CHAPTER 7

Physiological Responses of Wildlife to Disturbance

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Walter Cannon, at Harvard Medical School, was the first to systematically investigate the physiological responses of animals to disturbance. As early as 1929, he showed that disturbance produced dramatic physiological changes that helped animals survive during an emergency. In the laboratory, when an animal was confronted with situations that evoked pain, fear, or rage, a well-defined set of physiological reactions that prepare it to meet the threat was activated. Cannon used the term "fight or flight response" to describe this event (Cannon 1929), a concept every student of physiology is familiar with.

The complexity of physiological and behavioral responses to disturbance has been studied by other investigators (Folkow and Neil 1971; Mayes 1979). A more descriptive term for the fight or flight response is the "active defense response." Some of the physiological adjustments described for birds and mammals include increased heart rate and respiration, increased blood flow to skeletal muscle, increased body temperature, elevation of blood sugar, and reduced blood flow to the skin and digestive organs (Fig. 7.1). A detailed list of physiological adjustments associated with the active defense response is shown in Table 7.1. Most of these adjustments are controlled by the sympathetic portion of the autonomic nervous system and involve release of adrenaline. Each of these alterations improves the chances of survival under conditions where prolonged strenuous activity might be necessary, as in fighting or fleeing.

One example is a rabbit disturbed by a predator. If the rabbit runs and is pursued by the predator, the rabbit is then running for its life, and its survival depends on speed, agility, and knowledge of the area. The rabbit makes sudden turns for cover to try to elude the predator. The physiological adjustments made by the rabbit include increased sympathetic activity, which

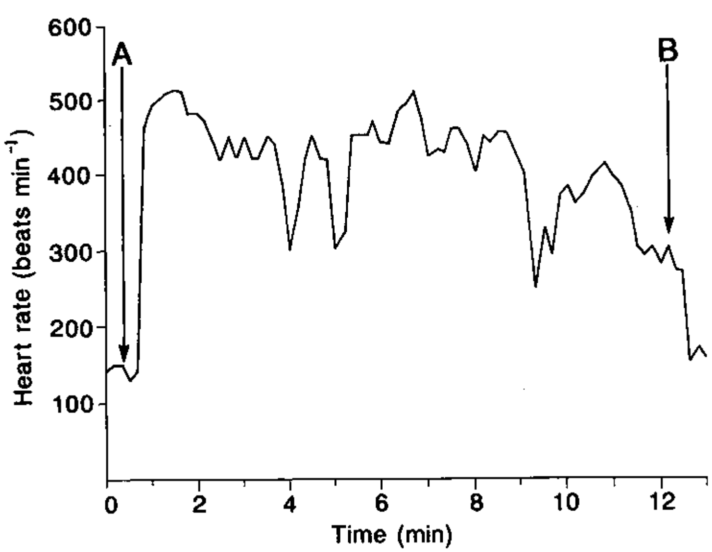

Figure 7.1 Heart rate response in a wild, nonincubating ptarmigan hen when approached by a human, showing the "fight or flight response." The disturbance begins at point A, and the human leaves the area at point B. From Steen et al. (1988).

Table 7.1

Physiological Changes Associated with the Active Defense Response

The Following Parameters Increase:	
Behavioral activity	Respiration rate
Heart rate	Respiration depth
Metabolism	Oxygen consumption
Blood sugar	Brain blood flow
Body temperature	Heart blood flow
Skeletal muscle blood flow	
The Following Parameters Decrease:	
Blood flow to the gut	
Gut motility	
Digestive secretions	
Blood flow to the skin?	

increases heart rate and cardiac output. Blood sugar is increased to support prolonged activity. Blood flow to skeletal muscle is increased to enable greater speed, agility, and endurance. Increased blood flow to the brain and sense organs heightens perception and reduces reaction time.

If an animal is cornered or caught by the predator, fear turns to anger or defensive aggression. Many animals will make threatening sounds or assume threatening postures ready to fight and defend themselves or their young. Even the most loving lap-cat arches its back, spits, and becomes a formidable combatant when approached by a strange dog. Again, the sympathetically dominated active defense response is involved. Many of the same physiological responses that enabled increased speed, agility, and sensory acuity while running prepare an animal for fighting.

Assume our hypothetical rabbit is feeding, grooming, or sleeping. Before it can run or hide, it must be aware of the danger. Any mild sensory stimuli will alert the rabbit. It may be sight, sound, smell, or some other sensory modality such as ground vibration from a person walking. Most mammals will look around, sniff the air, and move their ears. This behavioral response was called the "What is it?" response by Pavlov in 1927. Today it is called the "orienting response," and it usually precedes either the active or passive defense response (Fig. 7.2). The orienting response involves head and eye movements in which the animal orients the sense organs toward the stimulus, apparently in an attempt to identify it. If the stimulus is neutral, such as the distant call of a crow, the rabbit will continue its original behavior. If instead it announces the approach of a potential predator or a human, the animal will apply either the active or passive defense response.

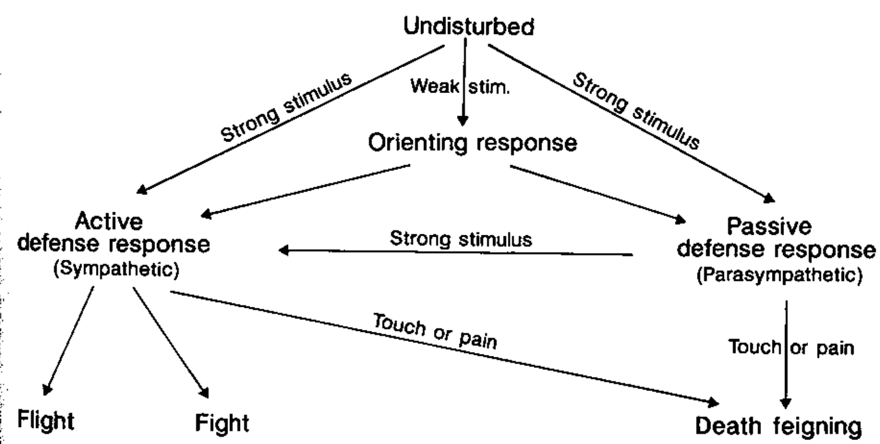

Figure 7.2 A schematic showing how disturbance affects wildlife.

The outcome depends on the age of the prey, the amount of cover, distance to the predator or human, and several other factors. Jacobsen (1979), for example, showed that the near approach of humans will cause newborn white-tailed deer to drop to the ground and hide. After the fawns are two-weeks old, the same stimulus will cause them to run.

The passive defense response involves profound physiological adjustments. Some of the major physiological adjustments for animals exhibiting the response include inhibition of activity, decreased blood flow to skeletal muscle, reduced blood flow to the digestive system, reduced heart and respiratory rate, and a reduction of body temperature. A detailed list of physiological adjustments associated with the passive defense response is shown in Table 7.2. Most of these alterations are controlled by the parasympathetic portion of the autonomic nervous system, and are opposite to the effects of the active defense response.

Two examples will illustrate the typical passive defense response. Perhaps the most insightful study of this response was done in Canada, with deer mice. Rosenmann and Morrison (1974) found that the response could easily be elicited by moving the shadow of a fan across the cage. In response to this stimulus, the mice would stop all activity for the duration of the stimulus. Respiration rate and depth decreased. Heart rate slowed suddenly and oxygen consumption was reduced. Body temperature dropped, especially when the ambient temperature was low, probably as a result of the reduced circulation to the muscles and skin area. Their study demonstrated the profound and far-reaching physiological alterations associated with the passive defense response.

The second example is from studies of willow grouse at Karlsøy, an island off the coast of northern Norway (Gabrielsen et al. 1977, 1985; Steen et al. 1988). Radio telemetry measurements of the heart rate of wild, incubating

Table 7.2

Physiological Changes Associated with the Passive Defense Response

The Following Parameters Decrease:	
Behavioral activity	Respiration rate
Heart rate	Respiration depth
Metabolism	Oxygen consumption
Blood sugar	Brain blood flow
Body temperature	Heart blood flow
Skeletal muscle blood flow	
Digestive blood flow?	
Skin blood flow?	

willow grouse hens varied from 120 to 140 beats per minute (bpm). Upon approach to a distance of two to four meters by a human or dog, the bird would become motionless, and the heart rate would drop to less than 30 bpm. On one occasion, the heart rate remained at 40 bpm throughout a five-minute period of provocation. The heart rate returned to pre-stimulus values when the human or dog retreated (Fig. 7.3). In both of these examples, the passive defense response was elicited by the apparent danger, and the animals remained motionless. It would appear from these and other studies that the response may help the animal remain hidden in the presence of perceived danger.

Hiding is not the only expression of the passive defense response. Under certain conditions many animals appear to faint or feign death. From antiquity, hunters no doubt observed prey species freezing or "playing dead" when approached. Death-feigning in the American opossum is so well known that the term *playing possum* has become widely used in American culture. Experimentally induced death-feigning was reported over 300 years ago by Kircher

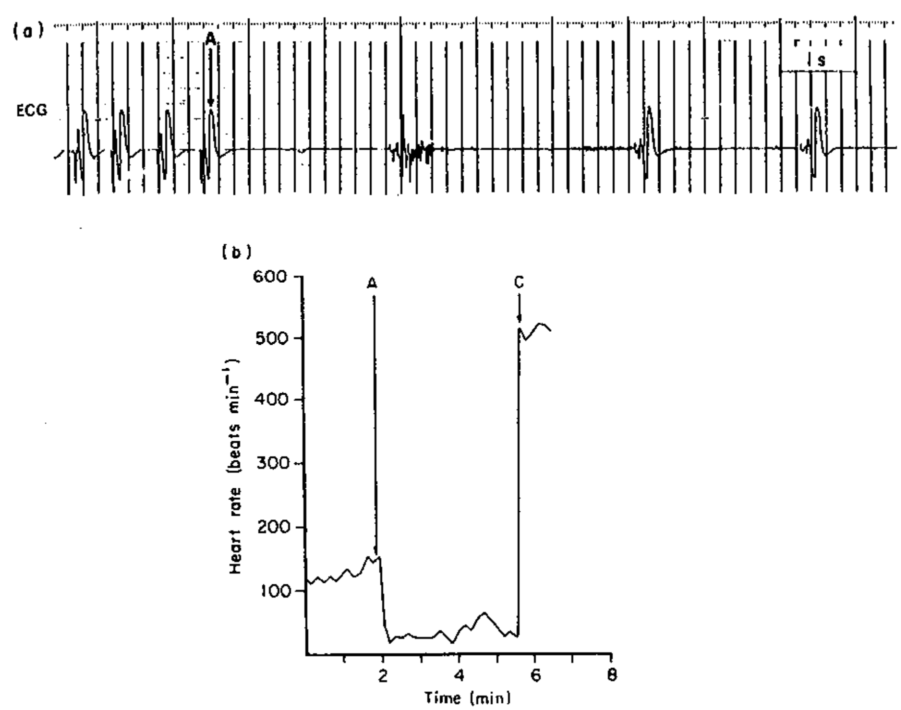

Figure 7.3 Provocation of a wild incubating willow ptarmigan hen. (a) ECG records from a wild incubating ptarmigan hen approached by one person. (b) Heart rate response in a wild incubating ptarmigan hen when approached by one person. The provocation starts at point A, and the hen flies away from the nest at point C. From Steen et al. 1988.

(1646). He found that certain manipulations of chickens resulted in "entrancement."

The passive defense response has been described for a wide array of vertebrates (Table 7.3). Fish stop swimming in response to ground or sound vibrations. Turtles become motionless when disturbed while free diving. Chickens become motionless and drop their heart rate at the sight of a hawk. Deer fawns become motionless, drop their heart rate, and stop breathing for minutes when alarmed by approaching humans. Regrettably, there are nearly as many

Table 7.3

Animals Showing the Passive Defense Response with Documented Bradycardia

Fish	Bluegill sunfish, *Lepomis marcochirus rafinesque*
	Chum salmon, *Oncorhynchus keta*
	Eel, *Anguilla anquilla*
	Ganoids, *Acipencer sturio*
	Atlantic cod, *Gadus morhua*
	Atlantic salmon, *Salamo salar*
Reptiles	Ornate box turtle, *Terepene ornata*
	Spectacled caiman, *Caiman crocodilus*
	American alligator, *Alligator mississippiensis*
Birds	Willow grouse, *Lagopus lagopus*
	Svalbard ptarmigan, (*L. mutus hyperboreus*)
	Pochards, *Aythya ferina*
	Tufted ducks, *Aythya fuligula*
	Common eider, *Somateria mollissima*
	Crested cormorants, *Phalcrocorax auritus*
	Canadian goose, *Branta canadensis*
Mammals	White-tailed deer, *Odocoileus virginianus*
	Red deer, *Cervus elaphus*
	Deer mouse, *Peromysus maniculatus*
	Swamp rabbit, *Sylvilagus aquaticus*
	Cotton tail rabbit, *Sylvilagus floridanus*
	Eastern chipmunk, *Tamias striatus*
	Ground squirrels, *Citellas armatus*
	Woodchuck, *Marmota monax*
	Fox squirrel, *Sciurus niger*
	Grey squirrel, *Sciurus carolinesis*
	Brazilian opossum, *Didelphis albiventris*
	American opossum, *Didelphis marsupialis*
	Harp seal, *Phoca groenlandica*
	Manatee, *Trichus manatus*
	Man, *Homo sapiens*

names given to the passive defense response as there have been workers investigating it. Kircher (1646) first used *entrancement*, but the term is too anthropomorphic to be accepted today. Throughout most of the nineteenth century, it was thought to be a form of hypnosis. At the turn of the century, Darwin (1900) introduced the term "death-feint." It is now generally accepted that this is one aspect of the passive defense response.

Recreational Influences

Over the last twenty years, we have telemetered a variety of wild animals, and investigated their behavioral and heart responses to humans or predators (Gabrielsen et al. 1977; Smith and Sweet 1980; Smith and Woodruff 1980; Causby and Smith 1981; Smith et al. 1981; Smith and Johnson 1984; Gabrielsen and Smith 1985; Gabrielsen 1985; Gabrielsen et al. 1985; Steen et al. 1988). In each case, if the animals had cover or a safe hiding place, they exhibited the passive defense response when threatened.

Woodchucks were telemetered and released on a small island on an Oklahoma lake (Smith and Woodruff 1980). When disturbed by a human or dog, they retreated toward their burrows and showed the active defense response, including increased heart rate. Upon reaching their burrows they immediately responded with the passive defense response, including reduced respiration and heart rate. The amount the heart slowed was stimulus dependent. When a dog or human approached the burrow and began digging, the heart rate would again slow down. Similar results were obtained with eastern chipmunks.

The next series of animals included fox squirrels, grey squirrels, swamp rabbits, and cottontail rabbits (Smith and Sweet 1980; Causby and Smith 1981; Smith and Johnson 1984). These animals were released on the same island. After an adjustment period ranging from a few days to a few weeks, their heart rate was measured by radio-telemetry with and without disturbance. Nondisturbance values were used to establish normal values. Measurements were made from a blind while observing the animals behavior. Animals were then approached by a human or a dog. If the animals were away from cover, they would first retreat to cover with the active defense response and increased heart rate, and then engage in the passive defense response. When the squirrels were disturbed, they would simply hide by slipping around the tree out of sight. Heart rate would often drop by 60%. If the human or dog retreated, the heart rate would return to predisturbance values. If the human or dog approached too closely, the animal would flee with increased heart rate and the active defense response. Heart rate was observed to increase from less than 200 bpm to over 450 bpm within a single heart-beat interval.

Similar results were obtained with rabbits, which would often hide by remaining motionless, lower their profile, and decrease their heart rate by about 60% to 80% (Causby and Smith 1981). If the intruder backed off, their behavior and heart rate would return to pre-stimulus values. If instead, the intruder approached the rabbit to within two to three meters, it would immediately switch over to the active defense response. Heart rate often increased from less than 50 bpm to over 200 bpm within a single heart beat.

Wildlife display either of the two fundamental strategies available to prey species when confronted with humans. Depending on the situation, either the fight-and-flight or the freezing/playing-dead response may be initiated. The physiological capacity for both options is available. Newborn deer or a ptarmigan hen on the nest will freeze. The deer's chance of being killed if moving and the hen's chance of losing her eggs if she is flushed are much greater than if they remain motionless. Both animals rely on cryptic coloration for camouflage. That this strategy is appropriate is attested to by the observation that neither a trained dog nor a keen researcher's eyes are of much use in finding incubating ptarmigan hens.

The passive defense response in squirrels, rabbits, opossums, deer fawns, and ptarmigan hens differ both behaviorally and physiologically. The deer fawn and opossum play dead; they will not move even if touched and can only be awakened by removing the provocation. Foxes hunting ground-breeding ducks (Sargeant and Eberhardt 1975) appeared to be fooled by this response, and cats would not bite a mouse as long as it remained still. In contrast, rabbits, eiders, and ptarmigan hens on the nest are fully awake and will switch to flight reaction once the disturbance becomes an immediate threat to their life.

A review of the literature suggests that the passive defense response is present in all animals: invertebrates, fish, amphibians, reptiles, birds, and mammals, when subjected to strong fear, pain, anger, sudden shock, or situations with few possibilities for escape. The passive defense response is related to age, and is well developed in newborn mammals. Passive defense may be as widespread as active fight and flight, and may be an important alternative behavioral and physiological response to disturbance. We suggest that both freezing or feigned death are developments of the more general passive defense response. We recognize that important differences exist between these responses and agree that more data from a variety of animals under natural conditions are needed.

Management Options for Coexistence

Behavioral and physiological research on the effect of human disturbance on wildlife has shown that several species are very tolerant of the noise from aircraft and from engines of cars, motorcycles, and snowsmobiles at a distance of one to two km. (MacArthur et al. 1979, 1982; Olsson and Gabrielsen 1990; Tyler 1991; Langvatn and Andersen 1991). At shorter distances, the active defense response may be activated when the vehicles head directly toward the victim. However, the most dramatic physiological defense response is observed when wildlife are provoked by humans (also see MacArthur et al. 1979, 1982). This is probably because mechanical disturbance is most often very brief, while humans walking take more time to cover the same distance, and thus have a much more profound effect. The magnitude of the response also depends on the distance, the movement pattern of the provoker, and the animal's access to cover. Most animals seem to tolerate disturbance better in woodland than in open terrain. They also seem to have a greater defense response to humans moving unpredictably in the terrain than to humans following a distinct path. To reduce the effects of human disturbance, permanent paths should be used or traffic should be restricted or reduced to certain times of the year in sensitive areas.

Studies of the effect of human disturbance on wildlife have revealed that there are two critical periods for many species of birds and mammals. The immediate postnatal period in mammals and the breeding period in birds are the most vulnerable. During these times, human disturbance should be prevented or reduced to a minimum. While most animals show active fear when disturbed and may respond by running, jumping, swimming, or flying away rapidly, there are some animals that, during a certain stage of the breeding cycle, show the passive defense response. Both the behavioral and the physiological responses are profound and are important to the individual's fitness.

This can be illustrated by incubating common eiders, which were studied in the high Arctic (Gabrielsen 1985; Gabrielsen et al. 1991). Female eiders do not eat for 25 days during incubation. To avoid predation and to maintain a constant egg temperature, they must rely on stored body reserves, mainly body fat, during the incubation period. At this time they lose 40% of their body weight. By seldom leaving the nest, and by using as little energy as possible, the eiders lose only 20 to 25 grams of body weight per day. Disturbance, including provocation by humans, and repeated reheating of eggs on their return to the nest, results in increased energy requirements, meaning further loss of essential energy needed later to raise their young. An increase in activity level of 10% per day would result in an extra daily weight loss of four to five grams. In time, this would result in a weight loss that would cause the bird to abandon incubation or to give up its chicks at hatching in order to save itself.

In the spring, people may find newborn deer freezing or playing dead. People should avoid touching these animals, because the parents may then abandon them. Human touch has a profound effect on animals. This can be illustrated using an example from studies of chinstrap penguins in Antarctica (Rory Wilson, pers. comm.). A breeding bird was provoked and touched for 30 seconds, but not removed from the nest. Such an event increased the stomach temperature by 2°C and it took two to three hours to return to normal (37.5° to 38°C). This clearly shows a great physiological effect of human disturbance on the penguin. Such an increase in body temperature is accompanied by an increase in energy expenditure. Depending on the bird's body resources and the number of provocations made during the breeding period, it would only be a question of time before such disturbances caused a reduction in the bird's breeding success.

Disturbance by humans also affects an animal's ability to habituate. Upon repeated stimulation, most behavioral and physiological concomitants decrease in intensity and gradually disappear. This is referred to as habituation, and it is probably why some species are better adapted to human activities and noises than others. Several studies of adult reindeer, deer, or moose that have habituated to mechanical sounds indicate that they have shorter flight distances than animals in remote areas not exposed to disturbances (Freddy et al. 1986; Tyler 1991). Similarly, birds nesting close to humans tolerate more disturbance than birds nesting in remote areas (Gabrielsen et al. 1985). However, both birds and mammals habituate more rapidly to mechanical noise than to human presence. Mammals and birds nesting close to human settlements seem to have built up a higher tolerance threshold toward vehicles and humans as a result of habituation than animals living in remote areas. Based on these preliminary results, less strict regulations may be needed to protect wildlife in areas close to human settlements.

Knowledge Gaps

Many questions related to the physiological effect of human disturbance on wildlife still need to be investigated in order to support good management of recreation and conservation. The use of physiological data from telemetered free-ranging animals will enable us to get much better data both from disturbed and undisturbed animals. Such data will be more precise and will enable us to quantify the impact of human disturbance on many wild species.

Physiological and behavioral research on the impact of human disturbance on wildlife is still lacking in many areas. There are, for example, few data on the effects of human disturbance on wildlife during migration, during the winter, and when animals experience drought or lack of food. In polar regions many animals must rely on stored body reserves and on maintaining low levels of activity to survive winter. Increased human activity in these areas due to in-

creased tourism or industry activity, for example, will certainly affect their behavior and physiology. The energetic cost of disturbance by humans and vehicles for both mammals and birds should also be investigated. Another interesting field for future research includes studies of the degree of habituation among wildlife. For example, do birds that breed close to human settlements, or near paths regularly used by humans, have lower energetic investments and higher breeding success than animals breeding in remote areas? There is also a need for studies of the effects of human disturbance on marine mammals breeding in coastal areas. Whether or not certain species of seals stop to breed in coastal areas as a result of increased human activity and the habituation of seal pups to the presence of humans are also in need of study.

Physiological and behavioral data gathered from a variety of wild animals strongly indicate that wildlife and humans can coexist in most situations. However, both birds and mammals have several critical periods that need to be identified. During these periods traffic and human disturbance should be regulated in order to prevent a reduction in the animals' reproductive success. Future research efforts should be directed towards such critical periods both in birds and mammals.

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