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Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size

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Abstract Knowing how far away animals can detect food has important consequences for understanding their foraging and social behaviors. As part of a broader set of field experiments on primate foraging behavior, we set out artificial feeding platforms (90 × 90 cm or 50 × 50 cm) throughout the home range of one group of 22 brown capuchin monkeys, at sites where they had not seen such platforms previously. Whenever the group approached such a new platform to within 100 m, we recorded the group's direction and speed of approach, and the identity and distance from the platform of the group member that detected the platform or came closest to it without detecting it. We used logistic regression on these data to examine the effects of group movement speed, platform size and height, and focal individual age and sex on the probability of detecting the platform as a function of distance. Likelihood of detecting a platform decreased significantly at greater distances – the probability of detecting a platform reached 0.5 at 41 m from the group's center and 25.5 m from the nearest group member. These results show that detectability of platforms by the entire group (9 adults, 13 juveniles) was less than twice that for single group members. Detectability at a given distance decreased severely as the group moved faster; at their fastest speed, individuals had to approach a platform to within less than 10 m to find it. The large platforms were significantly more likely to be detected than the small ones, suggesting that increased use of larger food patches by wild primates may not necessarily reflect foraging preferences.

Key words Food detection · Foraging · Travel speed · Sociality · Capuchin monkeys

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Introduction

Although rarely measured, the distance over which animals can detect previously undiscovered prey items plays an important role in several aspects of foraging behavior and socio-ecology. First, encounter rates with prey clearly depend on the distance over which they can be detected (Schoener 1971), which may vary according to prey type and size (e.g., Dukas and Ellner 1993; Getty and Pulliam 1991), predator species and age (Formanowicz 1987; Henderson and Northcote 1985), foraging tactics (Andersson 1981; O'Brien et al. 1990), habitat (Carlson 1985) or the predator's speed of movement, leading to predictions of an optimal speed of search (Gendron and Staddon 1983). Second, the benefit of remembering the locations of previously encountered or stored food items (e.g., food-storing birds: Balda and Kamil 1988; Krebs et al. 1990) depends on how easily these same items could be detected without using memory. If the detection field is large, "dumb" foragers can achieve prey intake rates only marginally lower than "smart" foragers (C.H. Janson, unpublished work). Third, the degree of food competition or foraging enhancement among individuals in a social group depends on how much food the group as a whole encounters relative to how much each individual alone could encounter (Altmann 1974; Clark and Mangel 1986; Janson 1988). If individual detection fields are large relative to distances between group members, then the group will detect only a little more food than solitary animals, thus engendering much food competition if food items are small (Ranta et al. 1993). Conversely, if detection fields are close to the same size as inter-individual distances, then every group member "pays its own way", food competition will be minimal, or there can even be foraging enhancement if the food items found can satiate more than one animal (Clark and Mangel 1986).

The issue of prey detection ability is especially vexing in interpreting the results of studies suggesting the existence of cognitive maps in primates and other animals. It has long been apparent to primatologists that non-human primates have seemingly complex abilities to remember and navigate among spatially fixed renewing or stable resources, be they fruit trees (Milton 1981; Garber 1989), water holes (Altmann 1974), or tools (Boesch and Boesch 1984). Although some of the parameters of cognitive maps have been analyzed experimentally for a few primate species in captivity (e.g., Menzel and Juno 1985) and the wild (Menzel 1991; Janson 1996), the vast bulk of data comes from observations on unmanipulated free-ranging primates. The kinds of evidence used to infer the existence of cognitive maps in the latter case focus on the preference of primate groups to visit the nearest available resource, to travel to it in nearly a straight line, and to restrict such apparently non-random visits to large productive resources rather than small unproductive ones (e.g., Sigg and Stolba 1981; Garber 1989). However, computer simulations (Garber and Hannon 1993; C.H. Janson, unpublished work) show that if primates tend to travel in straight lines for other reasons, such as avoiding areas previously foraged for insects, then even if they are ignorant of the locations of their food trees, they will still encounter preferentially and use the nearest available food sources *if their detection field for such food sources is sufficiently large*.Their tendency to use goal-directed travel only toward large resources is also easily explained if the detection field is larger for large, productive trees than for small unproductive ones. Thus, to distinguish goal-oriented movement based on a mental map from serendipitous discoveries of nearby food sources requires knowledge of the detection field of the animals for the resources in question. Although some intuitive guesses exist about the ability of monkeys to detect fruit trees in tropical rainforest (Terborgh 1983), none of these are based on experimental analysis of food discovery by free ranging animals. Here we report on experiments designed to establish the range of detection of artificial food sources (wooden platforms with fruit) by free-ranging capuchin monkeys in subtropical Argentina. The absolute results can be used to interpret the outcomes of other experiments using such platforms to explore spatial movement rules (Janson 1996), and the relative trends should be representative of a broader set of natural resources such as fruit trees.

Materials and methods

Study site and species

The study area is Iguazu National Park, Argentina. The site is adjacent to Iguazu Falls (54°W, 26°S) and is covered with subtropical forest in varying stages of recovery from human disturbance. Climate and fruit production are highly seasonal (see Brown and Zunino 1990; Janson 1996), with a pronounced low point in the winter months of June–August, when these experiments were carried out.

The study species is the brown capuchin monkey (*Cebus apella nigritus*), which lives in group sizes of 7 to over 30 individuals, with a ratio of about 3 adult males to 4 adult females, and about as many adults as juveniles (C.H. Janson, unpublished work). The study group used here was the Macuco group, which consisted in 1995 of 3 adult males, 6 adult females, 1 subadult, 8 juveniles, and 4 infants. They are omnivorous, with a diet showing strong seasonal variations from nearly exclusively frugivorous to a concentration on insects during the austral spring to almost totally folivorous during the austral winter when fruit is scarce (Brown and Zunino 1990).

Platforms and provisioning

Platforms were 95 × 95 cm or 50 × 50 cm structures with a wire-mesh bottom (0.6-cm squares), 10-cm-high wood sides and ca. 2 × 5 cm wood floor supports. Nylon cords were attached at the four corners and tied to a single heavier cord ca. 1.2 m above the platform. The heavier cord led through a pulley (tied to a tree branch) and then to an attachment site on a nearby tree trunk at chest height. The tree branches used for platform pulleys varied in height from 4 to 15 m above the forest floor; as precise measurements were not made on each platform, we used a simple categorization of heights to describe them in Table 1: $1 = 4 - 7$ m, $2 = 8 - 11$ m, $3 = 12 - 15$ m. Fruits were placed on a platform after lowering it with the rope to ground level; the platform was then raised as close to the support branch as the rope and pulley would allow (typically 1.2–1.5 m). The fruits used in these experiments were tangerines, with which the capuchins were already familiar because a few trees have escaped from cultivation and occur at the study site.

Platforms were used for two distinct sets of experiments: "routine" and "discovery". The routine platforms were always set up in pairs ca. 10 m apart, and fruits were provided either daily or twice daily, but only when the group had approached to within 30 m of the platforms; results from these experiments are not discussed here. The discovery platforms were set up singly in locations where the group had not previously received provisioned food either in 1995 or 1992 (see Janson 1996), and at least 100 m from any other concurrently-used routine platforms (for specific locations and dates of use of routine platforms, see Fig. 1). After a discovery

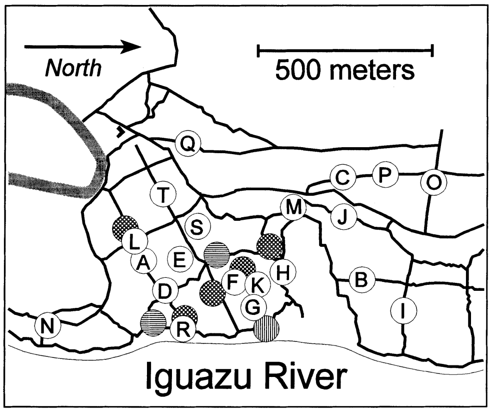

Fig. 1 Map of the study area, showing the access road (*shaded*), trail grid (*solid lines*), field station (*black L shape*), and positions of all platforms used during this study period. *Lettered* sites correspond to sites in Table 1. *Checkered* sites plus sites *A* and *D* were used as routine feeding sites from 29 June to 25 July 1995. The *horizontally striped* sites plus sites *D*, *E*, *F*, *G*, *R*, *S*, and *T* were used as routine feeding sites from 26 July to 7 August 1995. The *vertically striped* site plus sites *S*, *T*, *E*, *K*, and *L* were used as routine feeding sites from 8 August to 25 August 1995. Sites that were to become part of a routine design were treated as "discovery" sites prior to the group's first visit to them

Table 1 Data of every approach to less than 100 m by the study group to a discovery platform. Dates are expressed as month/date. Locations of the sites are shown in Fig. 1. Definitions of NAD and PD are given in Fig. 2. For measurement methods and other definitions, see Methods. Speed refers to group speed. Each site was used only until a discovery occurred, except for the two final cases where the platform was replaced after having been removed for a minimum of 14 days

Date	Site	NAD	PD	Detect?	Speed	Sex	Age	Platform size	Height category
06/29	A	10	0	Yes	5	♀	Adult	Large	1
07/15	B	60	85	No	2.5	♀	Adult	Large	2
07/17	B	15	40	Yes	7	♂	Subad	Large	2
07/21	C	8	30	No	10	♀	Adult	Large	2
07/25	D	6	5	Yes	10	♂	Adult	Large	3
07/27	E	50	55	No	7	♂	Adult	Large	2
07/27	F	6	30	Yes	7	♀	Adult	Large	1
07/27	E	45	65	No	8	–	–	Large	2
07/29	G	18	15	Yes	3	♀	–	Large	1
07/29	H	15	28	Yes	5	♀	Adult	Small	1
07/30	I	15	35	No	10	♂	Adult	Small	1
08/02	J	30	80	No	2	♀	Adult	Small	2
08/03	J	20	80	No	5	♂	Adult	Small	2
08/04	I	15	40	No	5	♂	Adult	Small	2
08/07	J	16	15	Yes	5	♂	Adult	Small	2
08/07	K	12	25	Yes	3	♀	Juv.	Large	2
08/08	E	34	15	Yes	2	♂	Adult	Large	2
08/09	L	20	40	Yes	5	♀	Adult	Large	2
08/09	M	30	60	No	1	♂	Adult	Large	1
08/10	N	5	45	Yes	2	♂	Adult	Small	1
08/11	M	12	10	Yes	6	♀	Adult	Large	2
08/12	O	22	20	Yes	5	♀	Juv.	Large	2
08/20	P	10	5	Yes	5	♀	Adult	Large	2
08/21	Q	10	12	Yes	5	♂	Adult	Small	1
08/22	C	20	30	Yes	1	♂	Juv.	Large	2
08/22	R	8	–	Yes	–	–	Adult	Large	1
08/24	J	8	20	Yes	2	♂	Adult	Large	2
08/25	B	60	70	No	5	♀	Adult	Large	2

platform was set up, it was provisioned with 15 (or sometimes 10) tangerines, which were left on the platform until the group discovered it, or we took down the platform (to move it elsewhere). We refer to the 95 × 95 cm platforms as large, and to the 50 × 50 cm ones as small.

Data collection

Pairs of observers followed the group from dawn to dusk, recording the spatial location of the group at least once every 15 min, the location and duration of all fruit-feeding activities, both at platforms and natural fruit trees, and 5-min interval records on the group's general activity, categorized into rest, feed (in food tree), forage, "forage-travel", rapid travel, and miscellaneous (cf. Terborgh 1983). When following the capuchin group, we stayed near the center or back portion of the group spread to avoid providing any anticipatory cues to the group about the location or provisioning status of any platform. When the edge of the group approached to within ca. 50 m of a discovery platform, we chose as focal animals for intensive observation the closest individual or pair of individuals to the platform. We followed these individuals until they found the platform or passed by it; in the latter case, we chose the individuals currently closest to the platform (but not beyond it) as new focal animals if the platform had not been discovered already. We avoided approaching the discovery platform to within less than 10 m.

Discovery of a new platform by a monkey usually could be recognized by several marked changes in behavior. First, the individual would stare fixedly directly toward the platform for several (2–10) seconds. Second, it would then start to travel rapidly through the tree(s) in a nearly straight line to the platform. Third, it sometimes began to vocalize with a distinctive "food-associated call" (M.S. Di Bitetti, unpublished work). Although some individuals did not perform the last step, the first steps were usually sufficient to determine when and where the monkey first found a platform. When a platform was discovered, we noted the distance from the platform to the discovering individual at the moment of discovery, measured by the observer's pacing between the two locations on the forest floor; no estimate of vertical distance was attempted. Accuracy of pacing was checked frequently against measured distances along measured trails (Fig. 1). We also noted the number of neighboring individuals, time delay to the first food-associated calls, and how many tangerines were consumed by any group member that visited the newly-discovered platform. From the associated background notes on group positions, described relative to the trail grid (Fig. 1) at 15-min (or shorter) intervals, we calculated the speed of movement of the group (straight-line distance between successive locations on the trail grid, divided by time between observations). Absolute coordinates (relative to the field station, Fig. 1) of mapped positions on the trail grid were obtained with the mapping software Tracker (P. Lee, 1995; available from the senior author upon request); straight-line distances between locations were obtained from the absolute coordinates via Euclidean geometry. Based on non-concordance between mapped locations of unique landmarks (e.g., the junction of two trails), the error in calculating straight-line distances with the Tracker software is estimated to be less than 5% of the true distance. By reference to mapped positions of the group during its approach toward a platform, we also calculated the shortest perpendicular distance between the major axis of group movement and the platform (PD in Fig. 2). The latter information is analogous to transect census methods in which an observer measures the shortest (perpendicular) distance from any discovered animals to the straight census trail (e.g., Burnham et al. 1980).

The senior author took opportunistic measurements of the group length and width whenever the group moved nearly parallel or perpendicular to a marked trail. The length was taken as the

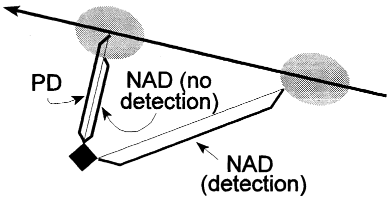

Fig. 2 Diagram showing the meaning of the distance measurements used in this study. The shaded areas depict the spread of the social group. Nearest approach distance (*NAD*) is either the distance at which the focal animal (usually at the edge of the group) detected the platform *or* the closest approach by any focal animal to the platform if the platform was not detected in a given approach. Perpendicular distance (*PD*) is the shortest distance from the major axis of group movement to the platform, regardless of whether the platform was detected or not

straight-line distance between the trail positions of the first and last observed individuals in the direction of group movement; width was taken as the distance between the two extreme points on the trail above which group members were observed to cross.

Statistical analyses

Clearly, the detection of a platform by any group member will not be independent of its prior detection by other group members. Therefore, each approach by the group to within 100 m of a discovery platform was considered a single independent data point, regardless of how many different focal animals we observed during the approach. Although detection of a platform was considered at the group level, it could depend on variables related to those individuals that were closest to the platform. To reduce possible dependence among the independent variables, we chose variables related to only one individual per approach. This individual was either the one that detected the platform or the individual that approached it most closely if no detection occurred; the corresponding variables are its age, sex, and the distance to the platform at which detection occurred or the shortest distance of approach if no detection occurred (NAD, Fig. 2). The remaining independent variables are either group-level traits (average foraging speed, the shortest perpendicular distance between the platform and the group's center) or characteristics of the discovery platform (large vs. small, height category). Because the dependent variable in logistic regression is a qualitative outcome (discovery vs. no discovery), plots of the raw data against an independent variable are hard to interpret; to present the results graphically, we averaged the frequencies of discoveries and non-discoveries over modest ranges of distances (0–10 m, 11–20 m, 21–30 m, 31–40 m, 41–60 m, > 60 m), subject to the constraint that there be a minimum of four observations per average.

Asymptotic parameter estimates and probability levels for each effect were calculated with the statistical package JMP 3.1 (1995, SAS Institute). The statistical significance of a variable in regression can be judged either by the probability level associated with its parameter or by the change in the overall goodness of fit of the model due to the addition of that variable. The latter procedure depends less on specific assumptions needed for parameter estimation and thus is preferred; we provide both the probability that a given variable's asymptotic parameter equals 0, as well as the total model goodness of fit (measured by the chi-square statistic against the null hypothesis of homogeneity). The program JMP also allows "inverse prediction" – the calculation of the expected value and confidence limits (using Fieller's method) of the independent variable corresponding to a given level of the dependent variable. We used inverse prediction to estimate the mean (and range) of distances at which the study group of capuchins had an even (1:1 or 50%) chance of discovering or not discovering the food platform. We performed this prediction for several group movement speeds within the range of speeds observed in our discovery data (2–10 m/min; Table 1).

Unless noted specifically, probability levels for each effect are two-tailed. In several cases, we have used one-tailed tests, because particular outcomes are either universally held to be true (detectability of a target decreases with distance, e.g., Burnham et al. 1980) or are logically implausible (it is hard to imagine that detectability could ever increase at faster movement speeds, see Gendron and Staddon 1983, or be lower for larger targets).

Results

Hypotheses

The null hypotheses are that the probability of detection of a platform by the group (i.e., by at least one group member) is the same regardless of the age, sex, or distance to the platform of the group member that detected the platform or came closest to it if it was not discovered (NAD, Fig. 2), the group's average movement speed during the approach, the shortest perpendicular distance between the platform and the center of the group (PD, see Fig. 2), or the size and height of the platform. The alternative hypotheses for one-tailed tests are that the probability of discovery should decrease with increasing distance (either NAD or PD) and be larger for large than for small platforms; no strong prediction could be made for platform height because its effects would presumably depend on the height of the foraging group, which we could not control for or measure systematically.

Foraging parameters

During the study, the Macuco group spent most of their activity period looking for or consuming food; resting and miscellaneous activities occupied only 5.9% of daylight hours. Of their food related activity, the group spent 20.9% ($\sigma = 8.6$, $n = 8$ dawn-to-dusk follows) feeding in food trees (including platforms), 46.6% ($\sigma = 10.6$) in slow foraging, 20.2% ($\sigma = 4.2$) in forage-travel, and 6.4% ($\sigma = 2.3$) in rapid travel. During foraging, the group maintained an average front-to-back length of 56.6 m ($n = 32$, $\sigma = 20.3$) and a width of 42.4 m ($n = 30$, $\sigma = 11.1$). The width of the group was inversely proportional to its movement speed (Kendall non-parametric correlation, $\tau = -0.32$, $n = 30$, $P = 0.036$), ranging from an average of 45.6 m ($n = 18$) during slow foraging down to 32.5 m ($n = 2$) during rapid travel. The length of the group was not predictably related to travel speed ($\tau = 0.17$, $n = 32$, $P = 0.24$). The rate of movement of the group's center during slow foraging averaged 2.56 m/min ($\sigma = 1.69$, $n = 83$), during forage-travel it averaged 4.95 m/min ($\sigma = 1.18$, $n = 16$) and during rapid travel it was 16.03 m/min ($\sigma = 3.84$, $n = 56$).

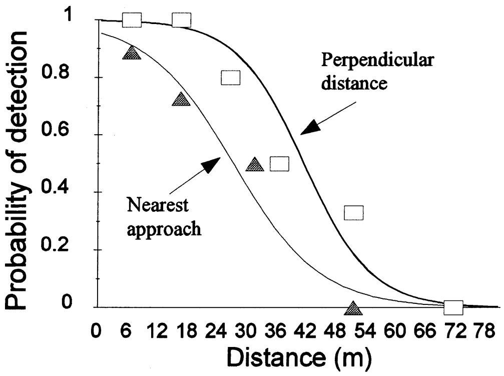

Fig. 3 Probability of detection of artificial feeding platforms as a function of the nearest approach distance (see Fig. 2) between the platform and group individuals (*triangles*) or of the shortest perpendicular distance (see Fig. 2) from the platform to the center of the group spread (*boxes*). *Data points* (based on Table 1) are calculated as the proportion of group approaches to a platform that resulted in detection, calculated within 10-m increments of the independent distance variable (see Methods for details)

Effect of distance

The Macuco group approached previously unused platforms to within 100 m 28 times during the study period (Table 1). The probability of detection of the discovery platform decreased significantly with increased distance, either the nearest approach distance (hereafter NAD) by a focal animal or the shortest perpendicular distance (hereafter PD) between the platform and the group's major axis of movement (Fig. 3). The relationship between detection probability and PD alone was much stronger than that with NAD alone (Table 2, models 1 and 2). In a multiple regression using both distance measures, NAD was not a significant predictor of detection probability (one-tailed $P = 0.35$), whereas PD retained a significant effect (one-tailed $P = 0.02$).

Effects of group movement speed

When controlling statistically for either measure of distance, detection probability decreased with increasing travel speed. For both NAD and PD, the addition of group movement speed significantly increased the model's fit to the data relative to the null model of no association (for NAD, Δ chi-square = 4.28, $df = 1$, one-tailed $P = 0.019$; for PD, Δ chi-square = 6.55, $df = 1$, one-tailed $P = 0.005$). In the model with NAD, the parameter associated with travel speed was significantly less than 0.0 (Table 2, model 3), while a similar strong trend was seen in the model with PD (Table 2, model 4). Ignoring travel speed, the NAD at which the group had an even chance of discovering or missing a food platform was 25.5 m (Table 3). However, when moving slowly (2 m/min), as they did during insect foraging, the corresponding NAD was increased 16%, whereas when traveling at 10 m/min, as they did when moving between previously known feeding platform sites, the NAD needed to assure 50% detection decreased 64% (Table 3). The PD needed to achieve a 50% chance of detection overall was 41.0 m, increasing 26% when the group moved at 2 m/min and decreasing 34% to 27.7 m when they traveled at 10 m/min (Table 3). The latter figure is not significantly different from the group's actual mean width of 21.2 m during travel ($n = 30$, $\sigma = 5.56$, $P = 0.25$). In other words, the faster they move, the narrower the detection swath in which they could detect food sources; at high travel speeds, they nearly had to trip over a platform to detect it.

Effects of age and sex of the focal animal

Neither alone nor in combination with either measure of distance did sex of focal animal significantly affect detection probability (alone: $P = 0.68$; controlling for NAD, $P = 0.5$; controlling for PD, $P = 0.91$). Likewise,

Table 2 Results of logistic regressions of probability of detection. NAD is the nearest approach distance of an individual to the platform prior to discovery, while PD is the smallest perpendicular distance between the group main axis and the platform at any time during the group's approach. Speed is in meters/min. Large is a binary variable with value 1 if the platform was large (95 cm) and 0 if the platform was small (50 cm)

Model	Variable	Parameter estimate (SE)	Probability (one-tailed)	Total model chi-square (*df*)
1	Constant	3.0298 (2.364)	–	11.54 (1)
	NAD	−0.1187 (0.0504)	0.0092	
2	Constant	6.0098 (2.369)	–	21.43 (1)
	PD	−0.1465 (0.0616)	0.0082	
3	Constant	8.2423 (3.856)	–	15.82 (2)
	NAD	−0.2383 (0.1189)	0.0225	
	speed	−0.6063 (0.3445)	0.0392	
4	Constant	19.1717 (11.588)	–	27.98 (2)
	PD	−0.3326 (0.2078)	0.0527	
	speed	−0.9970 (0.6159)	0.0547	
5	Constant	2.3040 (1.1956)	–	15.66 (2)
	NAD	−0.1486 (0.0601)	0.0067	
	large	2.2815 (1.2314)	0.0319	
6	Constant	9.4383 (5.8877)	–	19.91 (3)
	NAD	−0.3119 (0.1816)	0.0430	
	speed	−0.8740 (0.5998)	0.0725	
	large	2.6453 (1.5428)	0.0432	

Table 3 Expected values of distance at which the capuchin group had a 50% chance of detecting or not detecting a feeding platform, and associated confidence limits, calculated using inverse prediction by the statistical package JMP. Confidence limits could not be calculated for perpendicular distance with travel speed included, as the parameter estimates for this analysis were not significant at alpha = 0.05 (Table 2, model 4)

Distance measure	Expected value	U95%	L95%	U90%	L90%
Nearest approach	25.5	77.2	16.6	47.5	18.3
Perpendicular	41.0	77.8	29.7	58.5	32.6
Nearest, 2 m/min speed	29.5	–	–	54.6	22.6
Nearest, 10 m/min speed	9.1	–	–	30.7	0.0
Perpendicular, 2 m/min speed	51.65	–	–	–	–
Perpendicular, 10 m/min speed	27.7	–	–	–	–

no significant effect of focal animal age was detected (all Ps > 0.9), but there were very few (4) observations with focal animals as juveniles, because juveniles are rarely the animals on the periphery of the group (cf. Janson 1990).

Effects of platform size and height

When controlling statistically for either measure of distance, detection probability was greater for larger than for smaller platforms. Adding platform size significantly increased the fit of the model using NAD (Table 2, models 1 vs. 5, Δ chi-square = 4.12, $df = 1$, one-tailed $P = 0.021$), but did not for the model using PD alone (Δ chi-square = 0.4, $df = 1$, one-tailed $P > 0.25$). When platform size was added to the logistic regressions using travel speed along with NAD or PD, the increase in model fit was significant in both cases (for NAD, Δ chi-square = 4.1, $df = 1$, one-tailed $P = 0.021$; for PD, Δ chi-square = 3.91, $df = 1$, one-tailed $P = 0.024$).

The height category of discovery platforms (within the range used in this experiment) appeared to have little effect on the probability of detection. After controlling for detection distance and platform size, platform height category (see Methods) did not contribute significantly to the probability of detection (with NAD, Δ chi-square = 0.1, $df = 1$, $P > 0.50$; with PD, Δ chi-square = 0.84, $df = 1$, $P > 0.50$).

Discussion

Effects of NAD versus PD

It is not surprising that the results show that PD alone is a better predictor of detection probability than is NAD alone. PD is a "group"-level measure of distance and integrates across the entire approach of the group to a platform; note that PD is the same for a given approach to a platform regardless of which individual discovers or fails to discover the platform at whatever NAD. In contrast, NAD differs in meaning between cases in which detection occurred or did not (Fig. 2). When detection does not happen, the NAD is in fact the closest approach of the animal to the platform, and thus rather analogous to, albeit usually smaller than, the PD, which is measured from the group center. However, when detection does occur, NAD is the distance at which the detection took place, not the closest approach the focal animal would have made if the discovery had not occurred, which is of course not knowable. Thus, when detection does not occur, NAD is usually less than PD, but when detection does occur, NAD can often be greater than PD (as when the group is traveling straight at a platform, PD = 0, and the focal animal detects the platform from a considerable distance, NAD $\gg 0$). The stability and integrative nature of PD make it a far less variable and more robust estimator of detection probability than is NAD.

Nevertheless, NAD provides other information. Because NAD better reflects the discovery process of the individual, it is not surprising that its effect on detection is more sensitive to travel speed and platform size than is that of PD. After all, if PD = 0, the platform will almost certainly be discovered regardless of the group's movement speed or the platform's size, but the actual distance at which the focal animal detects the platform (NAD) will likely be affected by both variables, as shown in the Results. The integrative nature of PD makes it far less sensitive to variables that affect each individual's probability of detecting a platform.

Mean detection distance – implications for social foraging

A number of studies have demonstrated that individuals may increase their food intake when foraging in a social group (e.g., Caraco and Wolf 1975; Götmark et al. 1986; Hector 1986; Peres 1992). However, most of these examples concern predators hunting active prey that may escape, and the benefit of social foraging is thought to be in higher attack success rather than increased rate of prey detection. Several other studies have shown that individuals may encounter prey items more quickly when foraging in groups (e.g., Hake and Ekman 1988; Travers 1993), but in these studies the increase derives from individuals cuing in on the food discoveries of others (i.e., "scrounging": Vickery et al. 1991). Thus, the average per–capita food intake rate may decrease with group size even though the rate of individual food encounters increases, because individual food discoveries are "shared" among group members (Hake and Ekman 1988). To date, there exists little direct evidence about whether and how quickly total food encounter rates increase with foraging group size, a relationship crucial to most models of social foraging (Altmann 1974; Clark and Mangel 1986; Vickery et al. 1991; Ranta et al. 1993). In this study, a group of 22 capuchin monkeys had a 50% chance of discovering a food platform at a perpendicular distance (from the group's center) of 52 m during slow foraging. The average group spread during foraging of 42.4 m implies a group half-width of 21 m. The difference between the group's detection swath and its physical radius (52 – 21 = 31 m) agrees remarkably well with the mean NAD during slow foraging (29.5 m). Thus, it appears that the group's foraging swath is indeed increased by the amount expected from the foraging swath of its most peripheral group members. In any case, the group's expected rate of platform discovery is 1.76 (52 m/29.5 m) times as rapid as is expected of a single foraging animal. Although this increase in food discovery is appreciable, it can hardly pay back the costs of feeding 21 extra mouths (or excluding juveniles, 8 extra mouths), given that the majority of food trees used by this species are not productive enough to satiate even a lone individual (Janson 1988). Even with an increased detection field for food trees, it seems unlikely that group foraging is likely to be a major per-capita advantage of group living for these capuchin monkeys, even though it remains a theoretical possibility for other primates (Rodman 1988).

Tradeoff between movement speed and detection

The results from this study confirm the hypothesis of Gendron and Staddon (1983) that animals should not search for food at the maximum possible speed because the faster they travel, the narrower their search field will become. This reduced search field is not just a reflection of the group's being less spread out during rapid travel (see Results), because a significant effect of travel speed is seen also when the detection distance is measured as NAD, which does not depend on group width. The reduced search field at higher travel speeds is due presumably to some combination of reduced time exposed to platforms at any given distance and a tendency to focus more exclusively on choice of substrates.

In the case of these capuchins, faster travel was related to reaching a predefined, known goal (see Janson 1996). Rapid travel to fixed resources is likely to be an expression of indirect or scramble competition, because the first to arrive at the resource may obtain more food or feed more quickly than it could if it arrives later (cf. Janson 1985). The group's apparent decrease in detectability when traveling rapidly may be a reflection of their common focus on maximizing known future gains rather than maximizing unknown present ones. In any case, the lower detectability of rapidly traveling groups could provide an actual foraging cost to animals that use spatial maps for foraging, unless their target resources are quite predictable in yield or they can avoid traveling rapidly between targets. If the target resources often are emptied out by competitors, then it would be foolish to travel rapidly and pass up the opportunity to find and use unknown resources along the way.

Effect of platform size – implications for studies of cognitive maps

One of the kinds of evidence that animals have and use cognitive maps is that they encounter and use larger food sources at higher rates than smaller food sources (e.g., Garber 1989). While this observation is consistent with a rational foraging strategy based on knowledge of the locations of food sources, it is also consistent with a pure discovery process in which larger resources are detected more easily than small ones. In these experiments, larger platforms were found more easily at a given distance than were small ones. The magnitude of this effect is quite large – the mean NAD for large platforms was nearly twice that of small ones (30.9 vs. 15.5 m, from model 5, Table 2). This ratio of detection distances is nearly identical to the ratio of the dimensions of the platforms themselves (95 cm:50 cm), suggesting that detection depends largely on the visual angle subtended by the target (as assumed in several models of search strategies: Andersson 1981; Getty and Pulliam 1993). Because the number of tangerines and sizes of the rope and pulley for each platform did not differ systematically between large and small platforms, whatever difference we find in detection likelihood between the two sizes of platforms is either independent of these variables or is an underestimate of the effect due to platform size alone.

If detection ability correlates directly with resource size, as implied by our results, it is not outrageous to expect that large-crowned fruit trees (25 m diameter) might be encountered at random substantially more often than small-crowned ones (5 m diameter), all else being equal. Just how much more often is not easy to judge, as it is improbable that the entire fruit tree is the unit of discovery. In a dense forest, even large-crowned trees will have only a small portion of their crown exposed to a monkey group. In any case, without independent estimates of the detection radius for different-sized resources, one must be very cautious about interpreting an apparent preference for larger food sources as evidence for a cognitive map.

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