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Recognition of Visual Pattern Components in Squirrel Monkeys*

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Summary. In 4 mixed-age captive groups of squirrel monkeys the predator alarm behavior control by means of visual stimuli was studied, and the extent to which socially inexperienced infant squirrel monkeys are capable of species-specific alarm behavior.

By means of color film projection it was shown that both the socially experienced and inexperienced subjects recognized two-dimensional representations of real objects or situations. Behavioral reactions to visual stimulus patterns of terrestrial predators and graded controls revealed that recognition involves complex perceptional processes and is dependent on social experience. Using a series of systematically varied spot patterns, it was found that the monkeys generalize within a wide but well-defined range of stimuli.

There was a clear-cut gender difference in alarm responses, with the males exerting a leading role both in onset and ceasing of terrestrial predator alarm.

Both the socially experienced and inexperienced subjects responded with the species-specific avian alarm and flight reaction to fast moving patterns. Only the speed, not the shape, was relevant.

Key words: Squirrel monkey – Visual recognition – Stimulus control – Motion picture – Social experience

Introduction

Recognition of visual stimuli is a substantial part in the process of dealing with environmental conditions. There is much evidence that socially organized primates recognize each other individually by means of facial patterns. The processing of visual cues of familiar conspecifics has been investigated both on behavioral (Rosenfeld and Van Hoesen 1979; Plimpton et al. 1981; Bauer and Philip 1983) and neuronal levels (Desimone et al. 1984; Perrett et al. 1985).

Of special importance for survival is the reliable recognition of predators and food items. In squirrel monkeys, two distinct behavioral sequences are known in response to terrestrial and avian predators (Winter et al. 1966; Thorington 1968; Winter 1972; Baldwin and Baldwin 1972; Herzog and Hopf 1984).

In designing and carrying out experiments on the effects of selected stimulus patterns, the high level of behavioral organization peculiar to primates, especially the learning capacity and flexibility, has to be considered. Attention should be paid to the behavioral characteristics of the species, to the environmental conditions and, in particular, the precise control of the stimulus presentation itself.

Predator dummies have been used in studying alarm behavior in primates by e.g., Kortlandt (1967), Vogel (1976), Cheney and Seyfarth (1981). Experiments with snakes and snake models suggest that social experience is required to recognize visual components of these terrestrial predators both in squirrel monkeys (Murray and King 1973; Huebner et al. 1979) and in rhesus monkeys (Mineka et al. 1980).

By presenting motion pictures, Klüver (1933) did not find any clear evidence that squirrel monkeys recognize two-dimensional complex visual stimuli. Marriott (1976, 1977) mentioned prey catching behavior in response to slides of insects.

The aim of the present investigation was to assess if squirrel monkeys recognize colored films of visual stimuli as representations of the real objects or complex stimulus situations. Provided they do, films will be used as standardized and repeatable stimulus material to further investigate which visual stimulus characteristics of predator cats are effective in eliciting alarm behavior. Finally, the question of which of the species-relevant pattern components of terrestrial and avian predators are innate and which have to be acquired by social experience was examined.

Subjects and Maintenance

Groups

Four groups were used, comprising both wild-born and laboratory-born individuals (1 ♂, 2 to 5 ♀♀, 1 to 4 subadults, 1 to 2 infants). The cages measured 4 × 2 × 3 m ("West") or 2 × 2 × 3 m ("East"). One wall of each cage consisted of a large window allowing full view from the adjacent laboratory. The cages were equipped with platforms, wire mesh, ladders and elastic hoses and chains suspended from the wire ceiling.

During daytime natural light came through a ceiling window (1 × 1.5 m). A light-dark cycle of 14:10 h was provided by additional artificial light, resulting in 65 lx reflected from the cage walls, and 4 to 6 lx during a dim light period before night hours. During daytime, the monkeys could look out

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both into a garden and into the sky. Cleaning and feeding took place between 7 and 8 o'clock in the morning.

Isolates

Six squirrel monkeys were reared in social isolation under enriched substitute stimulus conditions as part of a developmental study. A species-adequate mother surrogate which allowed self-feeding, daily presentations of objects and auditory and vestibular stimulations was provided. Contact with caretakers and experimenters was kept to a minimum in order to avoid interspecies attachment. For further details see Herzog and Hopf (1983) and Hopf et al. (1984).

Spontaneous Alarm Behavior in Captive Groups

As a precondition for the analysis of stimulus components thorough knowledge of the spontaneous behavior and the response levels in the subjects is necessary. Therefore, a brief summary of predator-related behavior is given here.

Spontaneous alarm situations could be observed 1 to 6 times per day, e.g., a rook crossing the ceiling window of the cage at a height of 3 m, caused the animals to utter alarm peeps, dash off in various directions, and freeze. After about 3 s, the adult male became active again; 10 s later he returned to the feeding bowl on the cage floor where he was joined, after 23 and 25 s, respectively, by two of the females. The end of the alarm was characterized by species-typical "comfort movements" (Baerends and Baerends 1950), such as scratching, back-rolling, urine washing, and rubbing the face against the wall of floor (Hopf et al. 1974).

Artificial objects, if moved rapidly above the cage or at floor level, could reliably elicit the same behavior. No other stimulus situation, however, led to this response. Even fast-flying birds, when they were at a sufficient distance (more than 10 to 20 m), hardly ever elicited alarm behavior.

In terrestrial predator situations, motor and vocal behavior differed completely from that in avian predator situations: as soon as one animal had seen the potential predator, it yapped and the entire group immediately fled to the upper part of the cage where the animals, some of them yapping, crowded together under the wire mesh of the ceiling. From there, they intently faced the predator stimulus and continued yapping until it disappeared or even longer. Frequently, the adult male approached the predator, vigorously shaking the cage bars ("Wutrütteln", Ploog 1963; Ploog et al. 1963, 1967). When the alarm ceased, usually the male was the first to return to the ground or food.

In terrestrial predator situations, dependent infants were always carried by a female. They did not take part in yapping. In avian predator situations, however, they displayed the complete flight and freezing behavior on their own.

When a spotted cat model (yellow with black dots, 40 cm in size) was presented to the test group, the monkeys' response was hectic flight and yap vocalizations. The alarm usually lasted for approximately 3 to 5 min, sometimes up to 15 min, regardless of whether the 10-s presentation took place in the laboratory, at a distance of 4 m, or in the courtyard of the institute, at a distance of 30 m. Yaps were also heard when the caretaker removed an animal from the cage or when he or someone else entered the laboratory carrying a catcher net.

A survey of typical behavior sequences in avian and terrestrial predator alarm is given in Fig. 1.

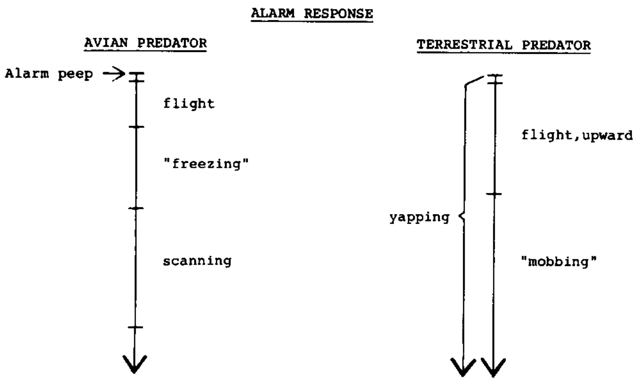

Fig. 1. Typical behavior sequences as response to avian and terrestrial predators

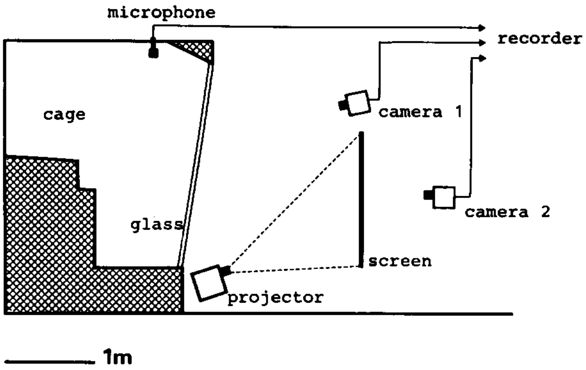

Fig. 2. Film projection in groups, and recording system for the ethometric analysis (camera 1) and stimulus control (camera 2)

Film Projection Study in Captive Groups

The previous investigations suggested that specific stimulus characteristics are effective in eliciting alarm responses. In this section, several of these characteristics were compared to pertinent control stimuli.

Procedure

A series of films was designed representing various predator patterns and relevant control stimuli. The films (Super-8 color film, Kodachrome 40) were presented to the squirrel monkey groups 1 and 2. A remote-controlled Bauer TS film projector, equipped with a halogen projection lamp (12 V/150 w), was used. The covered projector was placed immediately in front of the cage, the screen so that it faced the front window of the cage at a distance of 3 m and 1 m above the ground; the projected pictures were 1 m in width and 80 cm in height (Fig. 2).

Before a film presentation, the state of the group was assessed and recorded for 5 to 10 min. When some of the animals were aggressive or asleep, the presentation was postponed. A maximum of three different films (all of them taken with a Zeiss Ikon M811 Super-8 camera) were shown per day at intervals of 30 to 60 min. Each film began with a neutral background picture (Introduction) of about 30 s duration before the critical stimulus pattern appeared on this unchanged background. The stimulus patterns listed in Table 1 were presented to each group 3 to 5 times. Behavior was videographed, accompanied by a spoken comment from the experimenters.

Table 1. List of filmed stimulus patterns

Film no.	Contents
1, 2, 3	Spotted cat predators: ocelot, leopard, cheetah, passing frame in 5 s (0.2 m/s)
4, 5, 6, 7	Nonpredator mammals: capybara, guinea pig, rabbit, elephant, passing frame at 0.2 m/s
8	Dummy cat, yellow with black spots, is moved to and fro in the direction of observer (same object as in pilot study)
9	Control object: plastic bowl, yellow with 8 irregular black spots, is moved as described in 8
10	Same as 9, plain yellow, moved as described in 8
11	Living snake (Elaphe situla), brown with reddish spot pattern, curled position, then raising and thrusting head (catching movement)
12	Model of a boa constrictor, irregular black and red stripes, is moved as described in 8
13	Control object: wooden rod, natural color, size similar to 12, is moved as described in 8
16	Model of avian predator 1 (similar to the one used by Schleidt 1961): black silhouette on white background, moved horizontally at 0.5 m/s
17	Model of avian predator 2: as in 16, moved at 2 m/s
18	Model of avian predator 3: as in 16, moved vertically at 2 m/s
19, 20	Control models 1 and 2 of avian predator: black disc, black rectangle, on white background, moved horizontally at 2 m/s
21, 22, 23	Living avian predators, no locomotion visible: hawk, gliding, hovering; owl, perched
24, 25	Nonpredator birds: white hen, peacock, walking through frame
26	Food 1: peeling and cutting a banana
27	Food 2: cricket, walking through frame; green background
28	Food 3: fly, walking on window; light blue background
29	Human A, passive
30	Human A, passive, visible for 20 s, then reaching for a catcher net hidden behind a curtain and moving net in the direction of the observer
31	Human B, caretaker, male, "catcher 1": laboratory door closed (part of the usual outlook for the monkeys) for 20 s; then door opens and caretaker enters wearing his usual grey laboratory coat
32, 33	Humans C and D, controls: females wearing white laboratory coats, sequence as in 31
34	Human E, "catcher2", male, fully bearded, white laboratory coat, sequence as in 31, E standing for 15 s, then camera close-up of face
35,36	Humans F and G, controls to E: males, fully bearded, white laboratory coat, sequence as in 34

Vocal reactions were tape-recorded and selected samples analyzed sonographically.

Results

The subjects paid considerably more attention to the screen when films were shown, compared to the empty screen. In general, locomotor activities increased even during the introductory stage. When certain food or predator stimuli were presented, their visual interest was almost continuous, except for brief periods of locomotion.

The presentation of cat predators (films 1–3) and simple cat models (films 8–9) caused pronounced terrestrial predator reactions, flight to the ceiling area of the cage and repeated yapping (from 30 to 120 per test). Subsequent to only 10 to 15 s of stimulus presentation, it took the alarmed animals up to 9 (group 1) or 13 min (group 2), respectively, to calm down, with most frequent durations of 3 to 6 min.

The mammals (films 4–7) and the yellow plastic bowl without spots (film 10) caused only slight increase of facing, whereas, when the Capybara (film 4) appeared, close and tense attention and cackle calls were registered, but in no case was there an alarm response.

All displays of a living snake (film 11) and a realistic snake model (film 12) led to short-distance flight in both groups: in group 1 from 3 to 9, in group 2 from 6 to 18. The wooden rod (film 13) as a control object to snake patterns, had no specific effect on the animals' behavior.

Table 2. Number of alarm reactions to avian predators (AP) and control patterns (CP) per 5 presentations of each film to each group

Film no.	Stimulus pattern	Flight, scanning		Alarm peep	
		Group 1	Group 2	Group 1	Group 2
16	AP 1: horizontal, 0.5 m/s	4	4	1	–
17	AP 2: horizontal, 2 m/s	5	4	5	3
18	AP 3: vertical, 2 m/s	5	5	4	3
19	CP 1: disc, horizontal, 2 m/s	5	5	4	4
20	CP 2: rectangle, horiziontal, 2 m/s	5	5	4	5
21, 22, 23	Living AP, stationary: gliding, hovering or perched	–	–	–	–

Of the avian predator models, only those shown in films 17–20 (2 m/s) caused flight reactions and alarm peeps (Table 2). The model of an avian predator, moved at a speed of 0.5 m/s (film 16) evoked an alarm peep only once in group 1, but in all presentations the animals responded by flight, scanning (for up to 1 min) and cackling.

Table 3. Survey of behavioral reactions of groups to filmed food stimuli and humans associated with specific experience to the monkey

Film no.	Stimulus pattern	Behavioral responses	
		Motor	Vocal
26	Food 1: fruit	Active, approach	Twitter
27, 28	Food 2: insect, walking	Active, approach, prey-catching movements	Twitter
29	Human A	Neutral	–
30	Human A with catcher net	Flight, mobbing	Yapping
31	Caretaker ("catcher 1")	Flight, mobbing	Yapping
32, 33	Controls	Neutral	–
34	Human E ("catcher 2")	Flight, mobbing	Yapping
35, 36	Controls to E	Active, then relaxed	Cackle

The motor and vocal behavior patterns observed during the presentations of films 26–36 are depicted in Table 3. Film 26 shows the preparation of food. When shown this film, the animals reacted exactly in the same way as they did in the actual familiar situation: upon seeing the food, they increased their locomotor activities, jumped around in the cage, came near to the window and uttered long series of twitter calls. When insects were shown (films 27–28), they behaved similarly; some of the animals were observed jumping against the window, directing catching movements to the picture.

Comparative data were also available for evaluating the monkeys' behavior when confronted with human beings (films 29–33 in both groups, films 34–36 in group 1 only). The appearance of the caretaker at other than feeding times (film 31, "catcher 1"), who, among others, was responsible for occasionally removing animals from the group for medical examination, caused yaps and immediate flight. The same observations were made when persons carrying a catcher net entered the laboratory (films 29–30). In group 1, "catcher 2" had recently removed a dead neonate. When shown the "catcher 2" film (34), the group behaved as in a terrestrial predator situation. To the control persons shown in films 35 and 36, the animals responded with signs of motor tension and cackled. When close-ups of the control persons' faces were shown, the monkeys relaxed, which became apparent by their return to the feeding bowls on the ground.

Film Projection Study in Isolates

Procedure

As soon as the socially inexperienced subjects had developed a well coordinated locomotion (usually during their 2nd month of life), they were shown the filmed stimulus patterns. For film projection, the opaque front screen of the rearing chamber was used. The behavior of subjects D and F was observed and protocolled directly, that of H, I, J, and K was videographed (Fig. 3) and subsequently evaluated.

During the days before the start of the experiment, the monkeys were familiarized with dimming the light from the usual 60–70 lx to 5 lx, and with the noise of the running projector. Each test began with a 2-min pretest observation to determine the subject's state of activity. A maximum of three stimulus patterns were shown per day. Each subject saw the following films three times: predator patterns: film nos. 1, 3, 8, 11, 16, 17, 18, 19; food items: film nos. 26, 27, 28.

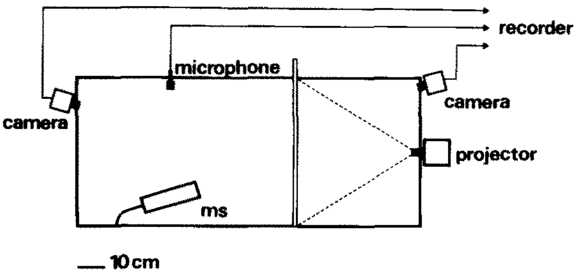

Fig. 3. Film projection in isolates

The behavior of the subjects was videographed and their vocalizations recorded.

Results

When the presentations began, the subjects usually climbed on the mother surrogate and, with typical fixation movements of the head, looked at the screen. After a few seconds, they left the surrogate, approached the screen, investigated the structures shown, tried to lick them (oral inspection), touch them or climb them. Neither the terrestrial predator models (films 1, 3, 8, 11) nor the food stimulus "fruit" (film 26) caused any changes in this behavior (Table 4).

In most of the experiments, the fast moving avian predator models (films 17–18), and the disc (film 19) evoked alarm peeps, flight, freezing and scanning behavior, but not so the slowly moving avian predator model (film 16).

When shown living insects (films 27–28), the subjects displayed prey catching behavior: they watched the moving insect intently for a while, then cautiously approached it and suddenly jumped towards the screen in an attempt to grab the insect. There were three instances in which the subjects, after jumping and grabbing, put the closed fist on the mouth and made a few chewing movements. The same behavior had been observed occasionally in the monkeys when flies, for instance, had entered the rearing chamber. At that age, however, they had not been able to consume solid food.

In Table 5 the behavioral reactions of socially isolated and socially experienced monkeys to various filmed stimulus patterns are compared.

Table 4. Number of species-specific responses per 3 presentations to each of 6 infant subjects reared in social isolation

Film no.	Stimulus pattern	Isolate subject					
		D	F	H	I	J	K
1, 3, 8	Cat	0	0	0	0	0	0
11	Snake	0	0	0	0	0	0
16	Avian predator, 0.5 m/s	0	0	0	0	0	0
17	Avian predator, 2 m/s	2	2	2	3	3	2
18	Same, vertical movement	–	–	2	2	3	3
19	Disc, 2 m/s	3	2	3	3	2	3
26	Fruit	0	0	0	0	0	0
27	Cricket	2	2	3	2	3	3
28	Fly	2	3	3	3	3	3

– not tested

Table 5. Behavioral responses to visual stimuli in socially experienced and inexperienced subjects

Film no.	Stimulus pattern	Wildborn adults (groups 1, 2)	6 Isolates
1,3,8	Cat	+	–
11	Snake	+	–
16	Avian predator, horizontal, 0.5 m/s	–	–
17	Avian predator, horizontal, 2 m/s	+	+
18	Avian predator, vertical, 2 m/s	+	+
19	Disc, 2 m/s	+	+
26	Fruit	+	–
27,28	Cricket, fly	+	+

+ Species-specific; – indifferent

Ethometric Analysis of a Visual Stimulus Quality of a Terrestrial Predator: Spot Pattern

According to the results of film presentations of natural cat predators (with spotted fur) and unicolor and spotted control objects (films 9–10), a quantitative analysis of the quality "spotted" was carried out.

Procedure

A series of yellow rectangles with 60 regular black spots was designed and filmed, with the spots covering 0.5% to 90% of the surface, plus the two unicolor patterns (= 0 and 100%, respectively). In the films, these patterns passed the frame horizontally in 5 s (= 0.33 m/s), between the green introductory and the end stage (20 s each) used for the predator film no. 1. An additional control stimulus film showed only the green color for 30 s. Each film was presented 10 times to groups 3 and 4. No more than three stimulus films were shown per day, including maximally one resulting in alarm. For comparison, film no. 1 (natural cat predator) was presented, under the same standardized conditions, as the 10th test to both groups.

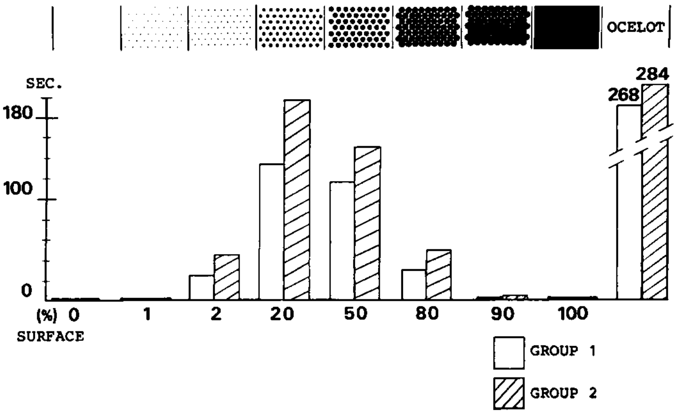

Fig. 4. Average duration of alarm responses to spot patterns (Mann-Whitney *U*-Test, one tailed: 2% vs 20% and 50%: $P \leq 0.01$; 80% vs 20% and 50%: $P \leq 0.01$)

Film presentations took place at the end of the day at dim light (2–6 lx), provided the group was awake and not extremely aroused. A small amount of sunflower seeds was scattered on the cage floor 10–15 min before a film presentation in an attempt to standardize the group activity (opening and eating seeds on the cage floor). The behavior of the group was videographed, their vocalizations recorded on video sound track 1, and the experimenters' comments on sound track 2 (Fig. 2). Evaluation focussed on five wild-born adults.

Results

The patterns of 2%, 20%, 50%, and 80% black portion were effective to elicit terrestrial alarm responses, with a maximum duration of alarm at 20% and 50% (Fig. 4). No clear-cut habituation effects were noted. The longest durations of alarm reactions occurred in both groups when young infants were present.

In most cases, the male initiated the alarm behavior by yapping. If a female yapped first, alarm behavior of the rest of the group did not ensue immediately in all cases, though females often yapped more frequently. During mobbing, males frequently vigorously jumped vertically or shook a movable object. It was also the male who ended the alarm behavior first.

Discussion

It was demonstrated that wild-born captive squirrel monkeys respond to filmed stimulus constellations with the same species-specific behavioral patterns as to the corresponding real situations. Thus it can be concluded that squirrel monkeys recognize color films as representations of highly varied objects and even complex situations.

In all cases, the film presentations of avian and terrestrial predators evoked adequate alarm and flight behavior. When the subjects were confronted, for comparative purposes, with stimulus constellations of an indifferent nature or featuring herbivorous animals, their neutral behavior clearly showed that the film projection technique itself did not stimulate the animals in an alarming and/or excitatory manner.

A matter of dispute in a series of psychological experiments was the primates' ability – or inability – to recognize photographs of stimuli. While Winner and Ettlinger (1979) and Ettlinger (1981) found that chimpanzees were not able, without special training, to match artificial "junk" objects to the respective photographs, Davenport and Rogers (1971) and Davenport et al. (1975) came to the conclusion, on the basis of similar tests, that their subjects could.

Species-typical responses to photographed food and predator stimuli were observed in New World monkeys, e.g., Cebus (Klüver 1933) and Saguinus (Wendt 1979). Recognition of facial characteristics of familiar conspecifics was shown, for instance, in rhesus monkeys (Rosenfeld and Van Hoesen 1979; Bruce 1982), hamadryas baboons (Kyes and Candland 1984) and chimpanzees (Bauer and Philip 1983). Obviously, with respect to processing of visual cues, the primates' cognitive abilities can best be investigated using species-relevant stimulus patterns.

Noteworthy in the study reported here is the fact that the subjects recognized faces alien to the species: they responded differentially to the "catcher 2" (film 34), even more than 3 months after the interference (removing dead neonate).

The responses in the test groups 1 and 2 to various bird presentations (films 15–25) demonstrated that the decisive factor in releasing alarm peep vocalizations and flight behavior was not the shape configuration but the speed component. Bird stimuli without locomotion did not influence the animals' behavior. Baldwin and Baldwin (1972) reported that wild squirrel monkeys did not seem to be alarmed by large birds as long as these were sitting on the branch of a tree. In response to a slowly moving bird model (film 16), the animals of both test groups were hesitant in their flight behavior but scanned the area of the screen for a considerable time. When the presentation was over, the animals uttered cackles instead of alarm peeps, a vocalization also heard when they were shown certain mammals or one of the less effective predator patterns. Songbirds are reported to display similar motoric alarm behavior, i.e., with the alarm call missing. According to Curio et al. (1973), a lower predator-determined level of excitation could account for graded alarm reactions which have been observed only in mildly alarming situations. The pied flycatcher is known to display such "silent" alarm behavior not only when alarmed by a predator but also when confronted with a rival. Similarly, the cackle of the squirrel monkey is a vocalization uttered in the course of agonistic social interactions before and after fights (Winter et al. 1966). According to the observations by Baldwin and Baldwin (1972), wild monkeys frequently utter cackle calls in avian predator situations; details as to the development of the accompanying motor behavior, however, were not given.

A dual function of the alarm peep and the yap, i.e., as a warning call and as a signal in social interactions, as described by Klump and Shalter (1984) for alarm calls of various songbird species, has not been observed in squirrel monkey so far.

Further information on the control of alarm behavior, especially on the genetic disposition of releasing mechanisms involved, was gained by stimulus experiments with animals reared in social isolation. The infant squirrel monkeys, which were provided with artificial substitute stimuli, exhibited the age-appropriate behavioral development (Ploog et al. 1967; King et al. 1974). Consequently, the influence of predator and food stimulus patterns on their spontaneous behavior could be examined.

The prompt display of the entire species-typical alarm response – alarm peeps and motor reaction components – clearly demonstrated that an Innate Releasing Mechanism (IRM) (Schleidt 1962) was involved in the visual identification of avian predator stimuli. Likewise, film presentations of insects initiated well-coordinated prey catching movements. The responses of the subjects to filmed neotropical cats and snakes suggested the absence of an IRM in the recognition of terrestrial predators.

As squirrel monkey populations living in different types of habitat have to cope with different terrestrial predators (Baldwin and Baldwin 1972), it seems likely that the visual characteristics of a particular predator species have to be learned by social experience. In squirrel monkeys reared in social isolation (Herzog and Hopf 1984) only the combined presentation of an object with the alarm call yapping resulted in prompt flight and sustained avoiding behavior. In the present study, the ethometrical analysis of spot pattern configurations representing a typical coat feature of neotropical feline predators yielded an elucidating example of a variable but well-defined "Acquired Releasing Mechanism" (Schleidt 1961, 1962).

Seyfarth and Cheney (1980) reported that in juvenile vervet monkeys a sharpened categorization of predator classes must develop over a number of years. A highly adaptive process of cultural transmission of enemy recognition generally should be important for primate species with a wide range of distribution.

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