ADAPTATION UNTO DEATH: FUNCTION OF FEAR SCREAMS

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Fear, or distress screams are emitted by animals in utmost danger, sometimes not until seized by a predator. The screams are far-reaching, long-lasting, and consist of irregular bouts including high and low frequencies (fig. 1), which make them easy to locate. They are also remarkably similar for different species. Fear screams are found mainly among birds and mammals, including man, although many species remain silent when captured. This differential propensity to scream in desperate situations has led to the formulation of the following hypotheses of fear scream function and evolution.

1. Fear screaming warns kin and is an altruistic act if it reduces the screamer's chance of surviving. As Perrone (1980) noted, however, conspecifics largely ignore the screams instead of fleeing or seeking cover. Also, a successful predator is harmful only to its captured prey.

2. Screams may startle the predator into loosening its grip, thereby giving the caller a chance to escape (Driver and Humphries 1969). If this effect were important, screams should be brief and explosive, but they are not. Another prediction from this hypothesis is that all similar-sized species should scream equally (see below).

3. Screams are calls for help, directed at kin or reciprocating animals (Rohwer et al. 1976), the latter not necessarily being related to the screamer. The caller's desperate situation makes reciprocation unlikely, unless the help provided has great survival value (Trivers 1971). Help in the form of distraction of, or attacks on predators is restricted to parents defending their young. Stefanski and Falls (1972) found that responses in sparrows (*Emberizidae*) declined rapidly after the reproductive period. Perrone (1980) found that fear screams did not attract conspecifics in the nonbreeding season. Therefore, this hypothesis explains the existence of fear screams in dependent young, but not in full-grown individuals during most of the year.

4. Screams are directed at other predators, which approach the arena in the hope of an easy meal (the screamer or the primary predator; see Curio 1976, p. 98). During the ensuing dispute between the predators, the prey will get a chance to escape.

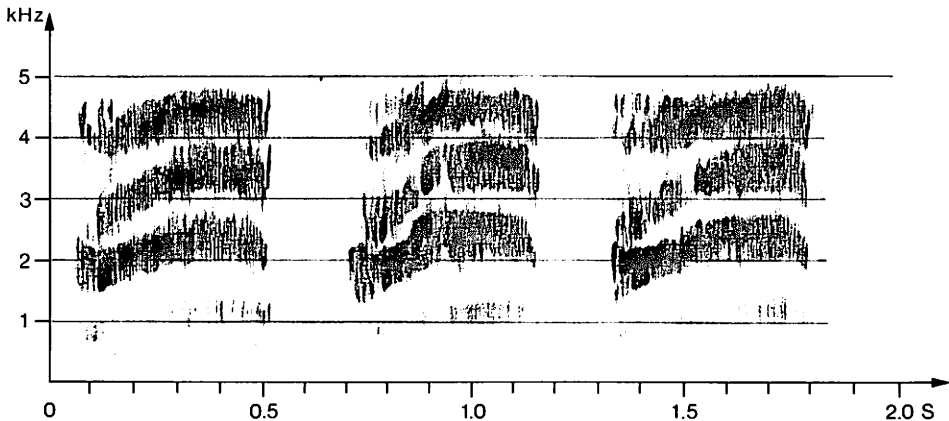Piracy is common among avian and mammalian predators, which use both

FIG. 1.—Fear screams of the European starling *Sturnus vulgaris*.

visual and acoustic cues to detect the capture (Kruuk 1972; Brockmann and Barnard 1979). Support for this hypothesis comes from Perrone's (1980) casual observation of raptors being attracted by fear screams. Incidentally, hunters formerly lured wolves to a screaming pig (Anon. 1872).

I suggest that fear screaming is a selfish trait, a cry for help directed at any animal capable of interfering with the threatening predator, be it an altruistic parent, a reciprocating individual, or a selfish, secondary predator (pirate). Here I report on the response by predator species to the playback of fear screams, examine how screaming propensity is influenced by various factors, and discuss how this behavior may have evolved.

PREDATOR RESPONSE TO FEAR SCREAMS

The predator attraction hypothesis was tested by broadcasting fear screams of the European starling *Sturnus vulgaris* from a concealed loudspeaker. Once a predator was detected, the loudspeaker was hidden at a distance of 100–250 m from the animal being tested. At the start of the experiment the observer was approximately 200 m perpendicular to a line between the predator and the loudspeaker, ready to measure the duration of the approach.

As seen in table 1 most predator species responded positively, the only exception being the kestrel *Falco tinnunculus*, a comparatively small and weak raptor. It seems that predators have to learn to associate fear screams with easily obtained food; eight young (2.5–3.5 mo) common buzzards *Buteo buteo* showed no response to broadcast screams, whereas 14 out of 24 unaged birds of the same species responded positively ($P < .01$; Fisher exact probability test). Probably, such an association is learned at an earlier age in predators which train their young with live prey (see Newton 1979, p. 162).

To prevent the prey from being swallowed or silenced and carried away, secondary predators should hurry toward the scream. Approach speeds for five common buzzards, corrected for wind velocity, were 12.3, 13.7, 15.2, 15.7, and

TABLE 1

PROPORTION OF PREDATORS APPROACHING BROADCAST FEAR
SCREAMS OF THE EUROPEAN STARLING *Sturnus vulgaris*

Species	Approximate Weight (g)	N	% Approaching
Common buzzard, *Buteo buteo*	900	32	44
Rough-legged buzzard, *Buteo lagopus*	1,000	3	33
Goshawk, *Accipiter gentilis*	1,300	1	100
Sparrowhawk, *Accipiter nisus*	200	4	50
Hen harrier, *Circus cyaneus*	400	10	40
Kestrel, *Falco tinnunculus*	200	7	0
Red fox, *Vulpes vulpes*	7,500	4	100
Feral cat, *Felis domesticus*	4,000	3	67

16.2 m/s (mean speed approximately 15 m/s), which is faster than the speed of actively flying buzzards on migration, 9–12 m/s (T. Alerstam, personal communication).

SURVIVAL VALUE FOR THE SCREAMER

The probability that a captured prey individual will survive and escape because of interference from a secondary predator (p_s) is the product of the probabilities that a secondary predator interferes before the prey is disabled (p_d) and that the prey manages to escape in the ensuing dispute (p_e). Therefore,

$$p_s = p_d \cdot p_e .$$

The probability that a pirate interferes before the prey is disabled (p_d) can be restated as the probability that there is a scream-responding predator within a circle of radius r_d, the distance covered by such a pirate in time t_d (disabling time). Therefore,

$$p_d = 1 - e^{-\lambda r_d^2}$$

(see Pielou 1977, p. 149).

Here λ is the mean number of responding, potentially successful pirates within a circle of unit radius. As dominance largely follows size, λ represents the density of responding pirates that are larger than the primary predator.

The probability of escaping the disputing predators (p_e) is certainly small, though not zero (see Bent 1938; Walter 1979). In the following discussion this probability is not dealt with, but it should be kept in mind that the factors (relative size of prey, size of primary predator, and kind of habitat) discussed for p_d have the same effect on p_e, and therefore reinforce the predictions made from variations in p_d.

p_s is influenced more strongly by variations in r_d than in λ, because r_d is squared. r_d is determined by disabling time (t_d), and because larger prey, in relation to the

TABLE 2

PROPORTION SCREAMERS, MIGRATIONAL STATUS, AND WEIGHTS OF MIST-NETTED BIRDS

Species (m) = migrant (r) = resident	% Screamers	N	Weight (g)
Aerial or open-ground species			
Swift, *Apus apus* (m)	5	699	42
Sand martin, *Riparia riparia* (m)	7	111	15
Swallow, *Hirundo rustica* (m)	6	69	19
House martin, *Delichon urbica* (m)	3	71	19
Tawny pipit, *Anthus campestris* (m)	0	108	24
White wagtail, *Motacilla alba* (m)	0	22	21
Species in moderately exposed habitats			
Great spotted woodpecker, *Dendrocopos major* (m)	98	47	90
Tree pipit, *Anthus trivialis* (m)	10	29	22
European robin, *Erithacus rubecula* (m)	19	773	16
Redstart, *Phoenicurus phoenicurus* (m)	17	170	16
European blackbird, *Turdus merula* (r)	65	26	105
Song thrush, *Turdus philomelos* (m)	72	69	70
Lesser whitethroat, *Sylvia curruca* (m)	12	144	11
Whitethroat, *Sylvia communis* (m)	14	146	15
Blackcap, *Sylvia atricapilla* (m)	19	134	18
Chiffchaff, *Phylloscopus collybita* (m)	9	34	8
Willow warbler, *Phylloscopus trochilus* (m)	13	780	9
Spotted flycatcher, *Muscicapa striata* (m)	33	27	18
Pied flycatcher, *Ficedula hypoleuca* (m)	13	30	14
Redbacked shrike, *Lanius collurio* (m)	31	61	32
European starling, *Sturnus vulgaris* (m)	61	18	80
House sparrow, *Passer domesticus* (r)	20	20	30
Chaffinch, *Fringilla coelebs* (m)	6	47	23
Siskin, *Carduelis spinus* (m)	4	114	14
Species constantly living in dense cover			
Wren, *Troglodytes troglodytes* (m)	32	22	9
Thrush nightingale, *Luscinia luscinia* (m)	73	48	25
Marsh warbler, *Acrocephalus palustris* (m)	59	68	12
Reed warbler, *Acrocephalus scirpaceus* (m)	83	173	12
Icterine warbler, *Hippolais icterina* (m)	87	53	13
Garden warbler, *Sylvia borin* (m)	47	108	18

NOTE.—Main predators of these species are the European sparrowhawk and equal-sized falcons (*Falconidae*).

primary predator, take longer to kill, increasing relative prey size greatly increases p_s and therefore should promote screaming. Also, large size enables an animal to scream louder, thus reaching those distant pirates that are fast enough to interfere within time t_d. Therefore I expect increasing relative prey size of a given predator to be correlated with an increasing tendency to scream.

On the other hand, for a given prey species increasing size of the primary predator lowers λ, the density of responding pirates that are larger than the primary predator within a unit circle. For that reason I expect prey of large predators to scream less than prey of small ones.

In open habitats most pirates become aware of a capture by sight, whereas a

TABLE 3

PERCENTAGE OF SCREAMERS AMONG ADULTS (>9 mo old) AND JUVENILES (<3 mo old)

Species	Adult (N)	Juvenile (N)	P
Marsh warbler			
Acrocephalus palustris	60 (30)	58 (38)	>.90
Reed warbler			
Acrocephalus scirpaceus	84 (148)	76 (25)	>.40
Whitethroat			
Sylvia communis	14 (117)	14 (29)	. . .
Garden warbler			
Sylvia borin	49 (75)	42 (33)	>.60
Blackcap			
Sylvia atricapilla	18 (66)	19 (68)	>.90
Willow warbler			
Phylloscopus trochilus	12 (475)	14 (305)	>.30
European robin			
Erithacus rubecula	20 (410)	18 (363)	>.50
Song thrush			
Turdus philomelos	63 (16)	75 (53)	>.40

capture in more dense vegetation must be detected by acoustical cues. Therefore, prey species living in closed habitats should scream more than open-habitat species of the same size.

These predators were tested by comparing screaming frequencies of captured (mist-netted) birds, as shown in table 2. It should be noted that screaming rates are independent of handler (cf. Perrone and Paulson 1979) and of age of full-grown birds (tables 3, 4), the latter stressing the adaptive value of screaming all the year round. The species in table 2 are regular prey of small raptors, which are frequently harassed by pirates. Therefore, these prey species could be expected to scream according to the above predictions.

To analyze the effect of habitat exposure I divided the species in table 2 into three groups: aerial and open-ground species, species in moderately exposed

TABLE 4

PERCENTAGE OF SCREAMERS IN SAMPLES FROM TWO DIFFERENT HANDLERS
(All birds juveniles [<3 mo old])

Species	Handler 1 (N)	Handler 2 (N)	P
Garden warbler,			
Sylvia borin	39 (19)	57 (14)	>.50
Blackcap,			
Sylvia atricapilla	30 (20)	17 (36)	>.30
Willow warbler,			
Phylloscopus trochilus	12 (107)	13 (108)	>.80
European robin,			
Erithacus rubecula	17 (179)	17 (143)	. . .
Song thrush,			
Turdus philomelos	77 (31)	73 (22)	>.90

habitats, and species living the year round in extremely dense habitats. As expected, open-habitat species scream much less frequently than moderately exposed ones ($P < .001$; one-tailed Mann-Whitney U-test), and these in turn scream less frequently than the skulking species in the third group ($P < .01$; one-tailed Mann-Whitney U-test).

Within the group of moderately exposed birds there is a high correlation between screaming frequency and weight ($r_s = 0.75$; $P < .001$, Spearman rank correlation), which is consistent with the prediction that larger prey take longer to disable and can produce louder screams than do small prey, i.e., have a larger r_d. Perrone (1980) suggested that large prey struggle to free themselves, but that this behavior is less profitable for smaller prey. Struggling and screaming are correlated (Perrone 1980), both leading to a prolonged killing process (increasing t_d and r_d), but they are not restricted to large prey species. If the startling effect alone explains the frequency of screaming, we should expect a straight correlation between fighting ability (size) and screaming propensity, not obscured by habitat exposure. This latter factor has a great impact on screaming frequency (table 2) and since the adaptive value of startling the predator should be independent of habitat exposure, I conclude that the startling effect does not explain the variation in screaming propensity.

The effect of predator density cannot be evaluated here, but one would expect that prey species constantly living in low-density areas (e.g., taiga) would scream less than prey species in high-density areas. Also, in a predator-rich area, prey of the largest predators (e.g., lion) should scream less frequently than prey of smaller predators, but I know of no quantitative data on this point. However, Kruuk (1972) and Schaller (1972) mention that many smaller herbivores scream or bleat when killed, but no such remarks refer to adults of larger prey species.

Rohwer et al. (1976) suggested that captured birds scream in order to get help from relatives, and therefore predicted that resident species are more apt to scream than migratory ones, the former having more kin in their vicinity. However, the positive correlation between screaming frequency and residency they found may simply reflect the fact that resident temperate bird species tend to be larger ($P < .05$ in table 2 in Rohwer et al. [1976]; weights from Terres [1980]), and therefore scream more often than migratory species. I compared six pairs of ecologically similar residents and migrants of roughly the same weights (both members of a pair were taken from the same study since methods may have varied) and found no pattern of screaming propensity (table 5). Residents screamed more in three pairs (significantly more in one); migrants screamed more in two pairs (significantly more in one pair); and in one pair neither species screamed at all. I therefore conclude that residency does not promote screaming. It must be kept in mind that most animals disperse after the breeding season and that even moderate movements lead to much reduced probabilities of encountering kin, particularly in dense populations.

To attract potential pirates from a great distance, fear screams should be far-reaching and easily locatable. First, fear screams are sometimes emitted before the prey has been captured, leading to increased values of t_d and r_d. Second, screams are high-intensity calls of a moderate pitch, which maximizes their

TABLE 5

SCREAMING FREQUENCY IN RELATION TO MIGRATIONAL STATUS IN PAIRS OF ECOLOGICALLY SIMILAR SPECIES OF APPROXIMATELY SIMILAR WEIGHTS

Resident Species	% Screamers	N	Migrant Species	% Screamers	N	P	Source
House finch			Purple finch				
Carpodacus mexicanus ...	0	61	*Carpodacus purpureus*	70	10	<.01	Rohwer et al. 1976
Cardinal							
Richmondena cardinalis			Evening grosbeak				
Pyrrhuloxia	87	31	*Hesperiphona vespertina* ...	55	11	<.05	Rohwer et al. 1976
Pyrrhuloxia sinuata							
American robin			Varied thrush				
Turdus migratorius	82	11	*Ixoreus naevius*	55	11	>.10	Perrone 1980
Song sparrow			Fox sparrow				
Melospiza melodia	0	8	*Passerella iliaca*	0	14	. . .	Perrone 1980
European blackbird			Song thrush				
Turdus merula	65	26	*Turdus philomelos*	72	69	>.80	This study
House sparrow			Chaffinch				
Passer domesticus	20	20	*Fringilla coelebs*	6	47	>.10	This study

effective distance (Marten and Marler 1977). Finally, they are composed of several distinct frequency bands (fig. 1), a feature increasing locatability of the call (Knudsen 1980).

The selective advantage of fear screams is most evident for dependent young that benefit from parental protection. It is therefore tempting to interpret the existence of screaming among full-grown, solitary animals as an extension of a juvenile trait into adulthood. However, the high incidence of screaming in many species, independent of age (table 3), points to a continuous adaptive value of the behavior. Moreover, the fact that some anurans, which do not care for their young, produce fear screams (Rohwer et al. 1976), suggests that in some cases this behavior has evolved independently of parent-young relations.

SUMMARY

A high frequency of rapid predator approach to broadcast fear screams supports the predator attraction hypothesis in explaining the function of screaming. A high incidence of screaming in prey species that are relatively large in relation to their main predators and live in densely vegetated habitats is concordant with this view. Contrary to earlier reports, I therefore conclude that fear screaming is a nonaltruistic phenomenon and that it is not maintained through kin selection.

LITERATURE CITED

Anonymous. 1872. Kort handledning i jagt och djurfångst [Short introduction for hunting and animal capture]. Sigfrid Flodin, Stockholm.

Bent, A. C. 1938. Life histories of North American birds of prey. U.S. Nat. Mus. Bull. 170.

Brockmann, J. H., and C. J. Barnard. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487–514.

Curio, E. 1976. The ethology of predation. Springer, Berlin.

Driver, P. M., and D. A. Humphries. 1969. The significance of the high-intensity alarm call in captured passerines. Ibis 111:243–244.

Knudsen, E. I. 1980. Sound localization in birds. Pages 289–322 in A. N. Popper and R. R. Fay, eds. Comparative hearing in vertebrates. Springer, New York.

Kruuk, H. 1972. The spotted hyena. University of Chicago Press, Chicago.

Marten, K., and P. Marler. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav. Ecol. Sociobiol. 2:271–290.

Newton, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Berkhamsted, England.

Perrone, M. 1980. Factors affecting the incidence of distress calls in passerine birds. Wilson Bull. 92:404–408.

Perrone, M., and D. R. Paulson. 1979. Incidence of distress calls in mist-netted birds. Condor 81:423–424.

Pielou, E. C. 1977. Mathematical ecology. 2d. ed. Wiley, New York.

Rohwer, S., S. D. Fretwell, and R. C. Tucksfield. 1976. Distress screams as a measure of kinship in birds. Am. Midl. Nat. 96:418–430.

Schaller, G. B. 1972. The Serengeti lion. University of Chicago Press, Chicago.

Stefanski, R. A., and J. B. Falls. 1972. A study of distress calls of song, swamp, and white-throated sparrows (Aves: Fringillidae). I. Intraspecific responses and functions. Can. J. Zool. 50:1501–1512.

Terres, J. K. 1980. The Audubon Society encyclopedia of North American birds. Knopf, New York.

Trivers, R. L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46:35–57.

Walter, H. 1979. Eleonora's falcon: adaptations to prey and habitat in a social raptor. University of Chicago Press, Chicago.