Chapter 10

FOURTEEN SECURITY LESSONS FROM ANTIPREDATOR BEHAVIOR

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Knowledge is power, whether it creates new ways to control a situation, or whether it simply explains the biological basis of a situation. I believe that there are lessons about security that we can learn from the sheer diversity of ways that nonhumans avoid predation. I am a behavioral ecologist. Behavioral ecologists adopt an economic approach when we study animals in natural settings to understand the evolution, diversity, and maintenance of behavior. We expect that costly behaviors will be selected against, unless there are overwhelming benefits associated with them. We expect animals will make fundamental trade-offs in how they allocate time and energy, and that over evolutionary time those that make the proper trade-offs will persist, while others will go extinct. Below I derive 14 lessons from the study of antipredator behavior that are relevant to designing security systems to manage terrorist threats, dealing with insurgencies, as well as managing ongoing biosecurity challenges.

We can make sense of the diversity of antipredator behavior several ways. One useful way focuses on the predatory sequence (Endler 1986; Caro 2005). Predators encounter potential prey and must identify them as suitable. Then, they must approach and attack the prey, prevent them from escaping, and consume them. Antipredator defenses may work at any of these steps. With this predatory sequence in mind, we can examine the interactions between predators and prey. For instance, prey should engage in behaviors that reduce detection by predators: they should be cryptic, or active at times when predators are not around. Prey may engage in group defenses. A commonly hypothesized benefit of sociality is to reduce the risk of predation by either increasing the ability of prey to detect predators, or simply spreading the risk among more individuals (Krause and Ruxton 2002). Once detected, prey should make themselves less profitable to predators. Increasing the cost of attacking or handling prey is an effective means to decrease profitability (Krebs and Davies 1993). For instance, many species have spines or other defensive structures. Remember, from the predator's perspective, it is looking for a meal, so the economics of handling a difficult prey will reduce the prey's profitability. Prey may also communicate to predators that they have been detected (Blumstein 2007). Such detection signaling works when predators require stealth for success. When a prey signals that it has identified a predator, the predator's hunting success has just been massively decreased. Prey may gang up and attack a predator. Such mobbing is common in a variety of species, and it often successfully moves the predator away from a particular location. Individually fighting a predator, or fleeing from a predator is an action of last resort. Flight is both energetically costly and involves an opportunity cost in that animals must stop what they have already been engaged in. Fighting is risky and therefore something that should be avoided at all costs.

A common behavioral ecological paradigm envisions individuals trading off the probability of starvation versus the probability of predation (Mangel and Clark 1988). Imagine a refuging rodent, for example, a kangaroo rat that lives in the desert, or a marmot in an alpine meadow. It lives in a burrow but must come out to forage. If it remains in its safe burrow, it will ultimately starve to death. If it emerges, it faces some risk of predation.

Our first lesson is that *avoiding all risk is impossible*. Virtually all animals must live with some risk of predation at some point in their lives. What cues should they use to assess risk? How should they modify their foraging behavior based on these cues?

Animals may use direct or indirect cues of risk. Direct cues are those by which individuals detect a predator. Indirect cues are those where there is some probabilistic relationship with predation. For instance, if predators hide in dense cover, avoiding dense cover might be an effective way to avoid predation. Regardless of whether they are direct or indirect, all cues vary in their reliability. For instance, if a predator is sighted, the prey knows that it is around, whereas if the scent of a predator is detected, the predator may be around now, or it may have been around at some previous time. Thus, prey often face the problem of estimating the reliability of a particular cue or situation.

Our second lesson is that *overestimating risk is a good strategy in many circumstances*. Theoretical models (Bouskila and Blumstein 1992) suggest that when faced with a starvation-predation risk trade-off, and imperfect information about the true risk of predation, being conservative—that is, overestimating risk—is an optimal strategy. Thus, we expect that animals may use rules of thumb to estimate predation risk and that these rules should be systematically biased toward overestimating the risk of predation. Clearly, assuming there is a 100% probability of being killed will be nonadaptive (an individual will then starve to death), but a modest degree of overestimated risk can be adaptive.

Given that individuals must take risks, how can risks be avoided? Imagine you find yourself at an automatic teller machine (ATM) in the middle of a bad neighborhood. One strategy to reduce risk would be to approach the ATM cautiously and spend a lot of time looking around while there. By doing so, you will spend more time in an exposed position. An alternative strategy would be to run in and run out as quickly as possible. We see evidence that animals use both strategies in nature. Some species are more vigilant in risky areas, while others are less vigilant, and by being less vigilant, they are able to reduce their exposure to predators because they decrease the amount of time in risky areas. Our third lesson is thus that *it is possible to reduce risk by limiting exposure or by being very careful when in risky areas.*

When prey detect a predator, many species produce obvious visual, acoustic, or olfactory signals referred to as alarm signals. Such alarm signals may be directed to the predator (to signal detection) or to other members of one's species (to warn them about the presence of the predator). There is considerable interest in understanding the evolution and adaptive utility of such signals because they are obvious and potentially risky (they may expose individuals to some risk of predation if the predator decides to focus on the signaler). That said, we see that alarm signals are often produced only when individuals are safe. The marmots I study typically run back to a burrow before alarm calling. The wallabies I have studied foot thump only when I am not walking directly toward them (and thus, when they perceive themselves as not being directly targeted). Thompson's gazelles, an African ungulate, stott (bounce up and down in front of predators with a characteristic stiff-legged gait), but only once they are a certain distance away from risky predators (Caro 2005). Historically, in rodents at least, alarm calls evolved to signal detection to the predator (Shelley and Blumstein 2005). Such calls have subsequently been "exapted" to have a conspecific-warning function. An exaptation is a trait that initially evolved for one function but later has been adapted to a new function (Gould and Vrba 1982). We expect many traits to be exaptations because evolution by natural selection works from the set of existing traits. Evolution, as Francios Jakob once wrote, works by "tinkering" with what you have, rather than creating some ideal trait de novo (Jakob 1977).

Alarm signals provide our next three lessons. Fourth, *detection signaling is a good idea and may, in some circumstances, reduce predation risk by encouraging the predator to select another target.* Fifth, *individuals should signal when they are in a relatively safe position*: flee to safety then signal. Sixth, *exaptations are common.* Defenses are adapted from preexisting behaviors rather than building de novo structures. Clearly, humans can escape from this constraint in that natural selection acts on existing variation, but humans could create their own variation. In theory, we could build a completely new type of transportation vehicle, but such novel construction would itself have costs. Adapting our defenses to meet new challenges from what we already have might be an effective long-term defensive strategy. At times, however, there are novel offenses. A defining characteristic of exotic plants that successfully invaded North America is that they had novel phyotochemicals and thus were defended against resident herbivores (Cappuccino and Arnason 2006). Novel offensives may require novel defenses, but these will most rapidly evolve from preexisting defenses.

Risk assessment is imperfect, and it behooves those detecting alarm signals to pay particular attention to who is producing the signal. Imagine two individuals: Nervous Nelly, and Cool-Hand Lucy. Nervous Nelly produces alarm calls whenever she detects any movement. Nelly calls to falling leaves, rustling bushes, and sometimes, to real predators. Cool-Hand Lucy, on the other hand, is much more discriminating. She calls only when she detects a predator. Given systematic differences in the reliability of callers, it should behoove those responding to them to try to assess caller reliability. In many species, information from unreliable individuals is discounted. Thus, Nervous Nelly (who often "cries wolf") is ignored. In some species, however, reliability assessment works in a slightly different way. Reliable individuals that make mistakes are given the benefit of the doubt, and unreliable individuals, probably because they are unreliable, elicit considerable independent investigation (Blumstein et al. 2004b).

Our seventh lesson is that *it is very important to assess signaler reliability* and to behave accordingly. However, how one behaves may vary in that unreliable individuals may be discounted or elicit more independent investigation. Our eighth lesson is that *there can be qualitatively different responses to the same situation or problem* and that these different strategies may all ultimately be successful strategies. Evolution provides us with a plethora of ways to respond to risk.

When faced with an uncertain risk, what should individuals do? Many species inspect their predators to better estimate the true risk of being around them (Caro 2005). Clearly, predators are not always hunting. Satiated predators may have obviously full bellies (envision a lion resting after a large meal). Acquiring more information about the true risk of predation is important because it is relatively costly to flee a nonhunting predator.

Our ninth lesson, thus, is that *reducing uncertainty by predator inspection is an important way to reduce costly responses.* Individuals that engage in costly responses indiscriminately will be selected against, while those that respond in an optimal way by responding appropriately to risk may do better in the long run.

A common theme throughout this chapter is avoiding costly responses. And, nonhuman antipredator behavior provides several insights into how this can be achieved. In many cases, costly antipredator behaviors are lost when there are no longer any predators around. For instance, many species become less cryptic, less wary, or otherwise lose antipredator behavior when isolated on islands or other predator-free locations (Blumstein and Daniel 2005). Such responses are adaptive in that by no longer allocating energy or time to antipredator behavior, animals are able to allocate energy or time to other activities.

Our tenth lesson is that it is adaptive to *reduce defenses when risk decreases.* Maintaining high vigilance when there is truly no risk is costly, and individuals doing so will be out-competed by those that reduce defenses adaptively.

However, there are some situations where we see evidence of antipredator behavior persisting despite long periods of relaxed selection (i.e., isolation from predators). One hypothesis explaining this is something I have called the multipredator hypothesis (Blumstein 2006). Most species have more than a single predator, and this realization has several important implications. First, we might expect generalized defenses that work well against more than a single predator. Second, being able to survive one predator but not another does not make much sense, and we might, therefore, expect "packages" of antipredator behavior. Importantly, we should not expect the various traits that constitute an effective defense to assort independently. For instance, consider a baby ungulate, such as a pronghorn antelope, which relies on crypsis and immobility to survive. A cryptic pronghorn who bounces around wildly, would be killed by coyotes or eagles. Thus, these traits should not be independent. Similarly, an animal that is exposed to both eagle predation and wolf predation should not have their antipredator traits be entirely independent (surviving one only to be killed by the other would not be favored by evolution). At the genetic level, we may see evidence of genetic correlations, and we might expect linkage (whereby traits are colocated on chromosomes to resist independent assortment). Studies of kangaroos and wallabies provide some support for the multipredator hypothesis: species living without any predators quickly loose all antipredator behavior, but those living with at least one predator maintain antipredator abilities for other, absent, predators (Blumstein et al. 2004a).

Several lessons come from thinking about the multipredator hypothesis. Our eleventh lesson is that we should aim to *have generalizable defenses that work against more than a single threat.* Our twelfth lesson is that *unless there are great costs to maintaining a defense in the absence of a specific predator, it may be a good idea to maintain all defenses.* This of course, focuses us on estimating the costs of maintaining apparently no longer useful defenses. In some cases we should expect defenses to be independent, but in other cases, we should expect them to be linked.

There are several ways by which prey could not respond to ongoing nonthreatening situations. The multipredator hypothesis focuses on the evolutionary loss of antipredator behavior, but species can respond in much more dynamic ways based on experience. A fundamental response is to habituate to ongoing stimulation. Habituation is seen when the magnitude of responses declines with repeated nonthreatening exposures. For instance, the Arabs used habituation effectively against the Israelis in the 1973 war (Rabinovich 2004). Before attacking Israel, Egypt had 40 military exercises on Israel's borders. This led Israeli security analysis to discount the threat of a troop buildup on their border. However, habituation is not ubiquitous, and individuals may sensitize, or have higher-magnitude responses, to repeated exposures.

Maintaining vigilance in situations where there are many false alarms is difficult (see appendix). Our thirteenth lesson is that *we should often expect habituation when there are many false alarms.* Importantly, understanding the conditions under which habituation or sensitization occurs is a fundamentally important question in security studies.

Our final lesson is that *maintaining flexible responses is often a good idea.* There are clearly time, energy, and opportunity costs of assessing risk, and by having inflexible constituent defenses, individuals need not pay the costs of trying to adaptively deploy defenses. In some situations, either when the costs are low, or when there are limited benefits from proper assessment, we should expect fixed responses. However, flexible and adaptable responses that are deployed only when necessary, in the long run, may allow individuals to allocate less energy to defense and more to other important activities.

Policy Implications

Studies of antipredator behavior illustrate remarkable flexibility of mechanisms: there is no single way to solve a particular problem. The optimal solution will likely depend on specific constraints, as well as the costs of making mistakes.

Whenever possible, we should seek to adapt defenses from preexisting resources. For instance, rather than creating a novel and unique "Department of Bioattack Detection," health care systems can be better developed and communication among hospitals and government agencies improved, so that biological attacks could be quickly detected. Importantly, an improved public health system will have positive benefits for citizens even when there are no terrorist attacks, and a strong public health system will help us respond to natural pandemics. Similarly, first responders should be given radiological and chemical weapons monitors (as some are), rather than creating an entirely new agency tasked to detect a low-probability (but admittedly high-consequence) threat.

Raising the alarm with press releases describing "credible information of threats," changes in the DEFCON level, or the Department of Homeland

Security threat level should be expected to communicate to both opponents and allies. Detection signaling has a long and functional evolutionary history, and this realization could be used strategically. However, to use it strategically, we must better understand the conditions under which we habituate to repeated false alarms. Without a fundamental understanding of this, we are likely to have the unintended consequence of habituating those that we need to remain vigilant. Importantly, when specifically targeting opponents, it is important to signal from a position of safety. In a policy context, this would mean we signal when we are certain that there is something to signal about. Thus, it is essential to choose when to signal to opponents; crying wolf has its own costs!

Faced with uncertain threats, information acquisition is essential, and this is a fundamental characteristic of adaptive, flexible responses. This, itself, is not a novel suggestion, but a behavioral ecological perspective does emphasize the costs and benefits of information acquisition and response are key things to evaluate when selecting a response. If making a mistake is not that costly, we should tolerate mistakes. However, whenever mistakes are costly, we should be very discriminating. Interestingly, there seem to be two ways to respond to uncertainty: discount it or use it as an opportunity to acquire more information. For instance, the information from the FBI agent that warned about certain foreigners enrolling in flight schools contained little that was actionable. Using this as an opportunity to acquire more information, in this case, might have prevented the 9/11 attacks.

Maintaining not currently functional defenses may be, in the long run, a good idea, but we should be very sensitive to the opportunity costs of doing so. For instance, if it can be done economically, ongoing monitoring for controlled pathogens (smallpox, polio, etc.) will allow early detection and thus control. Maintaining general defenses, such as health care systems, will allow us to respond more efficiently to a biological attack.

While not novel, examining the diversity of antipredator adaptations highlights, from a perspective directly concerned with life and death, the fact that we must be comfortable living with risk. It is impossible to completely avoid risk, and by trying to do so, we will suffer other costs. One (admittedly not politically tenable) response to a major terrorist attack, like 9/11 or the attacks in Madrid and London, would be to ignore them. In all three countries, more citizens are killed by drunk drivers each year than die at the hands of terrorists. Targeting drunk driving, smoking, or obesity, rather than terrorist attacks, might be a better way to save citizen's lives. But humans overestimate the risk of large, rare events (Cohl 1997), and politicians must respond to this fear (we also are more fearful of novel events, human-made risks, risks we have no control over, uncertain risks, and risks that may kill us in shocking ways [Ropeik and Gray 2002]).

The ancillary costs of responding to terrorist threats may, in some cases, be very high. The United States struggles with the trade-off between losing individual liberties and employing sophisticated surveillance against people who might be U.S. citizens. With a fixed budget, funds allocated to defense cannot simultaneously be allocated to health care, science, or education. Thus, overreacting has its intrinsic costs.

We see clear evidence that humans recognize the multiple ways to reduce risk. Many vehicles traveling from the Green Zone to the airport in Baghdad do so at very high speeds—a time-minimizing strategy that reduces exposure. Military personnel patrolling Iraqi roads do so very carefully, examining piles of trash, dirt, and household items to determine if they hold improvised explosive devices. With experience, search images develop and personnel are better able to detect these hidden bombs (National Public Radio 2005). We also see that the constraints created by having to maintain a physical presence selects in the military personnel this highly vigilant behavior.

Also, while not novel, studying antipredator behavior illustrates the value and efficacy of increasing the cost of attacking (i.e., building defenses) as a viable deterrent. Of course, as airports, embassies, and government office buildings are hardened, terrorists will choose softer targets, such as marketplaces and hotels. Nevertheless, the lesson is that increasing the cost of attack is a viable defensive strategy to defend important resources.

Future Research Needs

While nonhuman antipredator behavior creates a toolbox of strategies for those who wish to apply it to human security issues, future research should develop the following:

Models to explain the condition under which unreliable individuals will be ignored or will elicit independent investigation. Results will help us develop better strategies for responding to uncertain events.

Models to explain the conditions under which habituation or sensitization occurs. Results will help us defensively by preventing a decline in vigilance/responsiveness, and offensively to better understand how to reduce the vigilance of opponents.

Models to explain the conditions under which maintaining potentially costly and no longer useful antipredator behavior is a good strategy. Results will help us allocate scarce resources efficiently.

A better understanding of the consequences of using a general defense as opposed to a specific defense. Assuming specific defenses cost more to develop, what is the added value obtained by developing them. Results will help us allocate scarce resources efficiently.

A better understanding about how, specifically, species respond to novel threats. Do novel threats require truly novel responses, or can generalized or exapted responses work well?

Appendix: An Analysis of Citizen Responses to Changes in Department of Homeland Security Threat Levels

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The Department of Homeland Security (DHS) threat level system was instituted in September 2002. It has five levels: 1 = low, 2 = guarded, 3 = elevated, 4 = high, and 5 = severe. Since its institution, it has remained at either level 3 or level 4. While it was originally developed to help responders plan for terrorist attacks, it was made public, allowing us to analyze how the public responds to changes in threat levels. The DHS states on its threat level Web page (http://www.dhs.gov/xinfoshare/programs/Copy_of_press_release_0046.shtm) that "raising the threat condition has economic, physical, and psychological effects on the nation"; however empirical evidence as to the nature of such effects remains scant. In particular, citizens are encouraged as part of this system to utilize the Web site www.Ready.gov and the DHS information line (1-800-BE-READY) as their primary sources of information on preparedness for possible terrorist attacks. In order to test the effects of this system on citizen responses, we conducted two analyses. First, using bivariate correlations, we looked at how public responses changed over time and as a function of the specific DHS threat level. Second, we fitted a series of general linear models to isolate the effect of DHS threat level, after explaining variation accounted for by date.

Our response measures included CNN/USA Today/Gallup polling data (from www.pollingreport.com/terror.htm) from the question: "How worried are you that you or someone in your family will become a victim of terrorism: very worried, somewhat worried, not too worried, or not worried at all?" This poll surveyed approximately 1000 Americans periodically since 9/11. We also included data provided to us from the DHS that summarizes the number of hits to the DHS Web site (www.Ready.gov) and calls to the DHS information line (1-800-BE-READY).

We found some evidence of habituation, a decline in responsiveness over time, and no strong evidence that American citizens responded to variation in DHS threat levels by increasing their fear (Fig. 10.1). Specifically, the percentage people reporting that they were "very worried" decreased as a function of the highest level DHS threat that month, and the number of people reporting that they were "not too worried" increased. There were also strong effects of time on responses: the number of page views to www.Ready.gov and phone calls 1-800-BE-READY decreased over time and were not sensitive

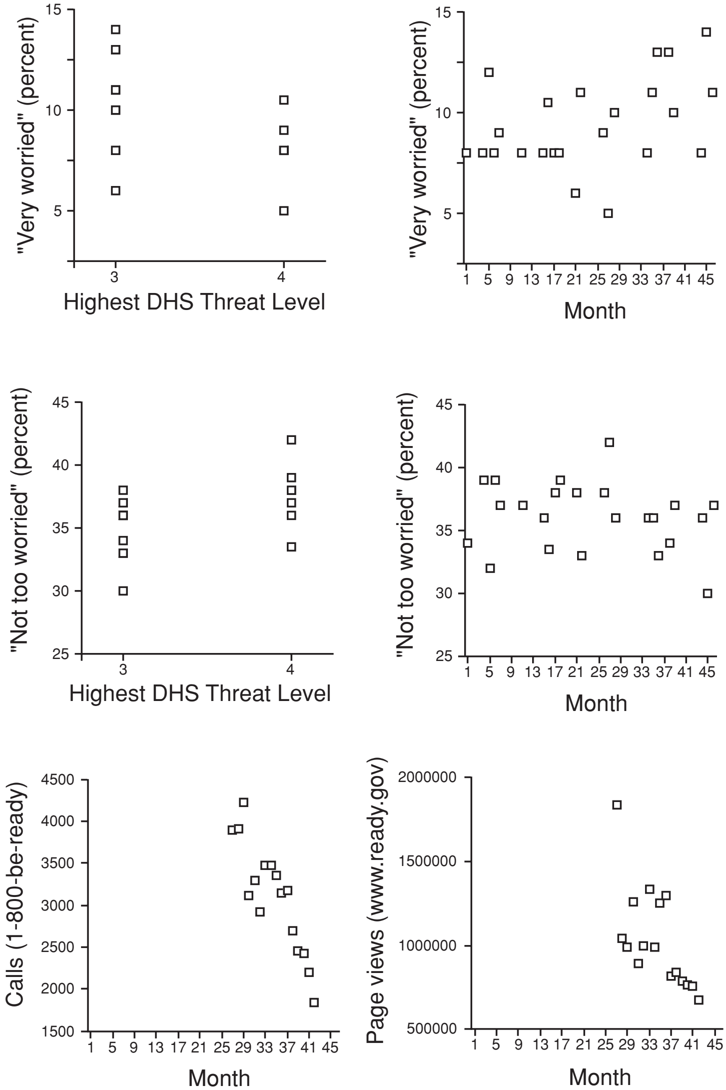

FIGURE 10.1 Response to Department of Homeland Security threat levels and over time. Month 1 = November 2001. Data for www.Ready.gov and 1-800-BE-READY prior to January 2004 were unavailable.

to variation in the highest level DHS threat that month. These results were supported by the results from the general linear models: after accounting for variation explained by month, threat level had no significant effect on page views or phone calls. Interestingly, there were no significant effects of either date or highest threat level on the responses to poll data.

American citizens seemingly obtained response to terrorist threat information early on from the DHS and stopped acquiring information over time. Changes in DHS threat level had no effect on acquiring information by going to these recommended DHS sources. We also found some evidence that the American public has habituated to DHS threat warnings since elevations in the DHS threat level led to, if anything, a decline in the number of Americans that reported themselves to be "very worried" about a possible terrorist attack. Our results highlight the point that habituation is a factor with which governments should be very concerned and to which effective homeland security systems will need to pay attention.

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