictions of models of efficient search behavior. These search-path characteristics enable Ruddy Ducks to locate and exploit prey patches more efficiently than if they had been moving at random through the aquarium substrate.

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