Cognitive Inference and Resulting Behaviors in Response to Ambiguous Threat in the Coyote, Canis latrans

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COGNITIVE INFERENCE AND RESULTING BEHAVIORS IN RESPONSE TO
AMBIGUOUS THREAT IN THE COYOTE, CANIS LATRANS

by

Sarah Shawnee Dawson

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Wildlife Biology

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2009
While antipredator strategies have been a focus of behavioral research for decades, scientists generally study the responses of prey toward overt, explicit threat. However, risk can also be significant when a threat is covert, such as when an ambush predator may be nearby or a secondary threat remains after a predator’s departure. Little is known about the mechanism that prey use to assess risk in a predator’s absence. Tests were conducted to determine the manner in which coyotes respond to these ambiguous threats. Specifically, I tested whether coyotes respond to prior anthropogenic activity that has occurred near their only food source, whether they investigate human activity at both profitable (feeding) and unprofitable (non-feeding) locations, and what sort of information coyotes are capable of gaining through their investigation. I explored these questions in three experiments spanning 4 years at the USDA/APHIS/WS National Wildlife Research Center’s Logan field station. Test subjects were eight pairs of captive
coyotes. Results showed that coyotes delayed or avoided feeding in response to prior anthropogenic activity, and that often a delay was due to investigation of human scent trails. Investigation of non-feeding areas occurred but was relatively brief. When coyotes were prevented from investigating locations of prior anthropogenic activity, foraging ceased altogether. In addition, coyotes were able to differentiate among the activity of different humans based on their association with negative, neutral, or positive threat levels, even in the presence of confounding visual and olfactory cues. They remembered these associations even after one month. This study is the first that provides evidence suggesting that canids gather and interpret complex information for cognitive inference about threat level associated with access to food.
DEDICATION

To my parents, for giving me all the tools I need to change the world.
ACKNOWLEDGMENTS

Funding and equipment were provided in large part by the USDA National Wildlife Research Center through cooperative agreements with Utah State University. Many thanks go to Mike Jaeger, Butch Brodie, Karen Beard, Fred Provenza, and Tim Shahan for guidance and patience throughout the duration of my time at USU.

Special thanks go to Aron Bauer for extensive help with data collection and results interpretation and McLaurin Dawson for volunteering time for research participation. Most of all, I would like to thank Peggy Dawson, McLaurin Dawson, Tesa Unger, and the rest of my family and friends for moral support, endless encouragement, and for picking me up off the floor when I thought I would never make it through.

Sarah Shawnee Dawson
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CHAPTER 1
INTRODUCTION

Several theories concerning the behavior of prey in response to predator activity, such as Helfman’s threat-sensitive predator avoidance hypothesis (1989) and Lima and Bednekoff’s predation risk allocation hypothesis (1999), suggest that prey should behave in a manner appropriate to the degree of threat that they are currently experiencing from predation. The ability to accurately gauge existing predation risk is advantageous because antipredator defenses are inherently costly (Lima 1998, Lima and Bednekoff 1999). Time and resources spent avoiding risky situations might alternatively be allocated to foraging and reproduction, and this tradeoff has probably driven the evolution of accurate and efficient risk-assessment capabilities (Lima and Dill 1990). In support of this concept, a large body of evidence has accumulated to suggest that prey have the ability to accurately assess the level of risk they are currently experiencing (Lima and Dill 1990). For instance, prey minimize their risk of predation by making fitting decisions about when and where to forage, how to handle food, what size group to maintain, and how often to look up from other activities to scan for predators (see Lima and Dill 1990 for a thorough review of the influence of predation risk on each of these behaviors).

Appropriate behavioral decisions are facilitated by relevant information (Inglis 2000, Dall et al. 2005). Accurate information aids in predicting the outcome of an action (Dall et al. 2005) by reducing uncertainty about the environment in which an organism subsists (Inglis 2000). When a threat is physically present, or “overt,” prey have access
to many cues that provide information that can facilitate apposite decisions (Stankowich and Blumstein 2005), including the predator species (Seyfarth et al. 1980), the individual predator within a species (Slobodchikoff et al. 1991), predator abundance (Helfman 1986), proximity (Cooper 1998, Stankowich and Coss 2006), approach speed (Cooper 1997, Cooper 2003, Cooper et al. 2003, Stankowich and Coss 2006), and directness of approach (Cooper 1997, Cooper 2003, Cooper et al. 2003, Stankowich and Coss 2006). Prey activity is subsequently reallocated from foraging and other vulnerable behaviors to appropriate antipredator responses (Lima 1998, Lima and Bednekoff 1999). These responses usually come from a predictable repertoire designed to either prevent detection (Kitchen et al. 2000, Werner and Peacor 2003) or avoid capture (Ydenberg and Dill 1986, Atwood and Gese 2008). A plethora of research has been conducted on antipredator behaviors elicited towards overt stimuli.

However, threat of predation may also be significant when predators are not perceptible. For instance, covert predation risk from ambush predators may be substantial even in the absence of visual cues. Covert threat is also inherent with scavenging at kill sites where a dangerous competitor may be concealed nearby. Additionally, prior activity by some predators (e.g., spiders or humans) can be associated with threat from secondary devices, such as webs, traps, or baits, which are dangerous even in the absence of the predator itself.

While information about ambiguous threat is usually less explicit than information about an overt threat, prey still have access to other indicators that may aid in the deduction of appropriate behavior through cognitive inference. Firstly, prey might
utilize any previous acquired visual information relevant to a situation. For instance, if prey previously observed suspicious activity from a departed predator that may have been indicative of the placement of a secondary threat, then this information can be integrated into future decisions as long as prey memory is durable and robust. In addition, animals are able to gain adaptive environmental information by spending time investigating their surroundings (Kats and Dill 1998, Grostal and Dicke 2000, Augustsson and Meyerson 2004, Dall et al. 2005). For example, predators often emit or leave behind chemosensory information that prey may utilize to facilitate germane decisions (Kats and Dill 1998, Grostal and Dicke 2000, Kusch et al. 2004, Dall et al. 2005).

As with overt threat, animals alter their behavior in the presence of more ambiguous threat (Lima and Dill 1990, Sih 1992, Lima 1998, Lima and Bednekoff 1999). In some cases, for instance, ambiguous threat can be completely avoided. Sequin et al. (2003) found that dominant, territorial coyotes (Canis latrans) were never photo-captured within their territories. The authors stated that coyotes tracked human activity as the camera stations were being installed and subsequently avoided the camera traps but not the areas around them. These coyotes never habituated to the camera stations even after 2 years, suggesting that their response might be one of wariness toward ambiguous threat associated with human activity as opposed to neophobia towards the cameras themselves.

In the aforementioned Sequin et al. (2003) study, there was no need for coyotes to approach the camera stations because they could be avoided without adverse consequences. In contrast, ambiguous threat in close proximity to an essential resource cannot be avoided without cost. In this case, animals must negotiate the risk to obtain the
resource. This type of situation provides an opportunity to determine whether coyotes are likely to use investigation and cognitive inference to overcome the problem.

The purpose of the present study is to determine whether cognition is likely to play an important role in the assessment of ambiguous threat by coyotes and, if so, how. Cognition is defined here as the mechanisms by which coyotes gather, evaluate, and act on information about potential threats (Shettleworth 1998). In the context of threat assessment, information gathering by coyotes would likely be performed through chemosensory investigation. Olfaction is a well-developed sense in canids; they use it to communicate (Gese and Ruff 1997, Allen et al. 1999) and easily recognize individuals based on scent alone (Dawson and Jaeger, in preparation).

If coyotes do gain valuable information about their environment through olfactory investigation (Kats and Dill 1998, Grostral and Dicke 2000, Augustsson and Meyerson 2004, Dall et al. 2005), then this acquired information can later be used to predict the risk associated with particular situations in lieu of direct testing. Trial-and-error learning is an inappropriate strategy for determining suitable behavior toward ambiguous threat because the consequences may be lethal if the threat is real and has been underestimated. A more prudent alternative might then involve initially overestimating of the potency of an ambiguous threat, collecting available information about the threat (Kats and Dill 1998, van der Veen 2002) through cautious investigation, integrating this newly acquired information with any prior knowledge that coyotes might possess about the threat, and the subsequent deduction of the most appropriate response (Owings 2002, Dall et al. 2005) through the use of cognitive inference. Thus, if coyotes rely on gathered
information in order to make behavioral decisions about ambiguous threat, we would predict their behavior to differ when they collect information versus when they are unable to gather any information. We might also predict that coyotes should behave in a manner that is appropriate to the semantics of the information, such that coyotes will avoid areas in which information indicates potential danger as opposed to areas at which information suggests a lack of threat.

Coyotes are good subjects on which to test the cognitive response toward ambiguous threat. As mesocarnivores, coyotes evolved in the presence of larger, more powerful predators that posed a threat to them (Palomares and Caro 1999). To compete successfully, coyotes developed strategies or learned techniques and heuristics that allowed them to decrease the likelihood of being captured or killed while foraging, particularly while scavenging at carcasses killed by larger carnivores (e.g., wolves, lions, and bears). While evidence suggests that coyotes avoid ambiguous threat when possible (Sequin et al. 2003), their response toward an ambiguous threat surrounding an essential resource remains unknown.

Several questions need to be addressed to determine if coyotes use cognitive inference to assess uncertain risk surrounding an essential resource; each will be answered in a separate manuscript for publication. In the following experiments, I will attempt to generate the perception of ambiguous threat for coyotes through prior anthropogenic activity in the vicinity of established feeding stations. The first question that I intend to address is the following: Do coyotes respond to uncertain threat at an established feeding station following human activity there and, if so, is this response
There are four plausible outcomes in this experiment. The first is that coyotes ignore prior human presence and subsequently eat at their feeding stations as soon as the food is delivered there. If this occurs, we can assume that coyotes do not perceive risk from prior human activity. On the other hand, coyotes might avoid the feeding stations and the food there without investigating prior human activity. Such a response would suggest that coyotes perceive unambiguous risk associated with prior human activity, and do not use cognitive inference to work around this threat. Alternatively, coyotes might initially show caution toward feeding but eventually overcome this caution through boldness or hunger, and during subsequent trials feed without hesitation. Overcoming caution in the face of prior human activity would suggest that coyotes may not perceive uncertain threat associated with this activity, but instead are initially cautious for some other reason (probably neophobia). This caution is subsequently overcome with trial and error learning. The final alternative is that coyotes always use investigation in response to prior human activity and never habituate to this ambiguous threat. In this case, we may conclude that coyotes do perceive the potential for threat from prior human activity and use investigation as a mechanism to acquire information about the risk.

The second question that I intend to answer is the following: In the absence of an essential resource, do coyotes differentially investigate recent human activity at areas that have previously been A) profitable, and B) unprofitable? One possible outcome of this study is that coyotes do not investigate recent human activity at either area when resources are unavailable. If this occurs, then we can conclude that coyotes do not gather information for its inherent value, but instead investigate only when they have to work
around uncertain threat in order to obtain an essential resource. Alternatively, coyotes might investigate all sites of recent human activity when resources are not available. Investigation of all areas of human activity suggests that coyotes value information about potential threats and do not perceive much risk in obtaining this information. Finally, coyotes might investigate human presence in the vicinity of feeding stations only. If this occurs, we can conclude that coyotes perceive uncertain threat associated with recent human presence, view investigation as risky, and subsequently investigate the locations at which they view information to be most valuable. Investigation before resource availability also suggests a predetermined decision to acquire information for future utilization. It should be noted that these scenarios are not mutually exclusive.

The final question that I intend to address is: Do coyotes differentiate between information from prior human activity that is indicative of various levels of threat? If coyotes respond similarly to all ambiguous threat of anthropogenic origin, then we can assume that coyotes do not differentiate between various levels of ambiguous threat, but instead only perceive the general potential for risk from prior human activity. Alternatively, coyotes might respond differentially to information from ambiguous threat indicative of different levels of risk. They might do this through either differential amounts of investigation, which is an information gathering mechanism, or through differential feeding latencies, which is decision making. If coyotes differ in their responses toward various ambiguous threats, we can conclude that coyotes possess sophisticated risk-assessment mechanisms for assessing ambiguous threat.
Our results must be conclusive to support the use of cognitive inference for negotiating ambiguous threat in coyotes. Firstly, coyotes should not habituate to ambiguous threat. Habituation would imply that an avoidance response is due to neophobia towards humans as opposed to the perception of risk associated with human activity. In addition, coyotes should use olfactory investigation as a mechanism to gather information and evaluate ambiguous threat. When prevented from performing this investigation, coyotes should avoid areas associated with human activity. If given the opportunity, coyotes should investigate ambiguous threat, regardless of whether or not a resource is currently available nearby. Investigation before resource availability also suggests a predetermined decision to acquire information for future utilization, as opposed to investigating due to the need to work around threat and get food. Finally, coyotes should be able to discriminate amongst information from different sources that are indicative of different levels of risk. Differential responses from coyotes would allow us to conclude that coyotes possess sophisticated risk-assessment mechanisms for utilization in the assessment of ambiguous threat. We could also then conclude that coyotes use cognitive inference as a mechanism to negotiate ambiguous threat.

It is our hope that this research will help to improve non-lethal control methods for coyote depredation of livestock. Thus far, control methods have attempted to deter coyotes without understanding the underlying biology of the depredation situation and have been mostly ineffective. Developing a highly successful non-lethal method appropriate for alpha coyotes requires first understanding the behaviors elicited by these animals and how to best exploit them. Predation deterrents are probably most effective in
a context that is ecologically meaningful to the prey species. Because coyotes evolved in the presence of large North American predators, they had to be able to work around the threat of predation in order to be successful. Therefore, avoiding frightening devices or developing learned aversions may not be as relevant for survival and fitness as avoiding predators. Capture by a predator is likely to result in death and therefore must be avoided the first time. This suggests that coyotes, like most prey animals, may have a better developed genetic predisposition for behaviors that help them to avoid capture than for learning to avoid “scary” objects. If cognitive inference toward ambiguous threat is supported, then the general strategy of research on non-lethal methods needs to be re-evaluated and oriented toward the coyote’s cognitive problem solving rather than toward finding aversive stimuli that the coyote will avoid. It is our belief that the key to deterring coyotes from depredation lies in exploiting the natural response of these coyotes towards their natural predators.

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CHAPTER 2
GAUGING THE UNKNOWN: COYOTES (*CANIS LATRANS*) ASSESS THE RISK OF AN AMBIGUOUS THREAT

Abstract

While it has often been documented that prey are capable of assessing current levels of predation risk in the presence of a predator, little is known about the mechanism that prey use to assess risk in a predator’s absence. Tests were conducted to determine whether hand and mother-reared coyotes investigate human scent and delay feeding when prior anthropogenic activity is associated with their only food source, whether that response differs depending on the time of day that the test is conducted or the interval between human activity and food availability, and whether the response changes after multiple presentations of the same threat. We explored these questions in a series of 16 treatments that were the product of four times of anthropogenic activity (03:00, 09:00, 15:00, and 21:00) and four times of food delivery (03:00, 09:00, 15:00, and 21:00).

Coyotes delayed feeding when anthropogenic activity occurred near their food source prior to food availability. While there was no difference in response between hand and mother-reared animals, coyotes exposed to activity from a more familiar human subject delayed feeding less than coyotes that were exposed to a less familiar human. Coyotes spent time investigating anthropogenic activity after food delivery and before feeding, and did not eat when food delivery occurred soon after anthropogenic activity. While coyotes decreased their feeding latency after multiple presentations of the same treatment.

* Coauthored by Sarah Dawson and Michael M. Jaeger
combination, a change in either time of anthropogenic activity or food delivery between weeks caused feeding latencies to increase again. We discuss the potential cognitive mechanisms involved in risk assessment towards ambiguous threat.

Introduction

According to the threat-sensitive predator avoidance (Helfman 1989) and predation risk allocation (Lima and Bednekoff 1999) hypotheses, prey should behave in a manner appropriate to the current level of predation risk. When a threat is physically present, or “overt,” risk assessment is relatively straightforward. Prey have access to many cues (Stankowich and Blumstein 2005), including predator abundance (Helfman 1986), proximity (Cooper 1998, Stankowich and Coss 2006) approach speed (Cooper 1997, Cooper 2003, Cooper et al. 2003, Stankowich and Coss 2006), and directness of approach (Cooper 1997, Cooper 2003, Cooper et al. 2003, Stankowich and Coss 2006). Prey activity is subsequently reallocated from foraging and other vulnerable behaviors to appropriate antipredator responses (Lima 1998a, Lima and Bednekoff 1999). These responses usually come from a predictable repertoire designed to either prevent detection (e.g., decreasing movement [Werner and Peacor 2003] or shifting activity to nighttime [Kitchen et al. 2000]) or avoid capture (e.g., vigilance [Atwood and Gese 2008] or flight [Ydenberg and Dill 1986]). Behaviors, such as these, are likely to be direct reactions to well-defined and conspicuous stimuli and therefore innate (e.g., Curio 1993, Kelley and Magurran 2003, Stoks et al. 2003) and relatively rigid. A plethora of research has been conducted on antipredator behaviors elicited towards overt stimuli.
Threat of predation may also be significant when predators are not perceptible. This “covert” threat can come in two forms. The first occurs when an ambush predator is not apparent but is suspected of being in the vicinity (“ambush threat”). As with overt threat, the underlying nature of ambush threat is explicit – it comes directly from a nearby predator. In contrast, sometimes covert threat can be less definitive. For instance, an animal may come upon a dead or distressed conspecific (see Curio 1993 for a review) or another sign that a predator has been in the area (see Kats and Dill 1998 for a review of prey responses to predator scents) in the absence of the predator itself, or a predator may have departed the area but its prior presence or behavior at the site is associated with potential threat from a secondary source (e.g., a trap or poisoned carcass). These “ambiguous threats” are indeterminate, and thus behavioral responses towards them are complex and less likely to be dictated by innate stimulus-response mechanisms (Blumstein et al. 2002, Kelley and Magurran 2003). Ambiguous threat is the subject of this chapter.

Although evidence suggests that animals alter their behavior in the absence of direct threat (Lima and Dill 1990, Sih 1992, Lima 1998a, Lima and Bednekoff 1999), the mechanism by which they assess and negotiate risk surrounding ambiguous threat remains largely unknown (Lima 1998b). In some cases, ambiguous threat can be completely avoided. For example, Sequin et al. (2003) found that dominant, territorial coyotes were never photo-captured within their territories. The authors stated that coyotes tracked human activity as the camera stations were being installed and subsequently avoided the camera traps but not the areas around them. These coyotes
never habituated to the camera stations even after 2 years, suggesting that their response might be one of wariness toward ambiguous threat associated with human activity as opposed to neophobia towards the cameras themselves.

In the aforementioned Sequin et al. study, there was no need for coyotes to approach the camera stations because they could be avoided without adverse consequences. In contrast, ambiguous threat in close proximity to an essential resource cannot be avoided without cost. In this case, animals must negotiate the risk to obtain the resource. Because an ambiguous threat is inherently vague, however, animals are likely to lack detailed information about it. Trial-and-error learning is an inappropriate strategy for determining suitable behavior toward ambiguous threat because the consequences may be lethal if the threat is real and has been underestimated. Therefore, a more prudent behavioral alternative would be a valuable asset for use in the negotiation of an ambiguous threat.

In this vein, research has shown that animals gain adaptive environmental information by spending time investigating their surroundings (Kats and Dill 1998, Grostal and Dicke 2000, Augustsson and Meyerson 2004, Dall et al. 2005); this acquired information can later be used to predict the risk associated with particular situations in lieu of direct testing. Therefore, prey might initially overestimate the potency of an ambiguous threat, collect available information about the threat (Kats and Dill 1998, van der Veen 2002) through cautious investigation, integrate this newly acquired information with any prior knowledge they might possess about the threat, and subsequently deduce
the most appropriate response (Owings 2002, Dall et al. 2005) through the use of cognitive inference.

We can make several predictions about the behavior of animals employing this risk-assessment strategy. First, animals possessing any prior information about an innocuous ambiguous threat might avoid it less so than would animals lacking this knowledge. In addition, well-fed animals with more opportunity to investigate this ambiguous threat may have shorter ultimate feeding latencies when food later becomes available nearby. Moreover, with repetitive presentation of the same ambiguous threat, we might expect to see a reduction in response strength as information about that threat is collected and the appropriate behavior towards it is inferred. These hypotheses have yet to be tested.

Coyotes are good subjects on which to test the response to ambiguous threat. As mesocarnivores, coyotes evolved in the presence of larger, more powerful predators that posed a threat to them (Palomares and Caro 1999). To compete successfully, coyotes developed strategies or learned techniques and heuristics that allowed them to decrease the likelihood of being captured or killed while foraging. While evidence suggests that coyotes avoid ambiguous threat when possible (Sequin et al. 2003), their response toward an ambiguous threat associated with an essential resource remains unknown.

Thus, the first objective of this study was to determine whether coyotes delayed foraging in response to an ambiguous threat (anthropogenic activity) in close proximity to their sole feeding station. Delayed foraging would suggest that coyotes view human activity as a potential threat. Because previous research has suggested that prey animals
in general (Lima and Dill 1990) and coyotes in particular (Kitchen et al. 2000) will increase nocturnal activity relative to daytime activity in areas where diurnal predators are common, we tested coyote responses to ambiguous threat at multiple times of day to determine whether coyotes view feeding under cover of darkness as less risky. Our second objective was to establish whether hand-reared coyotes behave differently towards anthropogenic activity than do coyotes that have limited previous contact with humans. A difference in response between these groups to subsequent anthropogenic activity would suggest that coyotes generalize previously obtained information to situations involving new humans when assessing risk, while no difference would suggest that coyotes recognize individual humans and the potential for threat from them. Our third objective was to ascertain whether coyotes investigate ambiguous threat prior to feeding. Prioritizing investigation over foraging suggests that coyotes employ investigation as a risk-assessment mechanism toward ambiguous threat and thus the use of cognitive inference is substantiated over trial-and-error learning. The fourth objective of this study was to determine whether coyotes, which had lengthy, as opposed to brief, opportunities for investigating an ambiguous threat near their feeding station prior to food availability, would feed there more quickly when food later became available. If they did, the importance of gathering information for risk assessment is supported. Our final objective was to determine whether coyotes change their response towards a harmless ambiguous threat after successive exposures to the same threat and multiple opportunities for information acquisition. Persistence in response strength would suggest that coyotes view this ambiguous threat as a perpetual risk, while a decrement in response strength
would indicate that coyotes recognize repetitive information about an innocuous ambiguous threat and adjust their response according to their previous experience with that threat.

Methods

Study Location

Tests were conducted at the USDA/APHIS/WS/NWRC Predator Research Center in Millville, Utah, U.S.A. The 68 ha facility houses 115 captive coyotes at an elevation of 1370 m above sea level. Tests were conducted during the spring and summer of 2006. Weather conditions throughout this time were generally arid and hot, with daytime temperatures averaging 27°C and nighttime temperatures averaging 9°C. Sunrise occurred between 05:52 and 06:35 during the study’s duration; sunset occurred between 20:27 and 21:06. The research center experiences a moderate level of human activity throughout the day – several studies take place at any given time, and general animal care activities occur daily. Besides the procedures noted in this study, no human activity occurred at night.

Tests occurred in eight hexagonal 0.66 ha outdoor enclosures (each side measured 54 m) (Fig. 2-1). Two gates for human ingress and egress were located at opposite ends of the enclosures. All enclosures contained two feeding compartments placed approximately two-thirds the distance from one end. Each feeding compartment was made from four horse panels (3.3 m x 2.6 m steel mesh fences). Compartments were
Fig. 2-1 Layout of a test enclosure showing position of feeding compartments
circular, 8 m in diameter, and had four equally-spaced 1.5 m openings for internal access. At the center of each compartment there was an automatic canine feeder (Sweeney Enterprises Inc., Boerne, Texas, U.S.A.) that delivered Black Gold dog food pellets (650 g/animal/day; Black Gold, Vienna, MO, U.S.A.) at a preprogrammed time (Fig. 2-2). Food that was not consumed immediately was generally eaten by scrounging magpies (Pica hudsonia). Ad libitum water was provided from an automatic bubbler at one end of each enclosure. Coyotes had access to two shade shelters located at the opposite end of the enclosure as the feeding compartments.

![Fig. 2-2 A feeding compartment within an experimental pen](image)

**Animal Subjects**

Coyote subjects (n=16) were seven male/female pairs and one male/male pair of unrelated adult (2 to 6 year-old) animals (one pair/pen). Eight animals had been hand-reared; the other eight were mother-reared and had minimal prior contact with humans. In two pens both animals were hand-reared, in two other pens both animals were mother-reared, and the final four pens had one animal of each rearing type. Twelve animals had not been used in any prior experiments; the other four animals had been used in non-
invasive behavioral studies. All animals had been placed in their outdoor enclosures 6 months prior to the study’s commencement and had no direct human contact during that time.

**Human Subjects**

In this study, ambiguous threat consisted of anthropogenic activity. Human subjects included one familiar 26-year-old female to whom the coyotes had been exposed (through neutral activities such as pen and feeder maintenance) for approximately 18 months and one unfamiliar 23-year-old male to whom the coyotes had not previously been exposed. Each human subject subsequently interacted with the same four pairs of coyotes throughout the study (i.e., four hand-reared and four mother-reared animals in four of the eight enclosures). Neither human had been involved in hand-rearing the animal subjects.

**Treatments**

During the study, animal subjects were exposed to 16 different daily schedules of treatments combining the independent variables of anthropogenic activity (03:00 [night], 09:00 [morning], 15:00 [day], and 21:00 [evening]) and food delivery (03:00 [night], 09:00 [morning], 15:00 [day], 21:00 [evening]) (Table 2-1). The resulting combinations produced four time gaps (investigation windows) of 0, 6, 12, and 18 hours. For all combinations, the measured dependent variables were latency to feed and time spent investigating human scent trails after the food drop. Investigation was defined as the amount of time a coyote spent either stationary or moving slowly with its nose to the ground at the exact area of anthropogenic activity, and was clearly discernable from other
behaviors. Each of the 16 combinations required 1 week to test, and repetition of independent variables in successive weeks was avoided whenever possible. The weekly schedule occurred as follows: Monday, feeders were programmed to deliver food at the appropriate time. Coyote subjects then had 4 days without interference to adjust to the new feeding schedule. On Friday, each animal’s feeding latency and investigation times were measured following food delivery – these were the control data. On Saturday (treatment day 1), Sunday (treatment day 2), and Monday (treatment day 3), the designated human subject entered the enclosure at the scheduled time and spent 10 minutes walking around the perimeter of each of the feeding compartments. The same routes of travel were followed each time. The dependent variables (feeding latency and time spent investigating following the food delivery) were measured when the food dropped at the scheduled time each day. Following the week’s final data collection on Monday, feeders were reprogrammed for the following week’s food delivery time. All observations were made via thermal-imaging cameras from a 3-story observation tower. Observations of each pen lasted for 1 hour following food delivery. Data were recorded with Noldus Observer Behavioral Software, Leesburg, VA, U.S.A.

To build an association between humans and ambiguous threat, each human buried a steel leg-hold trap within their assigned enclosures 1 hour after the food delivery on Fridays, > 30 m away from the feeding compartments. The trap had been disarmed by removing one of its two jaws so that if sprung, the remaining jaw would throw dirt but not hold the coyote’s foot. Animal subjects had not previously been exposed to leg-hold traps. Traps were always set at the same location within an enclosure and along the fence
such that the human could walk to and from the trap without ever going within 30 m of a
feeding compartment. The traps remained in the enclosure throughout the treatment days
(Saturday, Sunday, and Monday) and were visited and reburied (if excavated or sprung)
before the human subject visited the feeding compartments each day.

Table 2-1 Experimental design. Columns represent various times of anthropogenic
activity; rows represent various times of food delivery. Internal boxes represent duration
of investigation windows for combinations. The 16 resulting combinations were each
tested in a week

<table>
<thead>
<tr>
<th>Anthropogenic Activity</th>
<th>03:00</th>
<th>09:00</th>
<th>15:00</th>
<th>21:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food Availability</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>03:00</td>
<td>0</td>
<td>18</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>09:00</td>
<td>6</td>
<td>0</td>
<td>18</td>
<td>12</td>
</tr>
<tr>
<td>15:00</td>
<td>12</td>
<td>6</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>21:00</td>
<td>18</td>
<td>12</td>
<td>6</td>
<td>0</td>
</tr>
</tbody>
</table>

Data Analyses

Data were analyzed with SAS statistical analysis software, version 9.1, Cary, NC, U.S.A. A significance value of $p < 0.05$ was used for all tests. Data from a food delivery
time of 15:00 were excluded from analyses, because coyotes were inactive and never fed
at this time of day during either the control or treatment, probably due to extreme heat
and/or high levels of anthropogenic activity elsewhere onsite. Much of the time-to-event
(latency to feed) data was censored because feeding did not occur within the 1 hour observation window, and so it was analyzed via a Cox proportional-hazards regression survival analysis (proc PHREG application).

To examine the effect of ambiguous threat on foraging behavior, control feeding latencies (Friday) were compared to the overall latencies on treatment day 1 of each week (Saturday) with a survival analysis. We compared feeding latencies at various times of food availability on treatment day 1 (the difference between food delivery times of 03:00, 09:00, and 21:00) to establish whether coyotes were bolder at certain times of the day. We then performed two analyses to determine whether coyotes that had prior experience with humans responded differently to anthropogenic activity than those which did not. First, we compared the feeding latencies on treatment day 1 of hand and mother-reared animals with a survival analysis. We performed another survival analysis to compare the feeding latencies from treatment day 1 of animals exposed to anthropogenic activity from the more and less familiar human subjects. To ascertain whether there was a relationship between the amount of time coyotes spent investigating anthropogenic activity and their latency to feed after food delivery, we performed simple linear regression tests on data from treatment day 1 for individual treatment combinations (excluding the censored data). Because we only had direct investigation data for the hour following food delivery (and not the entire time between anthropogenic activity and food delivery), we limited analysis of the investigation data to this test alone in an attempt to prevent erroneous conclusions about the amount of investigation in particular treatment combinations. To determine if the amount of time available for investigation (i.e., investigation windows of
0, 6, 12, and 18 hours between anthropogenic activity and food delivery) affected latency to feed, we compared the difference in feeding latency between these intervals on treatment day 1 with a survival analysis. We tested for a change in response to ambiguous threat over the 16 weeks of the study (>54 days of exposure to anthropogenic activity around feeding compartments) by comparing feeding latencies on treatment day 1 in the final weeks of the experiment with those in the initial weeks using a survival analysis. In addition, we tested for a change in latency to feed within individual treatment weeks by performing a survival analysis to compare feeding latencies for treatment days 1 (Saturday) and 3 (Monday) overall and in all levels of treatment for both food delivery time (03:00, 09:00, and 21:00) and investigation windows (0, 6, 12, and 18 hours).

Results

Response to Ambiguous Threat

Results for the whole model survival analysis (control [Fri] v. treatment [Sat]) indicated that anthropogenic activity had a significant effect on feeding latency ($p < 0.0001, \chi^2 = 162.25, \text{hazard ratio} = 0.418, SE = 0.068$) (Fig. 2-3). Coyotes were 58.2% less likely to feed when humans had been near their food source within 18 hours. Anthropogenic activity caused a significant increase in feeding latencies for all times of food delivery over the control, including 03:00 ($p = 0.0002, \chi^2 = 14.35, \text{hazard ratio} = 0.558, SE = 0.154$), 09:00 ($p < 0.0001, \chi^2 = 50.76, \text{hazard ratio} = 0.255, SE = 0.192$), and 21:00 ($p < 0.0001, \chi^2 = 127.78, \text{hazard ratio} = 0.205, SE = 0.154$). In addition, there was a difference between feeding latencies for food delivery times of 03:00 compared to both
**Fig. 2-3** Feeding likelihood for combined control and combined treatment data. Solid line depicts likelihood of feeding for control data; dashed line depicts likelihood of feeding for combined treatment data.
9:00 (p = 0.0069, $\chi^2 = 7.30$, hazard ratio = 0.426, SE = 0.315) and 21:00 (p < 0.0001, $\chi^2 = 31.95$, hazard ratio = 0.338, SE = 0.192), but no difference between feeding latencies for food delivery times of 09:00 and 21:00 (p = 0.2515) (Fig. 2-4).

Effect of Prior Experience

A survival analysis confirmed that there was no difference in feeding latency response between hand-reared and mother-reared animals (p = 0.5965). However, animals treated with anthropogenic activity from the more familiar human subject fed significantly faster than did animals exposed to the less familiar human (p = 0.0003, $\chi^2 = 12.90$, hazard ratio = 0.491, SE = 0.198) (Fig. 2-5).

Investigation

A simple linear regression test showed that there was a positive relationship between time spent investigating human scent trails and feeding latency for all treatment combinations (p values ranged from < 0.0001 to 0.0953, $r^2$ ranged from 0.3947 to 0.9584, n ranged from 8 to 16) during the hour following the food drop (Fig. 2-6). The vast majority of this investigation occurred prior to feeding. Coyotes never investigated the areas around the feeding compartments prior to foraging on control days.

Investigation Window

Anthropogenic activity caused a delay in feeding latency for all investigation window durations over control feeding latencies, including 0 hours (p < 0.0001, $\chi^2 = 2858.66$, hazard ratio = 0.000, SE = 0.296), 6 hours (p < 0.0001, $\chi^2 = 46.83$, hazard ratio = 0.482, SE = 0.106), 12 hours (p < 0.0001, $\chi^2 = 68.81$, hazard ratio = 0.390,
Fig. 2-4 Likelihood of feeding for various times of food delivery. Dotted line depicts likelihood of feeding for food delivery at 03:00; solid line depicts likelihood of feeding for food delivery at 09:00; dashed line depicts likelihood of feeding for food delivery at 21:00.
Fig. 2-5  Likelihood of feeding after anthropogenic activity by familiar and unfamiliar humans. Solid line depicts the likelihood of feeding after anthropogenic activity from the familiar human; dashed line depicts the likelihood of feeding after anthropogenic activity from the unfamiliar human.
There is a positive relationship between the time that coyotes spent investigating human scent and their feeding latency. This scatter graph represents the relationship between investigation time and feeding latency for a treatment combination in which anthropogenic activity occurred at 15:00 and food delivery occurred at 21:00 ($p < 0.0001$, $r^2 = 0.9584$, $N = 8$).
Feeding latencies at an investigation window of 0 hours were different from feeding latencies at investigation windows of 6 ($p < 0.0001$), 12 ($p < 0.0001$), and 18 hours ($p < 0.0001$) for data from treatment day 1 (Fig. 2-7). Hazard ratios were incalculable for these comparisons, because coyotes never fed within the 1 hour observation period when the investigation window was 0 hours. Feeding latencies for an investigation window of 6 hours were not significantly different from those at either 18 ($p = 0.1556$) or 12 hours ($p = 0.0580$), but latencies at 18 hours and 12 hours were different from each other ($p = 0.0002$, $\chi^2 = 13.92$, $hazard\ ratio = 1.523$, $SE = 0.112$).

**Change in Latency to Feed Over Time**

Over the duration of the experiment, the coyotes did not decrease their latency to feed between weeks on treatment day 1 (Saturday). A survival analysis showed that the latency to feed after first exposure to anthropogenic activity was similar to the latency to feed after coyotes had been exposed to anthropogenic activity for 16 weeks ($p = 0.7269$, $\chi^2 = 1.55$, $hazard\ ratio = 1.185$, $SE = 0.136$).

Within individual weeks, however, latency to feed did decrease. When all treatments were combined, anthropogenic activity on treatment day 1 increased feeding latency by 65.5% over the control ($p < 0.0001$, $\chi^2 = 166.92$, $hazard\ ratio = 0.345$, $SE = 0.082$), activity on treatment day 2 by 55.8% over the control ($p < 0.0001$, $\chi^2 = 99.21$, $hazard\ ratio = 0.442$, $SE = 0.082$), and activity on treatment day 3 by 49.2% over the control ($p < 0.0001$, $\chi^2 = 63.81$, $hazard\ ratio = 0.508$, $SE = 0.085$). Feeding latencies on treatment day 1 were significantly different from those on treatment day 2 ($p < 0.0001$, $\chi^2 = 32.21$, $hazard\ ratio = 0.592$, $SE = 0.092$).
Fig. 2-7 Likelihood of feeding for various investigation window durations. Dotted/dashed line depicts likelihood of feeding for an investigation window of 18 hours; dashed line depicts likelihood of feeding for an investigation window of 6 hours; dotted line depicts likelihood of feeding for an investigation window of 12 hours; solid line (on zero on X axis) depicts latency to likelihood of feeding for an investigation window of 0 hours.
\( \chi^2 = 31.53, \text{hazard ratio} = 1.286, SE = 0.045 \) and treatment day 3 \( (p < 0.0001, \chi^2 = 57.85, \text{hazard ratio} = 1.484, SE = 0.052) \). Feeding latencies on treatment days 2 and 3 were also significantly different from each other \( (p = 0.0001, \chi^2 = 14.49, \text{hazard ratio} = 1.154, SE = 0.038) \).

When data were broken down by individual treatments, there was a decrement in response over treatment days for most, but not all, individual delivery times and investigation window durations. In a comparison of treatment days 1 and 3, a decrease in feeding latency was found for food delivery times of 03:00 \( (p < 0.0001, \chi^2 = 114.27, \text{hazard ratio} = 1.815, SE = 0.056) \) and 21:00 \( (p < 0.0001, \chi^2 = 18.92, \text{hazard ratio} = 1.883, SE = 0.146) \), but not for 09:00 \( (p = 0.1048) \). On treatment day 3, feeding latencies at all food delivery times were still significantly different from those for the control \( (p < 0.0001 \text{ for 03:00 and 21:00, } p = 0.0013 \text{ for 09:00}) \). A decrement in response from treatment day 1 to 3 was also found for investigation windows of 6 hours \( (p < 0.0001, \chi^2 = 62.74, \text{hazard ratio} = 2.594, SE = 0.120) \) and 18 hours \( (p < 0.0001, \chi^2 = 55.88, \text{hazard ratio} = 2.043, SE = 0.096) \), but not for 0 hours (values cannot be calculated because all data is censored) or 12 hours \( (p = 0.1031) \). On treatment day 3, feeding latencies for investigation windows of 0 hours \( (p < 0.0001, \chi^2 = 4627.64, \text{hazard ratio} = 0.000, SE = 0.286) \), 12 hours \( (p = 0.0024, \chi^2 = 9.19, \text{hazard ratio} = 0.552, SE = 0.196) \) and 18 hours \( (p = 0.0418, \chi^2 = 4.14, \text{hazard ratio} = 0.734, SE = 0.120) \) were all still different from the control feeding latencies, while the average feeding latency at an investigation window of 6 hours was no longer significantly different from the control feeding latency \( (p = 0.9479) \).
Discussion

Prior anthropogenic activity delayed foraging in coyotes by over 58% in these test conditions. This suggests that coyotes perceived some level of ambiguous threat associated with human activity within their enclosures, even after the humans had clearly departed. Therefore, antipredator behavior is not limited to response to overt predatory stimuli. In this experimental situation, a delay to feed did incur cost. Magpies were prolific onsite during the day, and they consumed food that was deposited from the automatic feeders when the coyotes were not feeding. In addition, one coyote would consume the food from both feeders if the other refused to approach. The longer that coyotes waited to feed, therefore, the less food they ultimately consumed.

While an increase in feeding latency occurred at all times of food delivery (03:00, 09:00, and 21:00), foraging was delayed to a greater extent in the morning (09:00) and evening (21:00) than at night (03:00). A lesser response at night indicates accurate risk-assessment capabilities by the coyotes (Helfman 1989, Lima and Bednekoff 1999). At night, humans have poorer vision and are rarely active onsite, providing a less risky environment (Lima and Dill 1990, Kitchen et al. 2000) that is more conducive to investigation. This conclusion is supported by the fact that there was a decrease in feeding latency response from treatment day 1 to 3 for food delivery times of 03:00 and 21:00; it was dark following both of these food delivery times, and onsite anthropogenic activity was nonexistent. Conversely, there was no decrease in feeding latency over treatment days for a food delivery time of 09:00, which was followed by a period of increasing daylight and onsite human activity. In addition, a scrutiny of thermal camera
data showed that coyotes approached human subjects at night instead of avoiding them as they did during daylight hours, suggesting that coyotes perceived risk from humans to be less in darkness (Lima and Dill 1990).

Although total avoidance of ambiguous threat was not an option for these coyotes because the threat surrounded their sole food source, it is still possible that the delay in feeding was caused by simple avoidance of the areas at which anthropogenic activity occurred. However, our data suggest otherwise. Instead of completely avoiding ambiguous threat, coyotes used the time between food delivery and feeding for olfactory investigation of human scent trails. They prioritized investigation over feeding, which suggests that they did recognize anthropogenic activity as a threat and that investigation might have been a necessary form of risk assessment. This reliance on investigation for assessing risk is indicative of the use of cognitive inference as opposed to trial-and-error learning when dealing with an ambiguous threat. Cognitive inference was an adaptive strategy in this case; it was better for coyotes to overestimate a possible threat and gather information about it before acting. Although coyotes may have foregone a feeding opportunity, the cost of a missed meal was minimal compared with the cost of death if the threat turned out to be genuine.

An analysis of data from the various investigation windows also provided support for the importance of investigation in risk assessment. When coyotes had no time for investigating anthropogenic activity prior to food delivery (a 0 hour investigation window), they never fed in the 1 hour observation period following food delivery. Coyotes fed most quickly with an investigation window of 18 hours, and at an
intermediate time with an investigation window of 12 hours. This evidence is again suggestive of the seminal importance of investigation in risk assessment; more time to investigate ambiguous threat led to a shorter ultimate feeding latency. These data also support the idea that animals gain adaptive environmental information through the investigation of their environments (Grostal and Dicke 2000, Augustsson and Meyerson 2004, Dall et al. 2005). If we assume that coyotes were using the time between anthropogenic activity and food delivery for investigation of anthropogenic threat, then animals with more time for this investigation should have had more information about the threat. Because the threat was not real in this case, the coyotes should have had more time to infer this and should then have subsequently fed more quickly than animals with less time for deduction.

It must be noted, however, that an investigation window of 6 hours was anomalous in this pattern. Coyotes fed more quickly with a 6 hour investigation window than they did with an investigation window of 12 hours, which does not fit with the hypothesis that the amount of time for investigation alone determines feeding latency. However, we do have a plausible explanation as to why this occurred. Observation indicated that investigation was bimodal. Coyotes investigated human scent trails a great deal for a few hours immediately following anthropogenic activity, less so in the subsequent hours, and then heavily again after food delivery and prior to feeding. We suggest that the first investigation period was for collecting fresh olfactory information to be used in risk assessment and the second investigation period was for confirming this information before approaching the ambiguous threat and feeding. When an
investigation window was 6 hours, coyotes used the majority of that time for initial risk assessment and the gathered information was relatively fresh at the time of food availability. Therefore, less confirmation was subsequently necessary prior to feeding. This hypothesis is supported by the drastic decrease in feeding latency over treatment days for the 6 hour investigation window. After 3 treatment days, the latency to feed for an investigation window of 6 hours had decreased to control levels, while investigation windows of 0, 12, and 18 hours were all still significantly different from control feeding latencies on treatment day 3.

Interestingly, while identical treatment combinations within weeks caused a decrease in feeding latency from treatment days 1 to 3, this decrement in response did not continue when the treatment combination changed between weeks. This suggests that coyotes did not generalize acquired information about one treatment combination to a new treatment combination, even though the actual ambiguous threat was identical. Further support for a lack of generalization comes from the fact that hand-reared coyotes did not respond differently to anthropogenic activity than did mother-reared coyotes, suggesting that their previous experience with other humans did not change their response to these particular human subjects. Conversely, coyotes that were treated with anthropogenic activity from a familiar human subject delayed feeding less than did coyotes that were exposed to activity from an unfamiliar human, suggesting that prior information specific to those individual humans was utilized during risk assessment. Together, these behaviors suggest that coyotes compile and utilize information about specific individuals but are reluctant to generalize this information to other people. This
aversion to generalization is probably ecologically adaptive in the context of risk. As noted above, it is best to overestimate the risk of a situation, especially when information about an ambiguous threat is sparse. While generalization is useful when one has learned about a real threat, it may be detrimental to generalize about the nonoccurrence of risk from an ambiguous threat based on previous experience. An erroneous assumption here could lead to the loss of life.

Together, these results imply that coyotes used information gathering as a risk-assessment strategy to negotiate an ambiguous threat that surrounded a necessary resource. While they initially delayed feeding to investigate, coyotes fed if they determined that the threat was minimal after their investigation. Although they utilized information specific to the treatment combination (time of anthropogenic activity X time of food delivery X particular human) to determine the appropriate behavior, they never habituated to the changing threat. This suggests that coyotes correctly perceived the potential for danger from human activity.

As an aside, we feel that it is important to note that coyotes responded very strongly to harmless activity by humans in this experiment. Other experiments that examine the effects of avoidance or antipredator responses and do not account for the effect of human activity on animal behavior may report erroneous conclusions. In addition, coyotes responded very differently to different human subjects. Experiments that fail to control for inconsistent responses to multiple human researchers might be excluding an important variable.
Our study could have been improved through the documentation of the investigatory behaviors elicited by coyotes immediately following anthropogenic activity, especially when this activity occurred during the evening (21:00) or at night (03:00) when coyotes would likely be active. We have planned future studies to determine the behavior that coyotes exhibit immediately following anthropogenic activity. In addition, we plan studies to ascertain the specific information coyotes are capable of discerning from covert threat.

References


CHAPTER 3
THE ROLE OF INFORMATION GATHERING IN RISK ASSESSMENT FOR
THE COYOTE, CANIS LATRANS

ABSTRACT

While antipredator strategies have been a focus of behavioral research for decades, scientists generally study the responses of prey toward overt, explicit threat. However, risk can also be significant when a threat is covert, such as when an ambush predator may be nearby or a secondary threat remains after a predator’s departure. Animals in complex environments may reduce the uncertainty associated with covert threat through chemosensory investigation. This information gathering may be especially important when prior predator activity occurred close to a necessary resource. We studied the investigatory behaviors of seven pairs of captive coyotes toward ambiguous threat within their “territories.” The threat consisted of recent anthropogenic activity at both feeding and non-feeding locations. At feeding locations, two distinct responses were observed. Five animals thoroughly investigated sites of human activity and subsequently fed there, while nine animals neither investigated these locations nor fed. Non-feeding locations were seldom investigated by any animal. From these results, we suggest that coyote behavior in response to uncertain threat at foraging locations may be qualified as either proactive or reactive. The proactive cohort investigated some feeding locations more than others and subsequently chose to feed at these locations. When the proactive cohort of coyotes was prevented from investigating anthropogenic activity,

* Coauthored by Sarah Dawson and Michael M. Jaeger
foraging ceased altogether. This study is the first that provides evidence suggesting that canids gather information for cognitive inference about threat level.

INTRODUCTION

In a dynamic environment, accurate information aids in predicting the outcome of an action (Dall et al. 2005) by reducing uncertainty about the environment in which an organism subsists (Inglis 2000). Information may lead to more appropriate decisions concerning what to eat (Stephens & Krebs 1986), where to forage (Stephens & Krebs 1986, Inglis et al. 2001), or with whom to mate (Mazalov et al. 1996). While this information may result in the accumulation of significant fitness benefits over the span of an animal’s lifetime, good information about threat, such as a predator’s identity (Seyfarth et al. 1980; Slobodchikoff et al. 1991), proximity (Ferrari et al. 2006), or temporal pattern of activity (Fenn & MacDonald 1995; Kitchen et al. 2000), aids in risk assessment and may make an instantaneous difference between life and death (Lima & Dill 1990; Kats & Dill 1998; Ydenberg 1998). Vulnerable animals should therefore highly value information about potential threats.

However, information gathering often entails some level of risk (Bouskila & Blumstein 1992). While salient cues are available in a predator’s presence, most of the prey’s attention must be put towards avoiding capture during direct confrontation. Alternatively, prey may gather residual chemosensory cues that remain available after a predator’s departure (Kats & Dill 1998). While this tactic is probably less dangerous, focusing on information gathering diverts attention from vigilance (Dukas 2002) and prey may become more vulnerable to ambush attack. In addition, recent presence of some
predators (e.g., spiders or humans) can be associated with threat from secondary devices, such as webs, traps, or baits, which are dangerous even in the absence of the predator itself.

With these competing pressures, prey may use any of several behavioral strategies in order to manage both information acquisition and risk minimization. On one hand, prey might disregard the risk associated with investigating a site. However, this sort of trial and error learning is impudent from a risk perspective; the result of such action may be an untimely death if a predator is nearby or a real secondary threat has been overlooked (Ydenberg 1998). On the other hand, if prey deem information gathering to be prohibitively dangerous, they might choose to avoid sites of predator activity altogether (Sequin et al. 2003). While this avoidance strategy is probably safest in the short term, prey sacrifice the chance to obtain valuable information which may be useful in prospective risk assessment (Ydenberg 1998). In addition, avoidance of sites of prior predator activity is impossible if the activity occurred near an essential resource (Dawson and Jaeger, in preparation). In this case, prey should adopt a strategy in which they minimize the risk associated with information gathering but still acquire knowledge about a predator and any associated threats that might be concealed nearby (Owings 2002). Acquired information may then be used when making decisions about the safety of exploiting areas at which predators have been active (Kats & Dill 1998).

Coyotes, *Canis latrans*, are good subjects on which to examine the role of chemosensory investigation in risk assessment. As mesocarnivores, coyotes co-evolved with larger carnivores (Palomares & Caro 1999) with whom they competed for food (e.g.,
carcasses). Consequently, we would expect coyotes to have evolved antipredator behaviors that aid them in risk negotiation at foraging sites. Furthermore, olfaction is an important sense in canids; they use it to communicate (Gese & Ruff 1997; Allen et al. 1999) and easily recognize individuals based on scent alone (Dawson and Jaeger, in preparation). We also found that in past tests, captive coyotes postponed feeding in order to investigate prior anthropogenic activity that had occurred near their feeding stations (Dawson & Jaeger, in preparation). Whether or not they investigated the locations in the time between human activity and food availability, and how they subsequently used the acquired information, remained unclear.

In an attempt to clarify the strategies that animals use in response to prior predator activity, we observed and measured the behavior of captive coyotes toward anthropogenic activity at multiple sites within their enclosures. First, we documented whether coyotes ignored, avoided, or investigated each of the sites of anthropogenic activity prior to food availability. If coyotes investigated prior anthropogenic activity, we measured the duration of this investigation at both feeding and non-feeding locations to determine whether coyotes emphasized investigation at areas surrounding a necessary resource. To ascertain whether coyotes relied on the duration of investigation when deciding on a foraging site, we recorded the amount of investigation they performed at each of two feeding stations and monitored at which location the animals subsequently chose to feed. We conducted a final test to determine whether or not coyotes would forage at sites from which they had been prohibited from collecting information in order to ascertain their dependence on information gathering in risk assessment.
METHODS

Study Location

Experiments were conducted during November 2006 at the NWRC Predator Research Center in Millville, Utah, U.S.A. The 68-ha facility sits 1370 m above sea level and houses approximately 115 captive coyotes. During the course of the study, daytime temperatures averaged 10˚C and nighttime temperatures averaged -10˚C. Sunrise occurred between 0659 hours and 0733 hours; sunset occurred between 1658 hours and 1722 hours. A low level of human activity occurred onsite during daylight hours. No human activity occurred at night.

Tests were conducted in seven hexagonal 0.66 ha outdoor enclosures (Fig. 3-1). Two gates for human access were located at opposite ends of the enclosures. Each enclosure contained two feeding compartments (Fig. 2-2) located approximately one-third the distance from one end that were constructed with four steel mesh fences, each measuring 3.3 m x 2.6 m. Compartments were circular and 8 m in diameter with four equally spaced 1.5 m gaps for internal access. An automatic canine feeder (Sweeney Enterprises Inc., Boerne, Texas, U.S.A.) was at the center of each compartment, and it delivered 650 g dog food pellets (Black Gold, Vienna, MO, U.S.A.) daily at 1900 hours (Fig. 3-3). Water was provided ad libitum from a fountain at one end of each enclosure. Two shade shelters were positioned opposite the feeding compartments.

Animal Subjects

Coyote subjects (N = 14) ranged from 2 to 6 years of age and originated from the facility’s own breeding stock. Animals were separated into six unrelated male/female
**Figure 3-1.** An experimental enclosure showing the feeding compartments (“2” & “3”), other treatment locations (“1” & “4”), and the trap location (“T”) from Experiment 1.
pairs and one unrelated male/male pair; each pair inhabited its own enclosure. All 14 coyotes had previously been used in observational studies that were noninvasive. All of the animals had been placed in their outdoor enclosures 14 months prior to the study’s commencement and had received no direct human contact during that time.

**Human Subject**

In this study, a 23 year-old male human performed the anthropogenic activity. All coyotes had been exposed to this human in earlier experiments, during which he preformed the same actions described below for this study but at different times of day and in different locations within the enclosures.

**Experiment 1**

*Treatments*

During the study, animal subjects were exposed to anthropogenic activity at four locations of interest within their pens (Fig. 3-1). Two locations were feeding compartments, and the other two were non-feeding (“other”) areas. The test occurred as follows: at 1700 hours, the human subject entered the pen and proceeded to the first non-feeding location (marked “1” in Fig. 3-1) which was located exactly opposite one of the feeding compartments (Fig. 3-1). This location was delineated with small pieces of string tied on the enclosure’s perimeter fence and was the same size as the feeding compartments (8 m in diameter). Once arriving there, the human spent 5 min walking around the perimeter of the non-feeding area. After the 5 min had elapsed, he proceeded directly to the nearest feeding compartment (marked “2” in Fig. 3-1) where he walked...
around the perimeter of the feeding compartment for 5 min. Following the activity at the first feeding compartment, the human went to the center of the enclosure (location “T” in Fig. 3-1) and buried a leg-hold trap to reinforce a negative association with human activity. The trap had been disarmed by removing one of its two jaws so that if sprung, the remaining jaw would throw dirt but could not catch the coyote’s foot. All animal subjects had been exposed to these same disarmed leg-hold traps in prior experiments and as a result were cautious of feeding following human presence around the feeding compartments, even though traps were never set nearby. After setting the trap, the human went to the second feeding compartment (“3” in Fig. 3-1) and walked around its perimeter for 5 min before proceeding on to the final non-feeding location (“4” in Fig. 3-1) and walking that perimeter for 5 min and exiting the enclosure.

Data Analyses

At each location, the measured dependent variable was the amount of time spent investigating human scent trails after the human activity and before the food delivery 2 h later (1900 hours). Investigation was defined as the amount of time a coyote spent either stationary or moving slowly with its nose to the ground at the exact area of anthropogenic activity and was clearly discernable from other behaviors. We also recorded whether or not the coyotes fed within a 1 h observation window after the food delivery and, if so, at which compartment the feeding occurred. Each pen was tested in a single day, with all seven pens being tested within 1 week. All observations were made via thermal-imaging cameras from a three story observation tower. Data were recorded with Noldus Observer Behavioral Software, Leesburg, VA, U.S.A.
Data were analyzed with SAS statistical analysis software, version 9.1, Cary, NC, U.S.A. A significance value of using $P < 0.05$ was used for all tests. To determine the strategies that coyotes use in response to prior anthropogenic activity, we measured the amount of investigation that they performed at the four sites (two feeding locations and two non-feeding locations) within their enclosures. First, we compared the amount of investigation that took place between animals that fed and those that did not feed with an independent samples t test. This was done to determine whether the duration of investigation influenced the decision of whether or not to feed. If coyotes investigated prior anthropogenic activity, we compared the duration of this investigation at feeding and non-feeding locations to test whether coyotes emphasized investigation at areas surrounding a necessary resource. This analysis was performed with a paired-samples t test. To determine whether coyotes used the quantity of collected information when deciding on a feeding site, we compared the amount of investigation that they performed at the feeding compartment from which they subsequently ate with the amount of investigation that took place at the feeding compartment from which they did not feed with a second paired-samples t test.

**Experiment 2**

In a subsequent experiment, we tested whether the five coyotes that investigated anthropogenic activity in the first experiment would eat from their feeding compartments if discouraged from investigating them prior to food availability. Fladry was used as a barrier between the coyotes and their feeding compartments. Fladry is made from a rope with 0.5 m pieces of red plastic flagging (1 m x 0.1 m) attached at 0.4 m intervals, and it
was strung across enclosures at a height of 0.33 m above the ground. The fladry was not a visual barrier, and was only used in an attempt to prevent coyotes from conducting proximate chemosensory investigation at the feeding compartments for 2 h.

In the control portion of this test, a different human hung fladry in the pens at 1700 hours at the locations marked “A” in Fig. 3-2. One strand of fladry was hung 10 m from the end of the pen closest to the two feeding compartments, while the other strand was hung 20 m from the opposite corner of the pen. For this control phase, both the coyotes and the feeding compartments were contained inside the two strands of fladry (Fig. 3-2). Immediately following the fladry suspension, the human subject entered the enclosure via the gate closest to the feeding compartments and spent 5 min walking around the perimeter of each feeding compartment before leaving the pen. The coyotes had full access to investigate the human activity. Two h later (at 1900 hours), the fladry was removed from the pen by the human that had hung it. This occurred just prior to food delivery and from outside the pens. Coyotes were then observed during the hour following food delivery to see if they fed.

For the treatment phase of this experiment, we hung fladry within the enclosures at the locations marked “B” in Fig. 3-2 at 1700 hours. This time, the fladry was hung 20 m from the end of the pen closest to the two feeding compartments and 10 m from the opposite corner of the pen. Here, the coyotes were contained within the two strands of fladry, but the feeding compartments remained outside. Again, the human subject entered the enclosure and spent 5 min walking around the perimeter of each of the feeding compartments. In this phase, the coyotes were unable to investigate the human
Figure 3-2. Location of the fladry for Experiment 2. “A” marks the location of the fladry for the control portion of the experiment in which the coyotes had access to investigate human activity. “B” marks the location of the fladry for the treatment portion of the experiment in which the coyotes did not have access to investigate human activity.
activity without crossing the fladry. Once more, the fladry was removed 2 h later, at 1900 hours, and just prior to food delivery. We again watched to see whether or not the coyotes fed in the subsequent hour. Animals within four pens were tested using both control and treatment phases, and each pen was tested with the control and treatment phases in 2 consecutive days. In this way, all four pens were tested in 8 days. Two pens received the control portion of the test first, while the other two received the treatment portion first.

RESULTS

Experiment 1

Coyotes had two different behavioral strategies to prior anthropogenic activity. Five animals (hereafter referred to as the “proactive cohort”) both investigated the locations where human activity was concentrated prior to food availability and subsequently fed quickly when food became available, while the remaining nine (hereafter referred to as the “reactive cohort”) investigated anthropogenic activity very little and did not feed within the 1 h observation window. Four males and one female were proactive, while the final four males and five females were reactive. Three pairs consisted of two reactive animals, one male/female pair was made up of two proactive animals, and the final three pairs consisted of a proactive male and a reactive partner. All proactive animals were 2 years old, while reactive animals ranged in age from 2 to 6 years. There was a difference between cohorts in the amount of investigation performed (Welch test for unequal variances: $t_{12} = -4.037, P = 0.0156$) (Fig. 3-3). The remaining analyses were performed
Figure 3-3. Mean investigation time (+/- 1 SEM) of proactive and reactive coyote cohorts towards prior anthropogenic activity.
only on proactive cohort \((N = 5)\). These animals investigated anthropogenic activity around feeding compartments more than around non-feeding areas (two-tailed paired-samples t test: \(t = 3.061, \ P = 0.0376\)) (Fig. 3-4). Each of the proactive animals fed from only one feeding compartment in the 1hr observation window following the food drop, and there was significantly more investigation at the used feeding compartment than at the unused compartment (two-tailed paired-samples t test: \(t = 3.011, \ P = 0.0395\)) (Fig. 3-5).

**Experiment 2**

All five coyotes in the proactive cohort fed in the control portion of this experiment (when they were not prohibited from investigating prior anthropogenic activity). However, none of the five coyotes fed in the 1 hr observation window when the fladry barrier successfully prevented them from investigating the feeding compartments. Coyotes instead used the hour for investigating prior anthropogenic activity that occurred near the feeding compartments (human scent near the fladry was largely ignored).

**DISCUSSION**

In our experiment, none of the coyotes rushed in to feed when food became available within their feeding compartments without first gathering information. This suggests that coyotes do perceive the potential for threat from prior anthropogenic activity (controls used in other experiments indicate that coyotes do not hesitate to feed when human activity does not occur near feeding compartments). However, coyotes did
Figure 3-4. Mean investigation time (+/- 1 SEM) of proactive coyotes towards anthropogenic activity at feeding compartments and other locations.
Figure 3-5. Mean investigation time (+/- 1 SEM) of proactive coyotes towards anthropogenic activity at the feeding compartment from which they chose to feed and the feeding compartment from which they did not feed.
use two strategies to deal with this uncertain threat. One group \((N = 9)\) investigated anthropogenic activity very little (or not at all) and chose not to eat when food became available within their pens 2 h later. Another group \((N = 5)\) investigated anthropogenic activity heavily (in some cases for almost the entire 2 h) and then fed very quickly after food became available. We have termed these groups the reactive and proactive cohorts, respectively. Sih et al. (2004) describe proactive animals as bold manipulators of their environments that readily explore their surroundings and often forage relatively quickly after predatory activity. Reactive animals, on the other hand, pay close attention to environmental changes but respond to them through passive observation (Sih et al. 2004). Depending on the environmental context, either of these behavioral syndromes may be the more adaptive. For example, in our study, the proactive cohort faired better because they investigated human activity, determined that no real threat was present and then collected food when it subsequently became available. If a real secondary threat had been left behind by the human subject within the pens, however, the proactive animals may have been captured or killed. Therefore, reactive animals may be favored in highly variable or risky environments in which high levels of exploratory activity could be detrimental (Sih et al. 2004).

Coyotes within our experiments were forced pairs; unlike in a natural setting, coyotes were not able to choose their mates or remain in a pack as a subordinate animal. Thus, it is plausible that natural pairs of dominant coyotes may enact a dual strategy such that one is proactive (usually the male) and the other reactive (usually the female); four of the five proactive animals within our experiment were males. This makes ecological
sense in terms of enhancing the chance that the female survives to provision the pups. This seems consistent with the Blejwas et al. (2006) finding that alpha males were the primary killers of sheep. Sheep are associated with human threat and depredation is risky.

Contrary to Sequin et al. (2003), the proactive cohort of coyotes in our study investigated all locations of prior anthropogenic activity proximately to some extent, which implies that the coyotes valued chemosensory information in general. This supports the hypothesis of Inglis (2000), which suggests that coyotes gather information in order to reduce environmental uncertainty in their surroundings. However, the proactive coyotes spent more time investigating anthropogenic activity that occurred around a necessary resource (their feeding compartments) than at other locations, suggesting that they may have recognized the risk inherent with investigation and attempted to minimize this risk while still gaining relevant information about potential threat near their feeding site. (In this case, the same information could presumably be learned through investigation at either feeding or non-feeding locations; hence coyotes were capable of “multitasking” by emphasizing investigation at feeding sites.)

In addition, the proactive cohort investigated the feeding compartment from which they eventually fed more than they investigated the other feeding compartment. This implies that coyotes recognized the amount of information that they had acquired at each of the feeding compartments and opted to feed at the location at which they had gathered the most information. Alternatively, coyotes made an a priori decision of the
compartment from which to feed, and then spent the majority of their time investigating the human activity that had occurred there to ensure that that location was safe.

When prevented from chemosensory investigation of prior anthropogenic activity surrounding the feeding compartments, the proactive cohort all opted not to eat in the subsequent 1 h observation window and instead used this time to investigate areas at which humans had been active. This behavior implies a reliance on chemosensory, not just visual, information gathering in the assessment of uncertain risk. When prey are uncertain of the risk level at a location, it is more adaptive to be overly cautious and delay an opportunity to eat than to underestimate the actual risk and lose one’s life.

Together, these results imply that coyotes are using cognition when dealing with uncertain threat from anthropogenic activity. The proactive cohort investigated the anthropogenic activity before food became available, suggesting that they used this chemosensory information. The information surrounding the feeding compartments was doubly valuable – not only would acquiring chemosensory information here allow coyotes to reduce environmental uncertainty surrounding an essential resource, but also it would allow the animals to learn the chemical signature of a potential threat which could be used in expediting decisions in future encounters.

Since we only carried this experiment out for 1 day in each pen, we are unsure of how the reactive cohort would have responded as days passed if we continued the treatment and their hunger level increased. Future experiments might target the ongoing behavior of both the proactive and reactive cohorts over time, noting any changes that occurred. In addition, experiments aimed at uncovering the actual content of acquired
information would bring us a step closer to identifying the capabilities of animals in chemosensory risk assessment.

References


CHAPTER 4
WHAT DO YOU KNOW? COYOTES (CANIS LATRANS) PROCESS
INFORMATION ASSOCIATED WITH HUMAN ACTIVITY AND
DISTINGUISH THE BAD GUYS FROM THE OTHER GUYS*

Abstract

Evidence indicates that prey are capable of assessing risk, even in the absence of a predator. However, the components of acquired information are largely unknown. Therefore, we designed an experiment to determine if eight pairs of captive coyotes investigate and/or delay foraging when presented with information indicative of different levels of threat. Prior to testing, three different male human subjects separately associated themselves with the coyotes positively (by leaving food), negatively (by leaving a trap), or neutrally (by standing) at designated areas within the coyote enclosures. Association occurred such that coyotes were presented with each human in separate roles; not all coyotes received the same human in each role. We then conducted three tests. In the Threat Level Test, the actual associated humans spent time near the feeding compartments and the same dependent variables were measured. In the Contradictory-Information Test, old scent from the associated human subjects was left by an unassociated human near the feeding stations in the enclosure; duration of investigation and feeding latency were measured at that site. In the Long-Term Memory Test, the Threat-Level Test was repeated after 30 days of inactivity. For all tests, latency to feed for the negative treatment was longer than for the positive or neutral treatments.

* Coauthored by Sarah Dawson and Michael M. Jaeger
Investigation time was higher for negative treatment than for positive or neutral in the Threat-Level and Memory Tests, but investigation times between treatments were equal in the Contradictory Information Test. These results suggest that coyotes are able to respond to conflicting information indicative of multiple threat levels, and that they retain this information over long periods of time. These sophisticated risk-assessment capabilities allow coyotes to successfully negotiate risk in the face of ambiguous threat.

Introduction

Several theories concerning the behavior of prey in response to predator activity, such as Helfman’s threat-sensitive predator avoidance hypothesis (1989) and Lima and Bednekoff’s predation risk allocation hypothesis (1999), suggest that prey should behave in a manner appropriate to the degree of threat that they are currently experiencing from predation. The ability to accurately gauge existing predation risk is advantageous because antipredator defenses are inherently costly (Lima 1998, Lima and Bednekoff 1999). Time and resources spent avoiding risky situations might alternatively be allocated to foraging and reproduction, and this tradeoff has probably driven the evolution of accurate and efficient risk-assessment capabilities (Lima and Dill 1990). In support of this concept, a large body of evidence has accumulated to suggest that prey do indeed have the ability to accurately assess the level of risk they are currently experiencing (Lima and Dill 1990). For instance, prey minimize their risk of predation by making fitting decisions about when and where to forage, how to handle food, what size group to maintain, and how often to look up from other activities to scan for
predators (see Lima and Dill 1990 for a thorough review of the influence of predation risk on each of these behaviors).

Appropriate behavioral decisions are facilitated by relevant information (Inglis 2000, Dall et al. 2005). In the presence of a predator, prey have access to many cues that are indicative of their current level of threat (Stankowich and Blumstein 2005), including predator species identity (Seyfarth et al. 1980), the individual predator within a species (Slobodchikoff et al. 1991), predator abundance (Helfman 1986), proximity (Cooper 1998, Stankowich and Coss 2006), approach speed (Cooper 1997, Cooper 2003, Cooper et al. 2003, Stankowich and Coss 2006), and directness of approach (Cooper 1997, Cooper 2003, Cooper et al. 2003, Stankowich and Coss 2006). The response of prey to each of these cues has been examined in some detail.

However, sometimes prey incur significant risk without direct confrontation from predators (Dawson and Jaeger, in preparation). For instance, predation risk from ambush predators may be substantial even in the absence of visual cues. In addition, prior activity by some predators (e.g., spiders or humans) can be associated with threat from secondary devices, such as webs, traps, or baits, which are dangerous even in the absence of the predator itself. In these more subtle risky situations, relevant information may be especially critical for avoiding capture (Kats and Dill 1998).

Although contemporary visual cues may be lacking in these situations, prey still have access to other indicators that may aid in the deduction of appropriate behavior. Firstly, prey might utilize any previous acquired visual information relevant to a situation. For instance, if prey previously observed suspicious activity from a departed
predator that may have been indicative of the placement of a secondary threat, then this information can be integrated into future decisions as long as prey memory is durable and robust.

In addition, predators often emit or leave behind chemosensory information that prey may utilize to facilitate germane decisions (Kats and Dill 1998, Grostal and Dicke 2000, Kusch et al. 2004, Dall et al. 2005). Although ample evidence indicates that prey exploit chemosensory information when making antipredator decisions (Kats and Dill 1998), few experiments have been conducted that establish the semantics of information encoded chemical cues. In a notable exception, Chivers and Mirza (2001) conducted a literature review which concluded that prey were able to distinguish the diet of predators through chemosensory information alone. In addition, Kusch et al. (2004) found that fathead minnows (*Pimephales promelas*) were able to determine the size of predators through the concentration of certain chemical cues. At present, however, it is unknown whether prey have the capability of determining anything besides the components of a predator’s diet and chemical concentrations through this chemosensory information gathering.

In a series of experiments, Dawson and Jaeger (in preparation) found that coyotes (*Canis latrans*) investigated sites of prior anthropogenic activity and would not forage at nearby feeding stations if they were unable to perform this investigation. This seems to indicate that coyotes did perceive the potential for risk from prior human activity and used information acquired through investigation to assess the associated threat and work
around this risk. However, the specific content of the information to which coyotes were responding remains unknown.

Coyotes are good subjects on which to test risk-assessment capabilities towards ambiguous threat. As mesocarnivores, coyotes evolved in the presence of larger, more powerful carnivores that posed a threat to them (Palomares and Caro 1999). In order to compete successfully, coyotes developed strategies or learned techniques that allowed them to decrease the likelihood of being captured or killed while foraging. As opportunists and generalists that often get food by scrounging at carcasses, coyotes must often be wary of larger unseen predators that may be lurking nearby. In addition, coyotes are often exposed to significant secondary threats from humans, including traps, snares, and laced baits, and have a proclivity to work around them. Coyotes rely on their sense of olfaction for communication (Gese & Ruff 1997; Allen et al. 1999), and previous studies (Dawson and Jaeger, in preparation) indicated that they investigated human scent trails before foraging near areas of anthropogenic activity.

The major objective of this study was to determine whether coyotes are capable of discriminating among various levels of potential threat following human activity at an established feeding site. In addition, we used contradictory visual and olfactory information to see whether coyotes were still able to distinguish among these threats. Finally, we tested the durability of this information by performing a memory test after 30 days. The ability to distinguish among different types of ambiguous threat and the retention of this information would demonstrate a highly sophisticated risk-assessment capability in coyotes.
Methods

Study location

Tests were conducted at the NWRC Predator Research Center in Millville, Utah. The 68 ha facility houses 115 captive coyotes and is located at an elevation of 1370 m above sea level. Tests were conducted during the summer of 2007. Weather conditions throughout this time were generally dry and hot, with daytime temperatures averaging 29°C and nighttime temperatures averaging 10°C. Sunrise occurred between 05:52 and 06:35 during the study’s duration; sunset occurred between 20:27 and 21:06. The research center experiences a moderate level of human activity throughout the day – several studies take place at any given time, and general animal care activities occur daily. Besides the procedures noted in this study, no human activity occurred at night.

Tests occurred in eight hexagonal 0.66 ha outdoor enclosures (each side measured 54 m) (Fig. 4-1) that were divided into three groups; group 1 consisted of three enclosures, group 2 consisted of two enclosures, and group 3 was made up of the final three enclosures (Fig. 4-2). Two gates for human access were located at opposite ends of the enclosures. All enclosures contained two feeding compartments placed approximately 2/3 the distance from one end. Each feeding compartment was made from four horse panels (3.3 m x 2.6 m steel mesh fences). Compartments were circular, 8 m in diameter, and had four equally-spaced 1.5 m openings for internal access. At the center of each compartment there was an automatic canine feeder (Sweeney Enterprises Inc., Boerne, Texas, U.S.A.) that delivered dog food pellets (650 g/animal/day; Black Gold,
Fig. 4-1 Layout of a test enclosure showing position of feeding compartments and locations of pre-test anthropogenic activity
Vienna, MO, U.S.A.) at 00:00 (Fig. 2-2). Food that was not consumed immediately was generally eaten by magpies (*Pica hudsonia*). Ad libitum water was provided from an automatic bubbler at one end of each enclosure. Coyotes had access to two shade shelters located at the opposite end of the enclosure as the feeding compartments.

![Diagram of experimental pens](image)

**Fig. 4-2** Eight experimental pens divided into three test groups. Each group received the same humans associated in the same roles, but roles for humans were different between groups.

**Animal Subjects**

Coyote subjects (*n=16*) were seven male/female pairs and one male/male pair of unrelated adult (2 to 6 year-old) animals (one pair/pen). All animals had previously participated in similar observational studies. The coyotes had been placed in their outdoor enclosures 18 months prior to the study’s commencement and had no direct human contact during that time.
**Human Subjects**

In this study, three types of ambiguous threat were used. Each was associated with three human males. The first of these (Human 1) was a 62-year-old who had built the feeding compartments within the enclosures 18 months prior; he had not been inside the enclosures since that time. The second human subject (Human 2) was a 57-year-old who had never encountered any of the coyote subjects or performed any activity within their pens. The third human subject (Human 3) was a 24-year-old who had intermittently spent time within the coyote enclosures during the preceding 18 months performing activities such as pen and feeder maintenance and setting mock traps (i.e., disarmed leg-hold traps that threw up dirt when sprung but could not hold a coyote). In addition, a fourth human (Human C, a 27-year-old female) was used to move scent cues, as explained below. She had also participated in the same activities as Human 3 during the preceding 18 months.

**Pre-test Association Phase**

A pre-test phase occurred daily at approximately 08:00 on the 4 days before the experimental testing began. During this time, coyotes were presented with three levels of threat: positive (+), neutral (0), and negative (-). For a positive association, the designated human subject entered the pen through the gate opposite the feeding compartments, walked along the interior fence to the location marked “+” in Figure 4-1, and left 0.5 kg of wet mink food there (food was purchased from a local slaughterhouse). He spent a total of 5 minutes at the location before leaving from the gate through which he had entered. For a neutral association, the designated human subject entered the pen
through the gate opposite the feeding compartments, proceeded along the interior fence to the location marked “0” in Figure 4-1, and simply stood or sat there for 5 minutes before exiting through the same gate. The negative association was achieved by the designated human subject entering the enclosure through the gate opposite the feeding compartments, walking to the location marked “-” in Figure 4-1, and burying a disarmed leg-hold trap there. The trap could not capture the coyotes, but it would spring up upon contact, throwing dirt and snapping shut. Coyotes had been exposed to these buried traps in earlier experiments and were wary of human activity associated with them. After spending 5 minutes at the location, the human subject exited the enclosure via the gate through which he had entered.

Animals within each group were subjected to identical treatments throughout the experiment, while treatments between groups were procedurally identical but utilized human subjects in different roles. Each of the three human subjects was associated in all three ways, but was only associated in one way for any group of animals (Table 4-1). In this way, Human 1 was associated positively for group 1, neutrally for group 3, and negatively for group 2; Human 2 was associated positively for group 2, neutrally for group 1, and negatively for group 3; and Human 3 was associated positively for group 3, neutrally for group 2, and negatively for group 1 (Table 4-1).

**Treatments**

To test the questions posed by this study, a series of three experiments were used. The first experiment (the Threat-Level Test) tested whether coyotes distinguished among
Table 4-1 Experimental design. Columns represent three human subjects; rows represent treatment types. Groups were superimposed onto resulting 9 combinations such that each human performed each of the three treatments but was not associated in more than one way for any group.

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<td><strong>Negative(^-)</strong> Treatment</td>
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<td>Group 1</td>
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For each threat level (+, 0, or -) the human that had been assigned to that particular treatment (Human 1, 2, or 3) entered the enclosure at 22:00 through the gate closest to the feeding compartments and spent 5 minutes walking around the perimeter of each of the feeding compartments before exiting through the gate from which he had entered. He did not visit the association locations or perform any sort of associating behaviors. The most recent association had occurred 38 hours prior to the test. The measured dependent variables were time spent investigating human scent around the perimeter of the feeding compartments between human treatment (22:00) and food drop (00:00) and latency to feed after food delivery. Investigation was defined as the amount of time a coyote spent either stationary or moving slowly with its nose to the
ground at the exact area of anthropogenic activity, and was clearly discernable from other behaviors.

The second experiment (the Contradictory-Information Test) addressed the question of whether contradictory visual and olfactory information would hinder the coyotes’ ability to distinguish among threat levels. Here, an unassociated human (Human C) entered an enclosure at 22:00 through the gate opposite the feeding compartments, walked to one of the pre-test locations (i.e., +, -, or 0), removed a shovel-full of dirt (approximately 1 liter) from it, and deposited it across the four openings of both feeding compartments within the enclosure (Fig. 4-1). At test time, the transplanted scent was approximately 14 hours old. Human C then left the enclosure via the gate closest to the feeding compartments. The measured dependent variables were time spent investigating human scent around the perimeter of the feeding compartments between human treatment (22:00) and food drop (00:00) and latency to feed after food delivery. Investigation was defined as the amount of time a coyote spent either stationary or moving slowly with its nose to the ground at the exact area of anthropogenic activity, and was clearly discernable from other behaviors. The measured dependent variables were time spent investigating human scent around the perimeter of the feeding compartments between treatment and food drop and the latency to feed after food was delivered.

The final experiment (the Long-Term Memory Test) tested whether the coyotes retained long-term memory of the different threat levels. Here, the same series of events occurred as in the Threat-Level Test – Human 1, 2, or 3 walked into the pen through the gate closest to the feeding compartments and spent 5 minutes walking around the
perimeter of each of the feeding compartments before exiting through the gate from which he had entered. This time, however, the coyotes had not seen the human or had any sort of association with him for 30 days. Once again, measured dependent variables were investigation time and feeding latency.

All observations were made via thermal-imaging cameras from a 3-story observation tower onsite. Observations of each pen lasted for 3 hours; they started after the treatment, encompassed the two hours until food delivery (during which time the duration of investigation was measured), and lasted for another hour following food delivery (during which time the feeding latencies were measured). Data were recorded with Noldus Observer Behavioral Software, Leesburg, VA, U.S.A.

Data Analyses

Data were analyzed with SAS statistical analysis software, version 9.1, Cary, NC, U.S.A. A significance value of $p < 0.05$ was used for all tests. For each of the three phases, a difference for the amount of investigation time between the positive, neutral, and negative treatments was examined with a repeated-measures ANOVA. A difference between feeding latency for the treatments in each of the three phases was analyzed with a repeated-measures Cox proportional-hazards regression survival analysis (proc PHREG application) because some of these data were censored.
Results

Threat-Level Test

Coyotes investigated the threat treatments in the Threat-Level Test differentially (repeated-measures ANOVA, $F_{2,30} = 13.44, p < 0.0001$) (Fig. 4-3). Tukey tests revealed that coyotes investigated negative treatments more than both positive ($p < 0.05$) and neutral treatments ($p < 0.05$), but that there was no difference between investigation of positive and neutral treatments. In addition, there was a difference in the feeding latency between treatments for the whole model ($p < 0.0001, \chi^2 = 30.47$); coyotes fed quickly for the positive treatment, 71% more slowly for the neutral treatment compared to the positive ($p = 0.0077, \chi^2 = 7.09, \text{hazard ratio} = 0.293, SE = 0.460$), and 88% more slowly for the negative treatment compared to the positive ($p < 0.0001, \chi^2 = 29.12, \text{hazard ratio} = 0.124, SE = 0.381$). There was also a difference between feeding at neutral and negative treatments, with coyotes feeding more slowly for negative treatments compared to neutral ($p = 0.0164, \chi^2 = 5.76, \text{hazard ratio} = 2.361, SE = 0.357$) (Fig.4-4).

Contradictory-Information Test

Prior to food delivery, coyotes investigated the soil associated with the positive, neutral, or negative human that had been transported to the entrances of the feeding compartments by Human C. However, there was no difference in the amount of investigation among them (repeated-measures ANOVA, $F_{2,30} = 0.27, p = 0.7652$) (Fig. 4-5). Nevertheless, there was a difference in the feeding latency between treatments for the whole model ($p < 0.0001, \chi^2 = 31.68$). Coyotes fed quickly for the positive treatment, 87% more slowly for the neutral treatment compared to the positive treatment.
Investigation times for negative, neutral, and positive treatments in the Threat-Level Test. Bar represents +/- 1 SEM. Coyotes investigated positive and neutral treatments the same amount, but they investigated negative treatments more than both positive and neutral treatments.
Feeding latency results for individual treatments in the Threat-Level Test. Dotted line depicts likelihood of feeding for a positive treatment; dashed line depicts likelihood of feeding for a neutral treatment; solid line depicts likelihood of feeding for a negative treatment. As with the chemosensory phase, coyotes fed most quickly when the treatment was positive, least quickly or not at all when the treatment was negative, with feeding latencies for neutral treatments falling in between. Feeding latencies for all treatments were significantly different from each other.
Fig. 4-5 Investigation times for negative, neutral, and positive treatments in the Contradictory-Information Test. Bar represents +/- 1 SEM. There was no significant difference in investigation between the treatments when associated human scent was left at the entrances to the feeding compartments.
(p < 0.0001, $\chi^2 = 15.15$, hazard ratio = 0.128, SE = 0.531), and 96% more slowly for the negative treatment compared to the positive ($p < 0.0001, \chi^2 = 31.48$, hazard ratio = 0.038, SE = 0.590). There was also a difference between feeding latencies for neutral and negative treatments, with coyotes feeding more slowly for negative treatments compared to neutral ($p = 0.0022, \chi^2 = 9.41$, hazard ratio = 3.398, SE = 0.402) (Fig. 4-6).

**Long-term Memory Test**

Results of the Memory Test were very similar to those of the first experiment that tested coyotes’ response to various threat levels. Again, coyotes investigated the treatments differently (repeated-measures ANOVA, $F_{2,30} = 7.53$, $p = 0.0026$). Tukey tests revealed that while there was no difference between positive and neutral treatments, coyotes investigated negative treatments more than both positive ($p < 0.05$) and neutral treatments ($p < 0.05$) (Fig. 4-7). There was again a difference in the feeding latency between treatments for the whole model (repeated-measures Cox proportional-hazards regression, $p = 0.0053, \chi^2 = 10.49$); coyotes fed quickly for the positive treatment, 47% less readily for the neutral treatment compared to the positive (not significant; $p = 0.0617, \chi^2 = 3.49$, hazard ratio = 0.482, SE = 0.335), and 74% more slowly for the negative treatment compared to the positive ($p = 0.0018, \chi^2 = 9.79$, hazard ratio = 0.255, SE = 0.428). Again, there was also a difference between feeding at neutral and negative treatments, with coyotes feeding more slowly for negative treatments compared to neutral ($p = 0.0092, \chi^2 = 6.78$, hazard ratio = 2.070, SE = 0.276) (Fig. 4-8).
**Fig. 4-6** Feeding latency results for individual treatments in the Contradictory-Information Test. Dotted line depicts likelihood of feeding for a positive treatment; dashed line depicts likelihood of feeding for a neutral treatment; solid line depicts likelihood of feeding for a negative treatment. Coyotes fed most quickly when the treatment was positive, least quickly or not at all when the treatment was negative, with feeding latencies for neutral treatments falling in between. Feeding latencies for all treatments were significantly different from each other.
Investigation times for negative, neutral, and positive treatments in the Long-Term Memory Test. Bar represents +/- 1 SEM. Coyotes investigated positive and neutral treatments the same amount, but they investigated negative treatments more than both positive and neutral treatments.
Fig 4-8 Feeding latency results for individual treatments in the Long-Term Memory Test. Dotted line depicts likelihood of feeding for a positive treatment; dashed line depicts likelihood of feeding for a neutral treatment; solid line depicts likelihood of feeding for a negative treatment. There was a significant difference between feeding latencies for the negative treatment compared to both the neutral and positive treatments, but no difference between feeding latencies for the positive and neutral treatments.
Discussion

In this study, coyotes were wary of feeding in the presence of ambiguous threat. Here, ambiguous threat was due to recent human presence nearby the coyotes’ feeding compartments. In this situation, threat was inferred as there was no actual threat (i.e. buried object near food). An earlier study (Dawson and Jaeger, in preparation) showed that coyotes will work around this threat when allowed the opportunity to investigate, but that they will not feed if prevented from doing so. What information do the coyotes need before they risk feeding? In this situation, they needed to distinguish not only among sources of ambiguous threat (e.g., a specific individual human) but also among threat levels from the same source (e.g., +, 0, or -). The results of this study provide three lines of evidence to support this risk assessment capability in coyotes.

The Threat-Level Test showed that coyotes were able to distinguish among the three levels of threat and focused their greatest attention on the most important threat level – the human associated negatively. In the two hours prior to food availability, coyotes spent significantly more time investigating the human presence associated with the buried trap. Following food availability, coyotes showed the longest latency to feed with the negative treatment and the shortest with the positive treatment. That coyotes made this distinction implies that they also investigated the three treatment locations at the opposite end of their enclosures from the feeding compartments.

Since animals encounter an ambiguous threat in the absence of an overt threat (like an actual predator), available information in the surrounding area has the potential to be complex. In the case of a secondary threat, such as a baited trap, other animals may
have also visited the area. In addition, trappers are known to apply the scent of coyote conspecifics to their traps in an attempt to draw animals in. Information available at the site may therefore be vulnerable to misinterpretation. Are coyotes capable of distinguishing threat level in the presence of confounding information? The Contradictory-Information Test demonstrated that coyotes perceived risk at feeding sites and distinguished among threat levels in spite of conflicting information. The scent of humans associated with each threat level was transported to the feeding enclosures in soil by a human unassociated with the threat treatments (Human C). In addition, Human C’s presence provided confounding visual and olfactory information. Interestingly, this treatment affected the relative proportion of time spent investigating feeding compartments prior to the food drop – equal time was spent investigating scent associated with all three threat levels. However, once food was present, coyotes were most cautious toward the negative threat and least cautious toward the positive threat, as was the case in the first experiment. This result suggests that olfactory cues for a recognized threat supersede contradictory visual cues and other confounding olfactory cues. This strategy for assessing risk associated with ambiguous threat would be difficult to defeat.

Effective risk assessment may be enhanced through the retention of information that has been acquired about particular ambiguous threats. This is because risk assessment itself may be dangerous – in addition to the possibility of triggering a secondary threat such as a trap, animals focusing on information acquisition are diverting attention from vigilance and may therefore become more vulnerable to ambush attack. Furthermore, time spent re-gathering information is time that could alternatively be used
for foraging and reproductive efforts; therefore, evolution should favor animals that are capable of efficiently maintaining information regarding threat over a period of time.

Results of the Memory Test indicate that coyotes remembered threat levels over a period of weeks. These results were also very similar to those in the Threat-Level Test, conducted a full month before.

The one difference between the Threat-Level and Memory Tests was that in the Memory Test, some coyotes did not feed for the positive treatment (whereas they all fed in the Threat-Level Test). This may indicate that coyotes tend to view humans as threatening in general, and will revert to this wariness as time passes after a prior positive association. This behavior is probably adaptive; when dealing with a potential threat, it is better to err on the side of caution by missing a meal rather than risk an early death (Lima and Dill 1990).

The results of these experiments indicate that coyotes were able to make erudite foraging decisions about ambiguous threat based on a variety of complex information. This suggests a highly sophisticated threat assessment capability in coyotes. Further research in this area will be facilitated by neurophysiologic studies capable of documenting amounts of acquired information, in addition to more behavioral studies aimed at discovering the specific content of information acquired through investigation and how this information is utilized in subsequent decision making.
References


Behaviour 137:1567-1599


CHAPTER 5
CONCLUSIONS

The goal of my research was to determine whether coyotes use cognitive inference to assess uncertain risk surrounding an essential resource. To address this topic, I asked three questions. The first of these questions was: \textit{Do coyotes respond to uncertain threat at an established feeding station following human activity there and, if so, is this response robust?} The first experiment demonstrated that prior anthropogenic activity delayed foraging in coyotes by over 58%. This suggests that coyotes perceived some level of ambiguous threat associated with human activity within their enclosures, even after the humans had clearly departed. In addition, there was no decrement in feeding latency between weeks, suggesting that coyotes did not habituate to ambiguous threat over time because they perceived the potential for danger from human activity.

Instead of completely avoiding ambiguous threat, however, coyotes spent time investigating human scent trails. They even prioritized investigation over feeding, and opted not to feed when given no time for investigation. These results suggest that coyotes used investigation as a necessary form of risk assessment. This reliance on investigation for assessing risk is indicative of the use of cognitive inference as opposed to trial-and-error learning when dealing with an ambiguous threat.

The second question that I asked was: \textit{In the absence of an essential resource, do coyotes differentially investigate recent human activity at areas that have previously been A) profitable, and B) unprofitable?} In this second experiment, the coyotes that investigated anthropogenic activity (the proactive cohort) investigated both profitable and
unprofitable locations to some extent, which implies that the coyotes valued chemo- 
sensory information in general. However, they spent more time investigating anthropo-
genic activity that occurred around a necessary resource (their feeding compartments) 
than at other locations, suggesting that they may have recognized the risk inherent 
with investigation and attempted to minimize this risk while still gaining relevant 
information about potential threat near their feeding site. Since the proactive 
cohort all investigated anthropogenic activity before food became available, this implies a 
predetermined decision to acquire information for future utilization from that group. When 
prevented from gathering information, all five animals in the proactive cohort opted 
not to feed, which again suggests a reliance on information gained through investigation 
to assess the safety of the feeding sites. Interestingly, the majority of coyotes neither in-
vestigated anthropogenic activity nor fed when food became available, indicating that 
they perceived significant threat from anthropogenic activity and probably viewed 
investigation of these sites as too risky.

The final question that I researched was: Do coyotes differentiate between information 
from prior human activity that is indicative of various levels of threat? In the 
fourth chapter, I provided evidence that shows that coyotes were able to distinguish 
among information indicative of different levels of risk. In fact, they were able to 
distinguish not only among sources of ambiguous threat (e.g., a specific individual human) 
but also among threat levels from the same source (e.g., negative, neutral, or positive 
associations). Coyotes focused their greatest attention on the human associated negatively; 
they spent significantly more time investigating the human activity associated

with the buried trap. In addition, coyotes showed the longest latency to feed after activity performed by the human associated negatively.

Moreover, coyotes were able to distinguish among threat levels in spite of the conflicting visual and olfactory information provided by an unassociated human (Human C) – although coyotes investigated the various associations equally, they were still most cautious (had the longest feeding latency) toward the negative threat. Results also indicated that coyotes remembered threat level over a period of weeks.

The results of these experiments together indicate that coyotes were able to make appropriate foraging decisions about ambiguous threat based on a variety of complex information. They used investigation to acquire this information, and would not feed when prohibited from gathering information. From these results, we can conclude that coyotes possess sophisticated risk-assessment mechanisms for utilization in the assessment of ambiguous threat.

These results are congruent with a cognitive interpretation of coyote behavior in response to ambiguous threat. Coyotes clearly inferred threat associated with prior human activity. Their investigation and avoidance did not diminish over time, which indicates that their response was not due to neophobia. When allowed to investigate anthropogenic activity, coyotes worked around it to obtain food. When prevented from investigation, however, coyotes did not approach areas of anthropogenic activity. These results indicate that coyotes use investigation as a mechanism to assess and negotiate ambiguous threat, as opposed to using trial-and-error learning. In addition, coyotes were able to distinguish amongst information indicative of different levels of threat, which
indicates that they are able to interpret semantic information encoded in chemical signatures from humans. Together, these results support the hypothesis that coyotes use cognitive inference to negotiate ambiguous threat.

Our research findings should be incorporated into the design of more effective non-lethal control methods for coyotes involved in depredation. Coyotes perceive human activity as threatening, and so this should be investigated further as a means of non-lethal control. Since our work implies that coyotes use chemosensory information to deduce appropriate behavior in response to ambiguous threat, the application of scent that is associated with humans that are viewed as threatening may be effective in deterring depredation. In addition, coyotes in our studies refrained from feeding when they were prohibited from investigating ambiguous threat. Preventing coyotes from performing investigative behaviors might keep them from attacking livestock.
CIRRICULUM VITAE

Sarah Dawson
(December 2008)

PROFILE

I’m a skilled wildlife biologist currently completing a doctorate with an emphasis in animal behavior and cognition. Specifically, I’m interested in cognitive aspect of antipredator behavior, such as the risk-assessment mechanisms that prey animals employ in negotiating a covert threat (e.g., when a predator is not physically apparent, but a predator sign or secondary threat, such as a trap, is detected). In that vein, I’m also interested in the importance of gathering information, the content of collected information, and how acquired information leads to subsequent behavioral decisions. In addition, I’m interested in the variable responses of individuals towards threat, or the prevalence of behavioral syndromes in an antipredator context.

I have a strong background in biological, ecological, and conservation sciences. I’m experienced in designing, implementing, and analyzing the data from research projects, and I’m very organized, with strong oral and written presentation skills. I have experience supervising and instructing both research technicians and students, and I work confidently both independently and on a team. I have extensive experience with animal husbandry.

EDUCATION

Doctorate of Philosophy in Wildlife Biology 2004-Present
Utah State University

Awards: Full-tuition Award, Research Stipend


Dissertation: Cognitive and behavioral responses of the coyote (Canis latrans) toward ambiguous threat

Bachelor of Science in Biology 1998-2002

College of Charleston

Awards: College of Charleston Foundation Scholarship, College of Charleston Full Academic Scholarship, Presidential Honors Scholarship, Americorps Educational Voucher, Honors College Graduate

Relevant Classes: Honors Biology I and II and labs, Mammology, Genetics, Animal Behavior, Organic Chemistry I and II and labs, Molecular Biology, Vertebrate Zoology, Biochemistry, Plant Physiology, Statistical Methods, Physics I and II and labs, Honors English I and II, Honors Psychology

Bachelor’s Essays: Musculature of the preorbital fossa of muntjac deer, Evolution of the sea otter

PUBLICATIONS

Cognitive inference and behavioral syndromes in the coyote (Canis latrans)
Dawson, S. and M. Jaeger, in press for the Journal of Veterinary Behavior
Coyote (*Canis latrans*) foraging behavior in response to ambiguous threat

Dawson, S. and M. Jaeger, in preparation for Animal Cognition
Behavioral syndromes and threat investigation in the coyote, *Canis latrans*

Dawson, S. and M. Jaeger, in preparation for Animal Behaviour
Information gained through investigation of ambiguous threat by the coyote, *Canis latrans*

Dawson, S. and M. Jaeger, in preparation for Behavioral Ecology
Musculature of the preorbital fossa of the muntjac deer, *Muntiacus reevesi*

W.J. Hillenius and S. Dawson, in preparation

SELECTED ORAL PRESENTATIONS

Dawson, S. and M. Jaeger. 2008. What do you know? Coyotes process information associated with human activity and distinguish the bad guys from the other guys. Presented at the Animal Behavior Society’s annual meeting, Snowbird, Utah, USA.


Dawson, S. 2005. The response of coyotes (*Canis latrans*) to prior anthropogenic activity. Presented to the Utah State University Department of Wildland Resources, Logan, UT, USA.

Dawson, S. and C. Keffer. 2001. Reliance on auditory and visual information in the domestic dog, *Canis lupus familiaris*. Presented to the College of Charleston Department of Biology, Charleston, SC, USA.

Dawson, S. 2000 oral presentation. Is handedness inherited? Presented to the College of Charleston Department of Biology, Charleston, SC, USA.

EXPERIENCE

**Student Researcher**

Utah State University’s Predator Research Center, Logan, UT

- Designs, implements, and analyzes research projects relating to captive coyote behaviors toward threat
- Participates in captive predator research, with experience in captures, handling, and husbandry
- Supervises research technicians
- Presents research ideas and data orally to students, technicians, and professors
- Successfully defended project proposal and passed oral and written comprehensive departmental exams
- Proficient with SAS and Medcalc statistical software and Observer behavioral software

**Animal Keeper**

2003
Smithsonian National Zoological Park, Washington, DC

Worked with many exotic animals in a captive setting

Fed and cared for cheetahs, Grevy’s zebras, Speke’s gazelles, bison, Malayan tapirs, kangaroos, peccaries, giraffe, camels, emus, and African cranes

Designed and implemented enrichment activities, including behavioral training

Carried out medical procedures and drug administrations, including via squeeze cage

Supplemental Instruction Teacher and Supervisor 1999-2002

College of Charleston, Charleston, SC

Attended high-risk biology classes and held post-class sessions to help students with lecture material

Assisted and instructed undergraduate students in classroom settings

Supervised other supplemental instructors in biology and chemistry and evaluated their work performance