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The Effects of Social Status and Learning on Captive Coyote (Canis latrans) Behavior

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THE EFFECTS OF SOCIAL STATUS AND LEARNING ON CAPTIVE COYOTE (*CANIS LATRANS*) BEHAVIOR

by

Lynne B. Gilbert-Norton

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

Approved:

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UTAH STATE UNIVERSITY
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ABSTRACT

The Effects of Social Status and Learning on Captive Coyote (*Canis latrans*) Behavior

by

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Many canids live within hierarchical social systems that could promote differences in learning or in behavior between ranked individuals. Differences in foraging and territorial behavior have been observed between ranked coyotes (*Canis latrans*), yet effects of learning and social status on coyote behavior are not thoroughly understood. I explored a) coyote response to an artificial scent boundary and whether response differed by status, b) how foraging coyotes tracked temporal resource change, and c) how coyotes find spatially distributed food, and the effect of dominance on foraging behavior. I used male/female pairs of captive coyotes at the National Wildlife Research Center Predator Research Facility in Utah. Prior to testing, I identified social rank within pairs by testing for food dominance. In study 1, I laid a scent boundary and monitored space use with GPS and observed behavioral responses directly. All coyotes investigated and crossed the boundary, but were repelled more by human presence. Subordinates investigated and marked the boundary more than dominants. Further investigation is needed to mimic natural boundaries for management purposes. In study 2, I gave eight individual coyotes an operant test with concurrent variable interval (VI) schedules. I varied the ratio of resources and measured the time spent on two choices, then fitted the generalized matching equation to the data. I found that all coyotes efficiently tracked changes in resource ratios and matched their relative rate of foraging time to relative rate of resources. Matching theory provides an effective methodology to explore foraging strategies and behavioral flexibility in coyotes. In study 3, I tested 16 coyotes in a spatial foraging task. Coyotes searched for food in eight potential locations, and were tested individually and in respective pairs. I recorded the area and number of locations searched, approach time, and frequency of marking by dominant and subordinate coyotes. Results showed individual subordinates increased efficiency by relocating, but their efficiency decreased when foraging in pairs. Dominant coyotes did not increase efficiency in company by following subordinates. Coyotes marked the correct feeder more than incorrect feeders. Results suggest coyotes use memory and odor (scent marks) to find food, but that social status overrules information use.

(112 pages)

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Lynne B. Gilbert-Norton

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CHAPTER 1

INTRODUCTION

Animals use a variety of methods to increase advantage in the face of social competition. They may use phenotypic traits such as social rank and size, or behavioral traits such as aggression (Drews, 1993). Traits may be correlated as high ranking individuals often have a larger body size and can use their competitive ability and aggression to maintain preferential access to resources (Wilson, 1975; Barta and Giraldeau 1998; Giraldeau and Caraco, 2000; Held et al., 2000; Liker and Barta, 2002; Lendvai et al., 2006).

Animals may also use behavioral strategies based upon past experience and learning to increase their advantage. Individuals can learn by pairing environmental events together such that a previously neutral event elicits a new or modified response (i.e., respondent or classical conditioning), or as a result of experiencing the consequences and context associated with a specific behavior (i.e., operant or instrumental conditioning; Skinner, 1938). When green anole lizards (*Anolis carolinensis*) and firemouth cichlid fish (*Thorichthys meeki*) learn food cues, they can gain food more quickly and defend food more successfully than individuals that do not learn the cues (Hollis et al., 2004). Similarly, animals are more likely to revisit areas if they previously found food there (Levine, 1959). Thus an animal gains information and experience as it interacts with its environment which it uses to guide subsequent behavior (Box and Gibson, 1999). The more diverse and unpredictable the environment, the more flexible an animal's response repertoire may be as a result of its experience. The resulting behavioral flexibility allows animals to respond appropriately to current conditions and alter responses as conditions change (Schlaepfer et al., 2002).

Animals may also learn about biologically important events by interacting with more experienced animals (Galef and Laland, 2005). Behavior such as foraging, territorial defense, predator avoidance and mate selection can be learned through social mechanisms (Heyes, 1994; Galef and Laland, 2005). Social interaction can take place between old and young animals, parent and offspring, and conspecifics (Box and Gibson, 1999), and learning can occur through observing another's behavior or through indirect cues associated with another's activity e.g., their location or scent-marking (Dall et al., 2005).

Some individuals within social groups may subsequently learn to exploit food resources found by conspecifics (Barnard and Sibly, 1981; Barta and Giraldeau, 1998; Giraldeau and Caraco, 2000). Differences in learning between individuals may be a function of social rank, among other factors (Barnard and Luo, 2002). Held et al. (2000) found dominant pigs *(Sus scrofa)* learn to follow and displace subordinate pigs from food and increase efficiency in foraging tasks. Dominant individuals have also been shown to outperform subordinate animals in learning tasks (Drea and Wallen, 1999; Nicol and Pope, 1994; Held et al., 2000; Barnard and Luo, 2002), which may be due to rank-related changes in motivational state. That is, all mice (*Mus musculus*) learn maze tasks equally before they form a dominance hierarchy, but dominant mice perform significantly better than subordinates afterwards (Barnard and Luo, 2002). Alternatively, differences in performance between the ranks may be in the expression of learned behavior rather than in learning ability per se (Nicol and Pope, 1994; Drea and Wallen, 1999; Held et al., 2000). For example, subordinate rhesus monkeys (*Macaca mulatta*) fail to respond to a previously learned task in the presence of dominant animals, but will engage in the task once dominant individuals are removed (Drea and Wallen, 1999).

Many canids live within social systems that may potentially enhance learning between conspecifics, and promote differences in learning ability or behavior between ranked individuals. Yet to date, there has been very little research on the effects of learning on wild canid behavior (Nel, 1999). The gray wolf (*Canis lupus*), Ethiopian wolf (*Canis simensis*), black-backed jackal (*Canis mesomelas*), African wild dog (*Lycaon pictus*), coyote (*Canis latrans*) and even the domestic dog (*Canis familiaris)* have highly defined social hierarchies (Nel, 1999). While many canids forage both individually and socially (MacDonald, 1984), dominant individuals usually have preferential access to resources. Similarly, many canids communally deter intruders, however dominant coyotes engage in the majority of territorial maintenance (Kleiman, 1966; Barrette and Messier, 1980; Gese and Ruff, 1997; Sillero-Zubiri and MacDonald, 1998; Allen et al., 1999). Dominant pups are likely to stay within family groups and be exposed to the behavior of experienced adults for longer periods than lower ranked individuals (Nel, 1999).

One of the most adaptable and highly successful canids in North America is the coyote. Originating from the south western plains and deserts, coyotes now range from Costa Rica (10°N) to Alaska (70°N latitude) and thrive in deserts, woodland, mountains, grasslands (Bekoff and Gese, 2003) and cities (Gehrt, 2007). Coyotes are generalist foragers and their diet includes fruit, insects, microtines, leporids, and ungulates (Litvaitus and Shaw, 1980; Bekoff and Wells, 1981; Boutin and Cluff, 1989; Gese et al., 1996a, 1996b; Quinn, 1997). Food resources vary according to season, habitat, weather and geographical region (Hamlin et al. 1984; Andelt et al., 1987; Gese et al., 1996a; Bekoff and Gese, 2003), and researchers have focused on the strategies coyotes use to forage efficiently. Some suggest coyotes are opportunistic and switch between prey irrespective of prey densities (MacCracken, 1984; Sacks and Neale, 2002), or hunt low energy options when high energy prey are available (Hamlin et al., 1984; Andelt et al., 1987; Gese et al., 1996b). Other researchers have suggested coyotes forage optimally, and choose high ranking foods regardless of availability and in preference to low ranking items (MacCracken and Hansen, 1987; Hernández et al., 2002). However, assumptions on foraging strategies have mainly been based upon indirect measures (but see Bekoff and Wells, 1981; Gese et al., 1996a, b), and decades of descriptive research has failed to explain how coyotes apportion foraging time and effort to available resources or how they track changes in resource distributions.

Further complications arise because of differences in foraging and territorial behavior between the dominance ranks in coyotes. Whether differences are a function of social status or learning, or a combination of the two, has yet to be determined. Alpha coyotes (particularly males) often instigate hunts and depredation attacks on domestic livestock (Conner et al., 1998; Sacks et al., 1999b; Blewjas et al., 2002; Mitchell et al., 2004) and preferentially control resources. Dominant coyotes are also more likely to directly and indirectly enforce territorial boundaries than lower ranking animals (Bowen and Cowan, 1980; Bekoff and Wells, 1986; Gese and Ruff, 1997; Gese, 2001). Scent lures are typically used for trapping, but interestingly, dominant coyotes are reported as being less susceptible to capture techniques than subordinates (Sacks et al., 1999a; Jaeger et al., 2001; Séquin et al., 2003; Mitchell et al., 2004). In contrast, subordinate coyotes may attempt to circumvent dominant individuals with a greater competitive edge. Transient coyotes of low social rank will alter behavior spatially and temporally to access carcass sites within occupied territory (Séquin et al., 2003). Subordinates may also gain advantage over more dominant animals if they can be first to a resource before being displaced. Johnson and Balph (1990) showed four month old dominant pups fed first and more often under familiar conditions while subordinates fed first under novel conditions before being displaced by the dominant pups.

In order to predict coyote behavior more accurately, we need a better understanding of the relationship between social status, learning and resource distributions. Behavioral mechanisms are assumed to be similar in captivity and in the field (Shettleworth, 1998) and controlled conditions provide an excellent test arena for isolating confounding variables that often plague field studies. I propose that observations of independent and social foraging, as well as territorial behavior under controlled conditions are warranted. To date there have been two controlled studies that have explored learning in coyote foraging behavior (Loether, 1978; Cheney, 1982), but none that have manipulated resources and social dynamics simultaneously.

My first objective was to explore indirect territorial behavior in established captive coyote pairs. Coyotes depredate domestic livestock in North America and managers often implement non-lethal techniques to reduce livestock losses (Knowlton et al., 1999). One technique used to deter herbivores from protected areas is an artificial scent boundary (Melchiors and Leslie, 1985; Swihart, 1991). Scent marks are also used by canids to signal territorial ownership and deter conspecifics from trespassing into occupied territories (Kleiman, 1966). Dominant coyotes are more likely to uphold their boundaries but test those of conspecifics (Bowen and Cowan, 1980; Bekoff and Wells, 1986; Gese and Ruff, 1997). I thus explored whether an artificial scent boundary could deter coyotes from a protected area. I also investigated whether coyote response to a simulated boundary differed according to social status. I hypothesized that dominant coyotes would spend more time investigating and scent marking an artificial boundary than subordinate coyotes.

My second objective was to investigate the ability of individual coyotes to track temporal resource change. I used an experimental paradigm known as the matching law (Herrnstein, 1961), which states animals match the proportion of responses, or time (i.e., output) to the proportion of obtained resources (i.e., input). Matching occurs across many species, behaviors and reinforcers (De Villiers and Herrnstein, 1976), stable and stochastic environments, and provides a well established and accurate measure of sensitivity to resource change. I tested captive coyotes using an operant two-choice test, which is analogous to simultaneous habitat patches with prey that replenish at variable rates (Kamil, 1978). I hypothesized that coyotes would match their relative rate of foraging time to relative rate of resource availability on either alternative.

My third objective was to investigate how coyotes find spatially distributed food resources and explore mechanisms they use to do so. Furthermore, I explored the effect of social status on individual foraging behavior and whether coyotes use social cues to increase foraging efficiency. Individuals often use strategies to locate spatially distributed food (Smith, 1974; Zach and Falls, 1976; Goss-Custard, 1977; Kamil, 1978), which can be affected by social competition and group dynamics (Box and Gibson, 1999;

Galef and Laland, 2005). Dominant animals may specialize in stealing food from conspecifics, because they can use their competitive ability and aggression to do so (Barta and Giraldeau 1998; Giraldeau and Caraco, 2000; Liker and Barta, 2002; Lendvai et al., 2006). I tested coyotes individually and in their respective pairs using a spatial foraging task in which animals searched for food in eight potential locations (as in Held et al., 2000). I predicted that individual subordinate coyotes would relocate a food resource, and that dominant coyotes would follow and displace subordinates with prior food location knowledge when foraging in pairs.

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CHAPTER 2

A SIMULATED SCENT BOUNDARY DOES NOT PREVENT COYOTE INTRUSION

Abstract

Highly territorial species such as coyotes use scent marks to delineate boundaries; thus, it is possible that coyotes could be repelled from livestock areas by simulating a pack boundary with artificial scat and urine marks. The objectives of this study were to determine a) if coyotes altered space use and avoided areas surrounded by an artificial scent boundary vs. a human-control treatment, and b) whether dominant and subordinate coyotes differed in their response to the boundary. I used eight coyotes (four breeding pairs) in four, 1-ha pens at the National Wildlife Research Center Predator Research Facility in Logan, Utah for the experiment. Social rank was determined using food dominance tests, space use was monitored using GPS collars, and behavioral responses were measured using direct observation. In treatments, a technician either a) walked along an artificial scent boundary or b) walked and laid coyote urine and scat along the boundary. I determined that all coyotes investigated the artificial scent boundary and crossed into areas marked by the boundary with no evidence of a repellent effect. Subordinates spent more time investigating the boundary and showed a trend toward marking the boundary at greater frequencies than dominants. Based on the results of our controlled experiment, I cannot recommend using simulated pack boundaries for protection of livestock or other resources from coyotes, but data weakly suggest a potential repellent effect from human presence.

1. Introduction

Scent marking is an integral part of the behavior of many species of mammals, in which glandular secretions are deposited within an animals' environment (Johnson, 1973). Possible functions of scent marking include conveying information on sex, age, social status, reproductive condition, and aiding individual or group recognition (Gorman, 1976; Gorman and Trowbridge, 1989; Rich and Hurst, 1999), use as an alarm signal (Ralls, 1971), and to facilitate orientation (Henry, 1977; Harrington, 1981). One of the principal functions of scent marking is to aid territoriality (Hediger, 1949; Mykytowycz, 1968).

Scent marking may be an important and less costly means of defending a territory than direct confrontation (Camenzind, 1978). Many species of carnivores use scent marking for indirect inter and intra-species contact at territorial boundaries by signaling territorial ownership and deterring conspecifics from usurping or entering an occupied territory (Smith et al., 1989; Allen et al., 1999; Stewart et al., 2001; Darden et al., 2008). In canids, territorial marking is well documented in feral dogs (*Canis familiaris*; Pal, 2003), gray wolves (*Canis lupus*; Rothman and Mech, 1979; Paquet, 1992), Ethiopian wolves (*Canis simensis*; Sillero-Zubiri and MacDonald, 1998), brown hyenas (*Hyaena brunnea*; Mills et al., 1980), and coyotes (*Canis latrans*; Barrette and Messier, 1980; Bowen and Cowan, 1980; Wells and Bekoff, 1981; Paquet, 1992; Gese and Ruff, 1997; Bekoff and Gese, 2003). Canids often deposit scat and urine at prominent locations along territorial boundaries to increase the probability of detection by conspecifics (MacDonald, 1980; Gorman and Trowbridge, 1989). Gray wolves will mark along well-used tracks and junctions to aid detection (Peters and Mech, 1975), and sympatric species such as wolves and coyotes may share the same scent marked locations on territorial boundaries (Paquet, 1992).

Within a social group, a strong association exists between scent marking and dominance (Ralls, 1971; Gorman and Trowbridge, 1989). Higher rates of marking by dominant animals have been observed in many carnivores, including tigers (*Panthera tigris*; Smith et al., 1989), gray wolves (Peters and Mech, 1975), Ethiopian wolves (Sillero-Zubiri and MacDonald, 1998) and spotted hyenas (*Crocuta crocuta*; Woodmansee et al., 1991). In coyotes, resident alpha males scent mark at higher rates than beta coyotes or pups, and at a greater rate on the periphery of their territory compared to core areas (Bowen and Cowan, 1980; Bekoff and Wells, 1986; Gese and Ruff, 1997). Allen et al. (1999) showed scent mark locations clearly defined coyote pack boundaries. Furthermore boundaries were rarely intruded upon by adjacent coyote pack members (but see Shivik et al., 1996). Photo-capture evidence also showed that coyotes adhered to territorial boundaries of adjacent packs when travelling outside of their own territories (Séquin et al., 2003).

Scent marked boundaries can alter the behavior of other species that come into contact with them, and it is well documented that predator scent can alter the behavior of prey species and deter herbivores from cultivated areas. Bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), wolf and coyote scent suppressed foraging in black-tailed deer (*Odocoileus hemionus columbianus*; Melchiors and Leslie, 1985). Similarly, bobcat and coyote scent successfully reduced woodchuck damage to crops (Swihart, 1991; Bean et al., 1995). Fox (*Vulpes vulpes*) scent deterred rabbit (*Oryctolagus cuniculus*), and

Australian brush tail possum (*Trichosurus vulpecula*) damage to seedlings (Morgan and Woolhouse, 1995), and western grey kangaroo (*Macropus fuliginosus*) were less likely to eat food placed near either dingo (*Canis dingo*) or coyote urine (Parsons et al., 2006).

In predator management, coyote scent is one of a range of olfactory attractants used mainly for trapping predators (Shivik et al., 2003). However, Windberg and Knowlton (1990) found that capture rates of adult and territorial coyotes were higher using commercial canine lures rather than coyote scent as an attractant. Thus an alternative use for coyote scent may be as a repellent. Current research by Wild Entrust International and The Botswana Predator Conservation Trust suggest mimicking scent marked territorial boundaries may repel carnivores from protected areas, and hence livestock (Apps, 2009). Furthermore isolation of the semiochemicals in predator urine is proposed for use as a 'Bio-boundary' to contain African Wild Dogs (*Lycaon Pictus*) within protected conservation areas (McNutt and Apps, 2009).

Predation upon domestic livestock by coyotes is a serious, ongoing problem to producers in North America, and managers continually strive to implement techniques that incorporate coyote biology and behavior, among other factors (Knowlton et al., 1999). Behavioral differences among coyotes are evident, and research has shown that dominant, territorial coyotes (particularly males) are more likely to instigate attacks and be the principal livestock depredator (Conner et al., 1998; Sacks et al., 1999b; Blejwas et al., 2002; Mitchell et al., 2004). Nine out of ten pack hunts on deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*) in Yellowstone National Park were initiated by the alpha male (Gese and Grothe, 1995). While Jaeger et al. (2001) found that one alpha pair was responsible for 46 kills during one lambing season and depredating stopped once the alpha male had been removed.

Thus before scent can be applied in the field, there is a need to determine if the use of conspecific scent repels coyotes, and given the differential depredation attacks between the social ranks, whether the desired effect of an artificial boundary holds for coyotes of different status. Furthermore, it is important to determine how humans who often apply non-lethal management tools impact those tools. Specifically it is important to know whether human presence affects the efficacy of artificial scent boundaries to repel predators. To investigate whether artificial scent boundaries repel coyotes I examined two hypotheses: 1) coyotes will avoid an area encircled by an artificial scent boundary, and 2) coyote response to an artificial territorial boundary will differ according to social status.

2. Materials and methods

2.1 Study area

My research was carried out at the National Wildlife Research Center (NWRC) Predator Research Facility in Logan, Utah during October 2006. Elevation at the field station is 1381 m above sea level. Mean annual temperatures range from –11º C to 32º C, and mean annual rainfall is 42 cm and snowfall is 82 cm. The NWRC holds a large population ($N = 106$) of coyotes kept individually and in pairs in a variety of captive environments ranging from small kennels (3.3 m^2) to experimental pens (0.1 to 6-ha). Each pen contained fallow-field vegetation (grass-alfalfa mixture), a wooden shade shelter and two kennels under the observation building.

2.2. Subjects and pens

My subjects were eight adult captive coyotes. Coyotes were kept and tested in four male and female breeding pairs in one of four adjacent 1 ha experimental pens. Pens were wedge-shaped and extended 160 m from a raised central observation building to an outer arc 125 m wide. Behavior of captive coyotes at the site was found to be equivalent to that exhibited by wild coyotes (Shivik et al., 2009). The social context of the pair is necessary and precludes isolating individuals for testing, thus coyotes were kept in established pairs to mimic wild coyote sociality and to strengthen inference of my results, although the sample unit in my experiments was an individual coyote.

Dominant coyotes in wild packs are referred to as the alpha pair and differ from associate pack members through preferential access to food resources and breeding rights, and maintain territories (Bekoff and Gese, 2003). Research has shown that alpha males are often the principal hunters and depredators (Conner et al., 1998; Sacks et al., 1999b; Blejwas et al., 2002; Mitchell et al., 2004) which suggests a difference in behavior within alpha pairs. Dominance between an established territorial pair can also be defined as an attribute of a relationship and measured via the asymmetric outcome of conflicts over access to a food resource, with the winner defined as the food dominant animal and the loser defined as the subordinate animal (Drews, 1993). This method has been used to assign dominance between established coyote pairs (Johnson and Balph, 1990; Mettler and Shivik, 2007).

Coyotes were given four weeks to adjust to the experimental pens. I then tested for dominance within pairs via four competitive food trials over a two week period. For each trial, five hotdogs were broken into small pieces and placed in a concentrated pile, 10 m from the observation building. The trial began when the first coyote started eating the food and ended when all food was consumed. The food dominant animal was the coyote which displaced the other from the food resource more over successive trials, and each interaction was reciprocal such that a win by one animal equaled one loss by the other animal.

I designated an area within each pen that was surrounded by a scent boundary. The size of the area was based upon visual references that I could reliably use to repeat the boundary treatment within the pen (e.g., exterior posts and an in-pen shade shelter). From the observation building, I measured a 57 m x 22 m x 57 m triangular area along the perimeter fence to a shade shelter in the middle of the pen. The total designated area encircled by the boundary was 697 m^2 and made up 6.95% of the total pen area (Fig. 2-1).

I applied two simulated boundary treatments. In the human control treatment, the technician walked along the designated area boundary from the observation building, along the perimeter fence to the shade shelter, and back to the observation building. In the simulated scent boundary treatment, the same technician walked the same boundary but placed coyote scat and urine at each corner and halfway along each length of the boundary (Fig. 2-1). Alpha coyotes in the wild mark an average of 1.8 marks per coyote km but may depend upon status and territory area (Barrette and Messier, 1980; Bowen and Cowen, 1980). My pens were considerably smaller and the protected area represented a model of more natural management conditions. Thus six marks were used to ensure they were placed in the same location throughout trials, and because as my

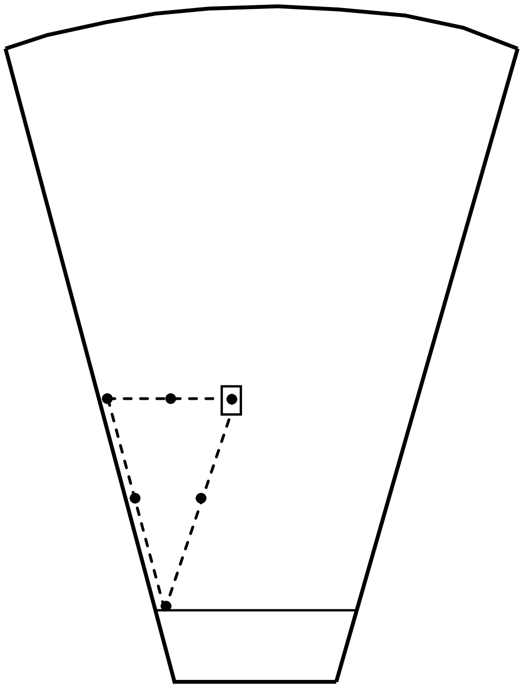

Fig. 2-1. Simulated scent boundary (- - -) within each pen, with position of scat and urine drops (•).

subjects had only resided in the pen for 4 weeks prior to treatment, thus I wanted to differentiate treatment marks from those of prior animals in the pen. I used scat and urine from two males and two female coyotes at the NWRC facility that were unrelated to the test animals. Scat and urine was collected one week before trials began and frozen until needed. The technician always used scat and urine from the same pair of animals in any one pen to mimic the contiguous boundary marking of an adjacent resident coyote pair.

The first trial period was from 5 to 18 October 2006. During this period, four (two randomly chosen pairs) coyotes received the human control, and the other four (two pairs) received the simulated scent boundary treatment. In the second testing period (19 October to 2 November) treatments were swapped for each pair so that all coyotes received both treatments, but in a counterbalanced repeated measures design. During each trial period, the technician walked the boundary on six nonconsecutive days at the same time each day (1000-1100). I collected data using two metrics: space use and behavioral response to boundary.

For space use analyses, six of the eight coyotes (two male and female pairs, plus the females in the remaining pairs) were fitted with GPS G2110 collars (Advanced Telemetry Systems, Isanti, MN, USA). I was not able to collar all eight coyotes due to logistical considerations. Collars were programmed to store locations at 20-min and 1-h intervals. I collected locations for three weeks before (11 September to 4 October) and three weeks during the treatments (5 October to 1 November), and converted them into UTM coordinates with ArcGIS 9.1 software using Nad 83 Zone 12N datum. Using the GIS software, I classified each coyote location as being within the designated area or outside of it, and then calculated the proportion of locations within the designated area during each trial period. I determined collar accuracy by calculating the mean percentage of error locations (i.e., an erroneous location occurred when a coyote was plotted outside of its pen) for the total number of locations taken over the six weeks.

In space use analyses, I used the proportion of each animal's locations inside the designated area as the dependent variable. I examined the effect of the simulated scent boundary by comparing the proportion of locations within the designated area versus the baseline period before the boundary was established. Similarly, for human control treatments, I compared the proportion of locations within the designated area during the treatment period versus the baseline period. I compared mean difference scores between the proportion of locations within the designated area during baseline and each treatment period using paired *t*-tests (Weiss, 2005).

For analysis of behavioral response to treatments, I observed coyotes using continuous focal animal sampling during treatments. Observations began when the technician finished walking the perimeter of the designated area and were terminated after 1 h. Each coyote was observed on six days during the 24 treatment days for a total of 6 h of observations per coyote. Behavior was recorded directly from the observation building using Noldus Observer® on a laptop computer.

I analyzed all behavioral data using non-parametric tests because our sample size was small when divided in to dominant and subordinate animals. Specifically, I analyzed latencies to approach the line (from the time the technician left the pen to when the animal was positioned on the boundary line) and the time spent (% of observation time) on the boundary by dominant and subordinate coyotes using Mann-Whitney U tests (Zar, 1999). Similarly, latency to enter the designated area (from the time the technician left the pen to when the animal crossed 1-m over the boundary line and within the protected area) and time spent (% of observation time) within the designated area by dominants and subordinate coyotes were analyzed using Mann-Whitney U tests. I classified when coyotes urinated, defecated, or scratched on the boundary as line marking, and analyzed the frequency of line marking by dominant and subordinate coyotes using a Mann-Whitney U test. I analyzed the frequency of marking on days simulated scent boundary was placed and days when the human control treatment was applied using a Wilcoxon signed rank test.

3. Results

3.1. Dominance

Males were the food dominant animal within all four pairs and displaced the subordinate from the food over competitive food trials (Fig. 2-2). The total number of displacements or wins varied across pairs (range = 14 – 71 events).

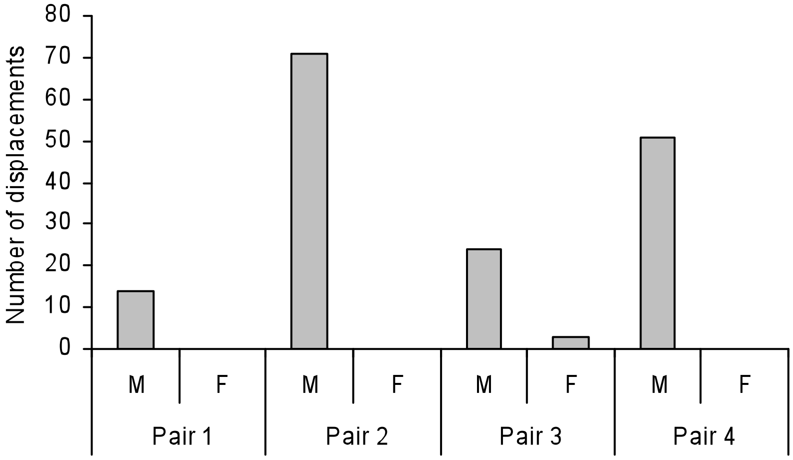

Fig. 2-2. Total number of displacements by males (M) and females (F) within established pairs (*N* = 4 pairs).

I collected 11,401 locations on the six individuals (range from 1090 to 3505). A minority of locations 9% (± *SE* = 4%) were discarded due to known error; the mean minimum distance away from the pen edge for known-erroneous locations was 3.61 meters (*SE* = 1.12 meters). In space use analyses, the mean difference score indicated that coyotes were located within the designated area 4.5% less during the simulated scent boundary treatment than before treatment, but the difference was insignificant (t_5 = .87, *P* = .42). Difference scores indicated that coyotes were found within the area 8.8% less during the human control treatment than before treatment ($t_5 = 2.14$, $P = .08$), indicating a possible trend toward repellency from human presence (Fig. 2-3).

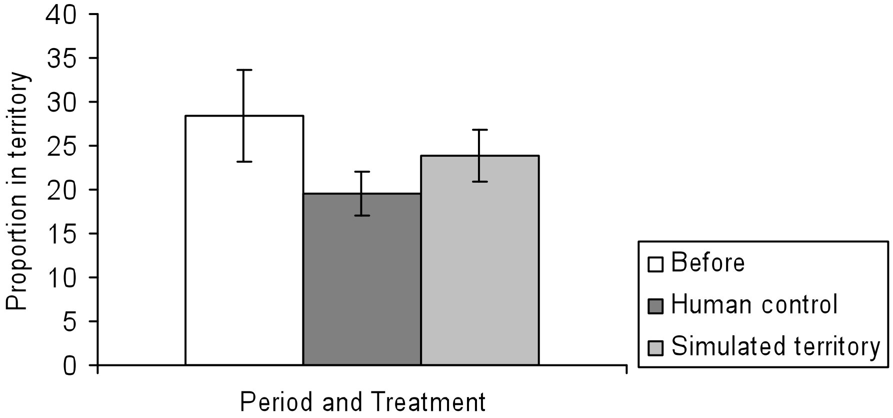

Fig. 2-3. Mean proportion of coyote locations (± *SE*) within the designated area before and during human control and simulated scent boundary treatments ($N = 6$).

When examining behaviors during the treatment phase (simulated scent boundary and human-control treatments combined), there was no difference in latencies to approach the boundary by dominant (median = 11.08 min) or subordinate (median = 14.47 min) coyotes ($U = 4.0$, $P = .29$). However, there was a difference in the proportion of time (% of observation) that coyotes spent on the boundary ($U = 0.01$, $P = .02$); subordinate coyotes were on the boundary more (median = 36.5%) than dominant (median = 25.5%) coyotes. I found little difference in the time that dominant (median = 13.47 min) or subordinate coyotes (median = 14.53 min) took to cross into the designated area ($U = 6.0$, $P = .56$). Similarly, dominant coyotes (median = 15.5%) spent a similar proportion of time inside the designated area as subordinate (median = 13.5%) coyotes ($U = 6.5$, $P = .66$).

Scent marking events by dominant (36 events) and subordinate (66 events) coyotes were not statistically different during the treatment phase (simulated scent boundary and human-control days combined; $U = 3.0$, $P = .15$). However, more marking by all coyotes occurred when simulated scent marks were applied (93 events) compared to human-control days (9 events; $Z = -2.38$, $P = .02$). There was a trend toward more marking by subordinate coyotes (62 events) compared to dominant coyotes (31 events) on simulated scent boundary days ($U = 2.0$, $P = .08$).

4. Discussion

I found that there was little effectiveness of using coyote scat and urine as a boundary to deter coyotes from a protected area. One possible explanation for the small repellency effect of the simulated scent boundary treatment was the amount of time between distributing scent marks. To approximate how artificial scent boundaries would be applied in a management setting, I laid scent marks once every two days; such a schedule would be practical from a management perspective, but it may not be representative of natural marking behavior in coyotes. That is, territorial coyotes in the wild often scent mark up to several times a day along their territory boundary, depending upon social status, time of year and territory size (Gese and Ruff, 1997). Therefore I may have observed a greater repellency effect by applying scent marks more frequently and mirroring marking rates in the wild, as the efficacy of marks may degrade over time. Studies with lapses in time between laying scents and subsequent coyote interaction have also shown poor results, which could be a function of mark degradation (Harris, 1983; but see Windberg and Knowlton, 1990). For example, Windberg (1996) laid scented lures 13–18 h prior to giving coyotes access, and only one out of 20 coyotes was attracted to the lures. Another possible explanation of the lack of treatment effect was the size of the designated area relative to potential error associated with the GPS collars. That is, the precision of location estimates was limited, which would reduce the statistical power of analyses. However, there is no reason to conclude that location estimates were biased and thus, combined with direct observations, our conclusions are valid.

To that end, I detected a differential response between baseline and treatment periods. Coyotes spent less time in the area to some extent during both treatments compared to the baseline but the effect was greater during the human control treatment, which suggested a potential repellent effect from human presence. In contrast, coyotes approached and over marked the scent that I laid during the simulated scent boundary treatment. Research shows that coyotes will alter temporal activity patterns in response to human disturbance or persecution (Kitchen et al., 2000; Mech et al., 2000; Bekoff and Gese, 2003; Gehrt, 2007), but will readily approach scent lures that humans place in their territory (Windberg and Knowlton, 1990). Differential motivation may dictate the direction of coyote movement, either away or toward a scent boundary. That is, most animals have an adaptive approach-avoidance response which is fundamental for survival and will move away from potentially harmful stimuli but toward potentially beneficial environmental ones (Elliot and Covington, 2001; Elliot, 2006).

Research shows scent marking does not always prevent intrusion into occupied territories. In canids, intrusions into scent marked territory have been recorded in foxes (MacDonald, 1980), hyenas (Mills et al., 1980), wolves (Sillero-Zubiri and MacDonald, 1998) and coyotes (Wells and Bekoff, 1981; Shivik et al., 1996; Gese and Ruff, 1997;

Allen et al., 1999). Coyotes in my study spent up to 28 percent of their time in an area that was only seven percent of the total pen area. One possibility is that of food motivation. The coyotes in my study may have associated the area with food because they had been fed close to the area in the past. In the wild, coyote home range use varies both spatially and behaviorally and the two factors may be interrelated. That is, Laundré and Keller (1981) showed temporal changes in space use occurred according to seasonal and dietary changes in behavior. Gese et al. (1996) showed the percentage of time coyotes spent within specific areas was related to the capture rate of small mammals in that area.

The motivation to trespass needs consideration from a management perspective. That is, the presence of livestock could potentially increase trespass attempts by coyotes and furthermore, may elicit a greater response from dominant individuals further limiting simulated boundaries as a predator management technique. Research has shown that dominant coyotes, particularly males, often instigate hunts and depredation attacks, with the probability of attack increasing when their territories overlap livestock pasture (Conner et al., 1998; Sacks et al., 1999b; Blejwas et al., 2002; Mitchell et al., 2004). Similarly, Bowen and Cowan (1980) found that adjacent coyote packs trespassed into conspecific territory when a carcass was present, and Shivik et al. (1996) showed a resident coyote followed sheep into another coyote's core area and that territoriality does not limit coyote access to sheep.

I found that subordinate coyotes spent longer investigating the line and showed a higher frequency of marking than dominant coyotes. The unexpected behavior of the subordinate coyotes in my study could highlight the problem of classifying social status, and determining which definition or concept is applicable for a particular situation or context (Drews, 1993). My coyotes were established pairs, housed in their own pen and dominance was classified by asymmetric outcomes during competitive food trials, as used in previous captive studies (as in Johnson and Balph, 1990; Mettler and Shivik 2007). However, alpha coyote pairs in the wild are more generally classified via a combination of preferential access to food, territorial holding power and breeding status, with both animals within a territorial breeding pair classified as alpha animals. Alpha females may uphold territorial boundaries as frequently as alpha males, as both male and female coyotes over-mark scent marks left by conspecifics (Gese and Ruff, 1997). That said, Windberg and Knowlton (1990) showed that both alpha and beta females had a high capture probability on or outside territorial boundaries, which implies that investigative activity by females of either status is disproportionately concentrated along boundaries.

A further explanation of why subordinates spent more time investigating the line compared to the dominant is that subordinate animals in many species are often less neophobic and take greater risks under novel situations, because dominants are control access to resources in familiar environments (Katzir, 1982; Johnson and Balph, 1990; Darrow and Shivik, 2009). Low ranking Japanese macaques (*Macaca fuscata*; Menzel, 1966) and jackdaws (*Corvus monedula*; Katzir, 1982) are quicker to detect and explore novel situations than dominant individuals. Thus greater exploration time and approach to scent by subordinates in my study may indicate reduced neophobia and my results may help explain the differential capture success often observed in coyotes in the wild (Windberg and Knowlton, 1990; Sacks et al., 1999a; Jaeger et al., 2001; Séquin et al., 2003).

One of the difficulties in using scent to delineate boundaries and deter predators from protected areas or livestock is that knowledge of the semiochemistry of scent marks, the information it conveys and its effect on predator behavior is currently limited (Gorman and Trowbridge, 1989). Thus how, and in what context scent marks alter conspecific behavior, or how territorial animals recognize neighbors from strangers through scent (Ydenburg et al., 1988; Temeles, 1994; Müller and Manser, 2007) has yet to be determined. Research is currently underway to isolate the chemicals in scent mark odor that signal territorial occupancy to use in bio-boundaries and repel African Wild Dogs from livestock (Apps, 2009), but further investigation is needed before we can successfully mimic natural territorial boundaries for the management of coyotes.

One way scent marks may deter coyote intrusion in to protected or occupied areas is if scent marks are experienced in conjunction with a perceived or direct threat. Scent marks in the wild often prelude aggressive behavior, especially when marks on boundary limits are left by unknown conspecifics (Ralls, 1971). Canids will defend their territories with a combination of marking, random threat and direct aggression (Gese and Ruff, 1997; Sillero-Zubiri and MacDonald, 1998; Gese, 2001). Thus animals subjected to repeated territorial encounters and continual defeats in conjunction with scent marked boundaries learn that scent marks signal a negative or aversive event i.e., aggressive threat. Thus over time, scent marks can acquire aversive properties which potentially deter intruders (Johnson, 1973; Jones and Nowell, 1973). Conversely, marks that are experienced in isolation of a negative event are more likely to be ignored over time through the same learning process (Beauchamp, 1995). Coyotes in my study did not experience a negative consequence of the scent marks I laid. Expecting coyotes to simply respond to artificial scents as if they signal a threat fails to take in to account the mechanisms by which animals learn about their environment. For artificial scent boundaries to function as actual boundaries and deter coyotes from livestock, it is likely that scent marks would have to be experienced in conjunction with a perceived or direct aggressive threat in order for coyotes to learn to make the desired response.

Captive coyotes readily crossed a simulated scent boundary. Factors such as motivation, the presence of a food resource, time of year, alternative prey availability, age, sex and social status of the coyote may also further influence on management success. Although scent boundaries may alter coyote behavior under natural conditions, our knowledge of how animals learn to respond to territorial boundaries and how such boundaries repel animals is currently limited. More research is needed before artificial scent marks can be employed as a non-lethal management technique to repel coyotes from domestic livestock.

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CHAPTER 3

COYOTES (*CANIS LATRANS*) AND THE MATCHING LAW

Abstract

Environmental change is accelerating due to anthropogenic influence. Species that have greater behavioral flexibility may be better adapted to exploit new or constantly changing habitats. There are few mammals and even fewer carnivores that better illustrate widespread adaptability and behavioral flexibility in the wake of human disturbance than coyotes (*Canis latrans*). Yet how such predators successfully track resources, enabling them to survive and extend their range in stochastic environments remains unknown. I tested eight wild-born, captive coyotes individually on an operant two-choice test using concurrent variable interval (VI) schedules. I held the overall rate of reinforcement constant but manipulated the ratio of reinforcement available from the two choices. I analyzed sensitivity of coyotes' tracking of resource change by fitting the generalized matching equation to the data. Results showed all coyotes efficiently tracked changes in reinforcement ratios within the first few sessions of each new condition and matched their relative rate of foraging time to relative rate of resources. I suggest the matching paradigm provides a methodology to explore coyote foraging strategies, and a potential framework to compare behavioral flexibility across species, by measuring the ability to track resource change under variable resource conditions.

1. Introduction

Human activity is changing the face of the landscape at a phenomenal rate as a result of agricultural practices and urban development. Perhaps the most dramatic rate of change occurs at the human-wildlife interface where urban landscaping that previously took decades to develop, can now be completed in five or six years, providing new habitats for select species to adapt and survive (Radeloff et al., 2005). Successful invaders of new environments may use behavioral flexibility as one mechanism to adapt under conditions of extreme change (Sol and Lefebvre, 2000; Sol et al., 2002, 2008). Behavioral flexibility is defined as the ability to respond appropriately to current conditions but alter responses as conditions change (Schlaepfer et al., 2002). A further factor that promotes species adaptation under anthropogenically modified habitats and resource change is having a generalist rather than a specialist approach to foraging (Dukes and Mooney, 1999). Such generalist, commensal species in North America include the raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), virginia opossum (*Didelphis virginia*) and the coyote (*Canis latrans*; Prange and Gehrt, 2004).

Indeed there are few large carnivores that better illustrate widespread adaptability in the wake of human disturbance than coyotes. Originally inhabiting the plains and deserts of the North American southwest, coyotes now range from latitude 10°N to 70°N on the continent. They can survive in environments as diverse as deserts, woodlands, prairies (Bekoff and Gese, 2003) and dense human cities (Gehrt, 2007). To that end, coyotes have had positive ecological impacts on urban systems; preying on smaller native and exotic carnivores, whose increase in numbers have resulted in a sharp decline of native bird abundance (Crooks and Soulé, 1999).

Coyotes incorporate a wide range of resources into their diets depending upon factors such as seasonal availability and habitat (Bekoff and Gese, 2003), which have been extensively documented in descriptive studies (Andelt et al., 1987). Furthermore, researchers have explored diet choice by focusing on potential foraging strategies that coyotes use. The literature is currently divided on whether coyotes are opportunist or optimal foragers. MacCracken (1984) found coyotes followed seasonal availability of resources which did not constitute a large proportion of their overall diet, which suggested an opportunistic strategy. In contrast, MacCracken and Hansen (1987), and Hernández et al. (2002) suggested coyotes choose high ranking foods regardless of availability and in preference to low ranking items, as predicted by optimal diet theory. However, the expectation that coyotes respond either opportunistically or optimally in environments that continually change may be unrealistic, and interpretations of feeding patterns have suffered from generalizations and over simplification (MacCracken, 1984). The problem is that determining coyote foraging strategies in the field is extremely difficult due to the illusive nature of coyotes. Indeed decades of foraging research have failed to explain how coyotes successfully apportion foraging time and effort, and efficiently track variable resources, increasing their ability to survive and expand their ranges in the face of intense urbanization, high exploitation and rapid habitat change.

Under stochastic conditions, a successful strategy which could increase foraging efficiency and that has not been considered in the coyote literature is to track resource change by continually sampling alternatives, and then exploit the resource with the higher ratio of return (Houston and McNamara, 1981). Species that have greater behavioral flexibility may be better adapted to exploit a sampling strategy. Because coyotes are such a successful behaviorally flexible species, I propose they are an excellent model for understanding behavioral adaptation in commensal species under variable resource conditions.

To accurately measure foraging efficiency at the local scale, I combined the ecological question of how coyotes track variability with a behavioral analytical approach based upon the matching law (Herrnstein, 1961). The matching law states an animal will match the proportion of responding, or time spent on a choice alternative, to the proportion of reinforcement obtained from that alternative. Matching has been shown across a variety of species, behaviors, and reinforcers (De Villiers and Herrnstein, 1976). As such, matching has great applied potential in studying foraging choice as changes in reinforcement frequency can be likened to changes in prey density within foraging patches in the wild. Furthermore, matching has been shown under both stable and stochastic resource conditions. Thus I suggest the matching framework provides an alternative method to traditional field methodology, one which can measure coyote foraging choice under both stable and more dynamic variable resource conditions. I hypothesized that to increase foraging efficiency within foraging patches, coyotes continually sample alternative resources and match their relative rate of foraging time to relative rate of resource availability.

2. Materials and methods

2.1 Subjects

Eight wild born, two-year-old captive coyotes (four males and four females) at the National Wildlife Research Center Predator Research Facility in Logan, Utah, were used as subjects. The coyotes were kept as four established breeding pairs, and each pair was housed separately in a 1 ha pen containing natural vegetation (grass), two shade shelters and two adjoining kennels. All research protocols were approved by the USDA/National

Wildlife Research Center's and Utah State University's Institutional Animal Care and Use Committees.

2.2 Apparatus

Two 8 m x 3 m fenced experimental pens were constructed, side by side, in each home pen. Thus coyotes within each pair could be tested simultaneously and without interference from their mate. Each of the experimental pens contained two identical operant footplates positioned 1 m apart. The footplates were constructed from a 5 cm x 15 cm^2 wooden box, and a 1 cm x 15 cm^2 PVC hinged lid which rested on a small steel spring in a raised position and acted as a lever, closing a micro-switch inside the box when de-pressed.

Reinforcers, consisting of 10 g of BlackGold 30-20 Super Blend dog food pellets (Black Gold Pet Food, Vienna, MO, U.S.A.), were delivered in to a metal food bowl equidistant between the footplates, via an aluminum chute attached to an automatic SuperFeeder™ (Model 6; Super-Feed Enterprise, Mansfield, TX, U.S.A). The feeder was housed in a 4 L plastic bucket, raised .5 m off the floor outside the experimental pen fence. Both the footplates and the bowl were attached to the fence via spring clips and removed after testing. All electronic input from the footplates (response and time counts) and output (schedules and reinforcement delivery) were controlled by a central computer using Med-PC® Version IV software (MED Associates Inc., St Albans, VT, U.S.A.).

2.3 Procedure

Coyotes were initially trained to respond on two concurrently available footplates using a fixed ratio schedule (FR 1). They were then introduced to concurrent VI 10-s schedules on each footplate, which were gradually increased over five weeks to concurrent VI 60-s schedules. Each schedule was composed of ten intervals from an exponential progression (Fleshler and Hoffman, 1962). Schedules were arranged so that when a time interval elapsed on one, both schedules stopped until reinforcement was collected (Davison and Jones, 1995). I held the overall rate of reinforcement constant across the two footplates, based upon an average delivery rate of two reinforcers per minute for each session, but I manipulated the ratio of reinforcement between footplates in five conditions. In the first and last conditions, reinforcement for the two footplates was presented with a ratio of 1:1. The other three conditions were presented randomly, and the left: right reinforcement ratios were 3: 1; 9: 1 and 1: 9 respectively. I included a change over delay (COD) so that coyotes were not immediately rewarded for switching between footplates (Herrnstein, 1961). Thus, after a switch from one footplate to the other, the first response to the new footplate started a 2 s delay during which an arranged reinforcer could not be earned.

Daily testing sessions lasted 20 min and the relative time on the left alternative ($T\text{L}/ [T\text{L} + T\text{R}]$) across sessions as a function of the VI condition was plotted on a graph for each subject (Fig. 3-1). Each coyote was exposed to the same condition until their responding on the left footplate reached behavioral stability. Behavioral stability was determined by statistically comparing the median of the proportion of left responses for each five day session to the median for the previous five day sessions (Eliffe and Alsop, 1996). Stability was reached when the medians varied by $\leq .05\%$.

Coyote sensitivity to changes in resource rates was analyzed by fitting the generalized matching equation (Baum, 1974) to individual data. The generalized matching equation is:

$$\log(T1/T2) = a \log(R1/R2) + \log b \qquad (1)$$

where T refers to time allocation, R refers to reinforcer frequency, a represents sensitivity which measures a change in log time ratio with a unit change in log reinforcement ratio ($a = 1.0$ represents perfect matching), while b represents a systematic bias for one of the alternatives (1 and 2 in subscript) that is unrelated to the reinforcement ratio.

I measured the amount of time spent on each footplate (timed in seconds, from the first response on that alternative until a response occurred on the other schedule throughout a session) to allow the strongest inference to natural predator foraging behavior. Time allocation and reinforcement ratios were analyzed in each session and Eq. (1) was fitted to the data from the last five sessions of each condition. The mean time spent and the mean number of reinforcers taken from the left footplate of the last five sessions were logarithmically transformed to the base ten. The transformed data for each individual animal, and as a group, were fitted to the generalized matching equation using least squares regression. I used t-tests to analyze if coyote sensitivity in changes of relative time with changes in relative reinforcement rate were significantly different from 0 (with $P < .05$).

3. Results

Results showed all coyotes tracked a change in reinforcement ratios within the first few sessions of each new condition (Fig. 3-1). After a change, all coyotes increased their foraging time toward the new richer schedule (higher rate of reinforcement) within two 20 min sessions of a change in condition. One exception to this pattern was coyote F21 that took four sessions to track one condition change (ratio 3:1 to 9:1). The greatest shift in time allocation between footplates resulted from changes between ratios 1: 9 to 9:1 and vice versa. Two coyotes, M21 and M24 (both males) failed to complete the last condition because testing coincided with coyote breeding season. However, as condition five was a repeat of condition one, the analysis of their individual data remained unaffected.

Data were described well by Equation 1, with > 96% of the variance accounted for in all cases (mean $R^2 = .98$) and *SEs* that ranged from .03 to .10. Sensitivity of log ratios of time allocation to changes in log ratios of reinforcement (i.e., a) ranged from .62 -.78 (Table 3-1). For all eight coyotes, *t*-tests showed sensitivity (a) in changes of relative time with changes in relative reinforcement rate were significantly different from 0 (with $P < .05$). Bias (i.e., b) was generally negligible and ranged from .23 to -.11, and *t*-tests showed bias was not significantly different from zero for six of the eight coyotes ($P > .05$; Table 3-1). Two coyotes showed a significant bias. M21 favored the right footplate and F22 favored the left.

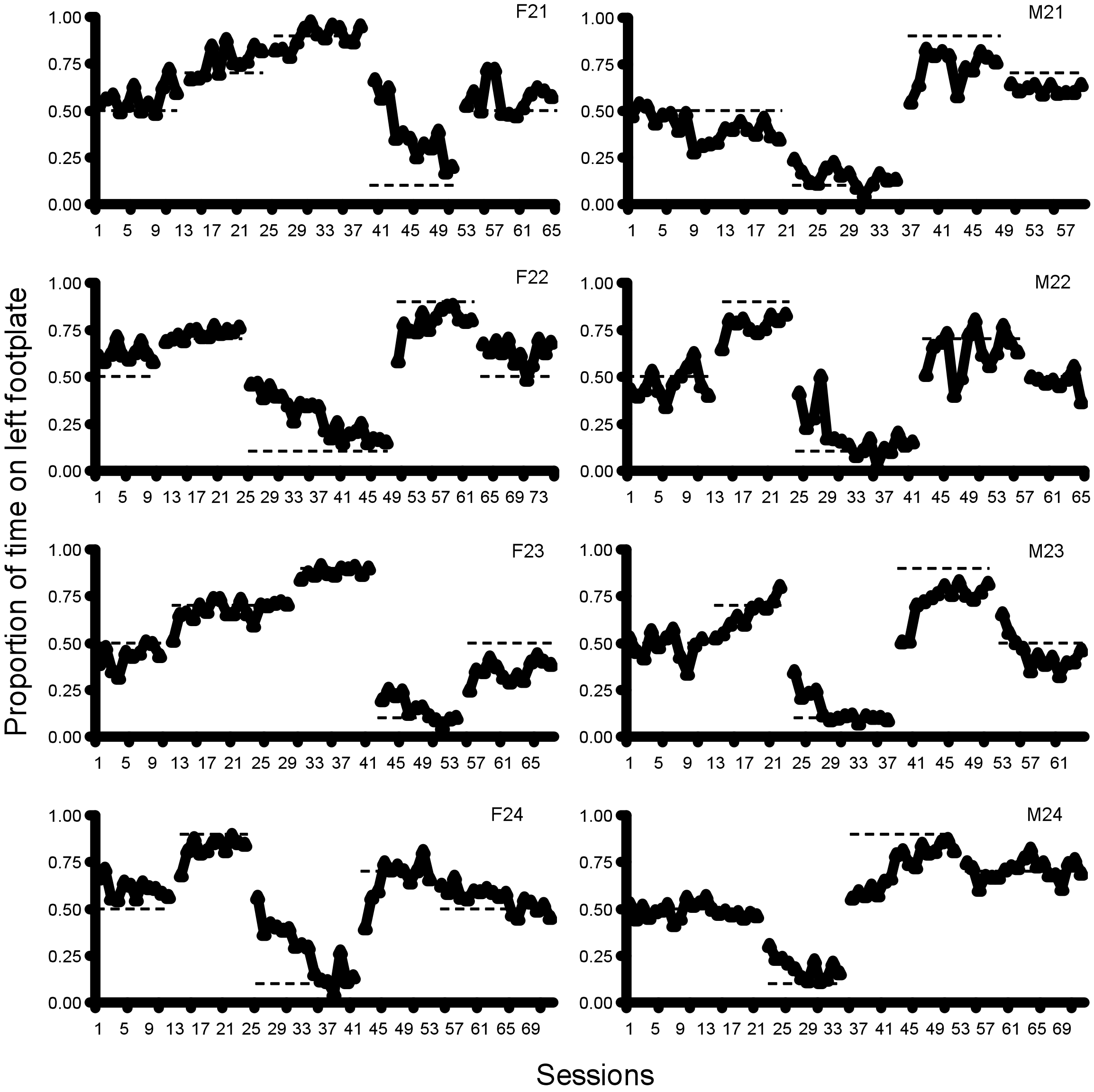

Fig. 3-1. Changes in the relative time (*T*L/ [*T*L + *T*R]) across sessions as a function of the VI condition on that footplate (*N* = 8). Dashed lines represent the reinforcement ratio for each VI condition for the left footplate. Breaks in the data represent condition changes.

Table 3-1
Results of log ratios of time allocation to changes in log ratios.

			Slope			Bias		
Coyote	%VAC	*SE*	*a*	*t*-test	*P*	log *b*	*t*-test	*P*
F-21	.96	.10	.71	6.98	.020	.23	2.78	.110
M-21	.99	.03	.74	28.49	.001	–.11	–6.30	.024
F-22	.99	.04	.72	20.38	.002	.12	4.49	.046
M-22	.99	.04	.68	16.95	.003	–.04	–1.49	.275
F-23	.99	.03	.76	24.42	.002	.02	0.56	.633
M-23	.98	.07	.78	10.53	.009	–.09	–1.71	.230
F-24	.99	.04	.78	19.20	.003	.05	1.56	.258
M-24	.98	.06	.62	9.74	.010	–.03	–0.69	.562

Percentage of variance accounted for (VAC: R^2) and standard errors (*SE*) of the lines of best fit fitted to individual response times. *t*-statistic and *P* values show whether changes in sensitivities (slope: *a* and bias: *b*) in relative time with changes in relative reinforcement rate were greater than zero ($N = 8$).

Coyotes also matched relative time to relative rates of reinforcement as a group. Plotting log time ratios against the log obtained reinforcement ratios as a group (Fig. 3-2) indicated that the sensitivity of time ratios to changes in reinforcement ratios was $a = .80$, which was significantly different from 0 ($t_1 = 22.64$, $P < .0001$). There was no systematic group bias for either footplate, $b = .03$ ($t_1 = .78$, $P > .05$). The line of best fit accounted for 90% of the variance and $SE = .03$ and described group data well.

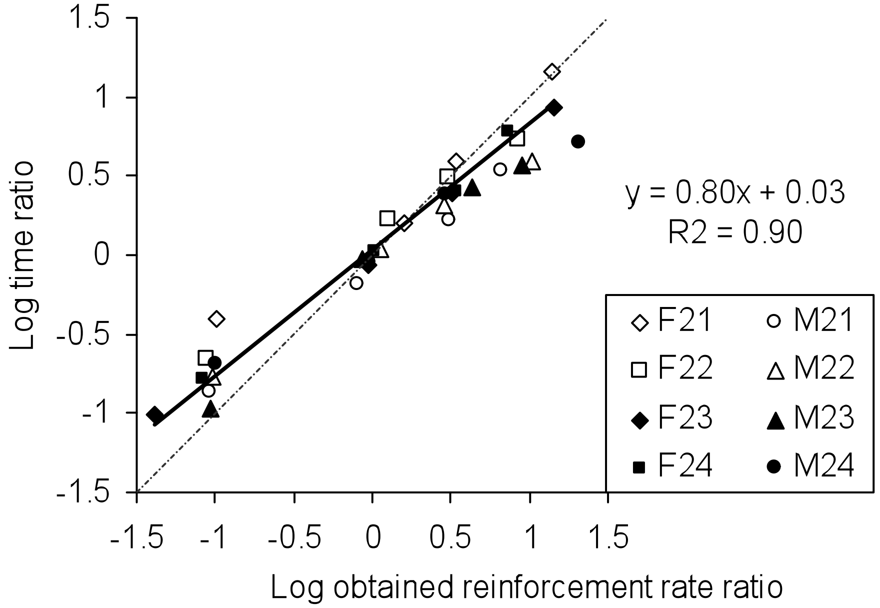

Fig. 3-2. The logarithms of time ratios plotted as a function of the logarithms of obtained reinforcement ratios (*L/R*) for all coyotes: F = female, M = male (*N* = 8). Each datum is the average time spent over the last five sessions of each condition. The solid line was fitted by the method of least squares. The slope gives the sensitivity, and the coefficient gives the log bias. The dotted line shows the locus of perfect matching (*a* = 1.0).

4. Discussion

This study represents a direct measure of coyote choice during foraging. Results showed that every coyote tested showed efficient tracking of temporal variability in food resources, and matched relative rates of foraging time to relative rates of resources. Furthermore, the generalized matching equation explained individual and group data well, as shown by the high R^2 values and low *SEM*s for individual coyotes and group alike. Matching is well established in laboratory data, and the equation parameters mean that comparisons across behaviors, reinforcers and species are possible. In a review of 53 studies that explored matching across responses and reinforcers in rats (*Rattus norvegicus*), pigeons (*Columba livia*), macaques (*Macaca speciosa*) and to some extent humans, the majority showed that variance accounted for (VAC) was >90% (De Villiers and Herrnstein, 1976). Furthermore, a handful of studies using less conventional subjects i.e., chickens (*Gallus gallus domesticus*; Sumpter et al., 1995), dairy cows (*Bos Taurus*; Matthews and Temple, 1979; Foster et al., 1996) and brush tail possums (*Trichosurus vulpecula*; Bron et al., 2003) showed that sensitivities (*a*) in changes of relative time to changes in relative reinforcement ranged from .51 to 1.0. Although methodologies may differ, I found that coyote performance was comparable to tested species, both in VAC and *a*, which suggests the matching paradigm is a valuable behavioral measure of foraging choice and strategies in canids.

By determining how coyotes allocate their time in relation to available resources and make foraging decisions, managers may be better able to predict coyote movements within territory. To date, conclusions on foraging strategies have been based on scat and prey surveys, or telemetry data in the field (MacCracken, 1984; MacCracken and Hansen, 1987; Boutin and Cluff, 1989; Hernández et al., 2002) and resulted in a lack of consensus as to whether coyotes are optimal or opportunistic foragers. I suggest the matching paradigm provides an alternative methodology to traditional field methods, and may potentially increase predictive power in coyote foraging research. That is, matching has been used to tease apart optimal and sub-optimal foraging strategies by exploring whether choice is under the influence of global (Shimp, 1966; Rachlin et al., 1981; Hinson and Staddon, 1983) or local rates of reinforcement (Herrnstein and Vaughan, 1980). Research has shown local rates of reinforcement have considerable influence on behavior (Vaughan, 1981), and recent models based upon local changes in reinforcement can accurately describe and predict behavior in dynamic foraging tasks (Sugrue et al., 2004).

Matching includes both steady-state and transitional behavior. By plotting coyote performance across daily sessions I found that coyotes detected change and adjusted their behavior rapidly (within the first few sessions of each new condition) during the transition periods between stable states. This is consistent with other studies that show log response ratios reach 95% of the new ratio values in three to eight sessions (Davison and Hunter, 1979; Hunter and Davison, 1985). How accurately or how fast animals detect and respond to change may be a function of the speed of environmental change. In a stable state, time and response ratios can improve with an increased number of sessions within a condition (Todorov et al., 1983), which can result in a slow behavioral change to new ratios because of a carryover effect from previous conditions (Davison and Hunter, 1979). When environmental change is rapid however, animals can adjust behavior and track current ratios much more quickly (Schofield and Davison, 1997; Bell and Baum, 2002). Davison and Baum (2000) arranged seven un-signaled ratios within a single session and found pigeons could adjust sensitivities to each new ratio after only six or eight reinforcers. To that end, I suggest a highly flexible species such as the coyote might be expected to match equally well under stable or stochastic conditions. To determine the extent of behavioral flexibility in coyotes, future research could consider measuring behavior during transition states and increase environmental variability within sessions.

Detecting change may also be a function of discernable differences between alternatives. I found that all coyotes exhibited large shifts in time allocation from one footplate to the other during extreme ratio changes (1:9 to 9:1 and vice versa), but small shifts in time allocation between ratios 1:1 to 3:1. My data are thus consistent with findings that show large differences between ratios are more discriminable and can be easier to detect and track than small differences in resource ratios. Mazur and Ratti (1991) found that pigeon's preference for the richer of two alternatives was faster when the reinforcement probabilities were large compared to when they were small. Large ratios may also be more discriminable because reinforcer rate per response is much higher (Mazur, 1992; Kyonka, 2008). Either way, coyotes did continue to adjust behavior across subsequent sessions and increase their foraging efficiency (sensitivity) and overall matched relative foraging time to relative reinforcement ratios.

Another finding was that all coyotes spent slightly less time on each footplate than the matching equation predicts for perfect matching ($a = 1.0$). Undermatching ($a < 1.0$) is often the observed norm and our data are well within the accepted range of past studies (Baum, 1979). Undermatching may be a procedural effect due to the length or effort associated with the changeover delay (Baum, 1982). Aparicio (2001) showed rats overmatched responses, but not time allocation when changeover required increased effort to climb over a barrier. It is possible that a two second delay is of little consequence to a predator that can spend anywhere between 24% and 60% of daily activity budgets traveling (Gese, 2004). Thus future research could explore travel effects on coyote foraging behavior and manipulate travel time or effort during trials.

An alternative explanation is that undermatching may be indicative of a sampling strategy (Shettleworth et al., 1988). When sampling two schedules, an animal can determine the current state of one alternative, but can miss an available reinforcer on the other. In my study, coyotes would lose efficiency in resource acquisition while sampling because they allocate time to investigating other potential resources. A field study by

Sacks and Neale (2002) showed coyotes killed lambs in proportion to sheep abundance, but did not specialize in killing lambs despite high availability. These results suggest coyotes were losing foraging efficiency, which although may be suboptimal in the short term, could provide coyotes, and potentially other species, with an adaptive response to determine fluctuating resource distributions and increase potential to exploit new and rapidly changing habitats.

Finally, my results showed two of the eight coyotes had a significant bias for one of the two footplates: one male for the right footplate, and one female for the left. Bias is often reported in studies and the cause may be difficult to determine (Baum, 1974). Coyotes are inherently wary of human presence and although they vary in individual response to risk (Darrow and Shivik, 2009), they will often alter their behavior to avoid contact (Kitchen et al., 2000). In my case, the bias may have occurred because the favored footplates in both cases were furthest away from the observation building, and hence the researchers presence. Alternatively, both footplates were the closest to the coyotes as they entered their experimental areas.

All the coyotes in my study were wild born animals which strengthen the inferences of my results to coyote foraging in natural environments. However, foraging does occur at different scales across space and time and our work specifically focused on patch selection at a localized scale. That said, the matching paradigm does have applied potential. A wild analogue of the method is that of depleting patches within a territory that are renewed after unpredictable amounts of time. In a situation where prey are simultaneously available, matching theory suggests that predators should match foraging time and behavior according to prey proportions, and this has been shown in the field.

Houston (1986) showed the generalized matching equation adequately described the foraging data of territorial pied wagtails (*Motacilla alba yarrelli*) in the wild. Similarly, data from 44 wild species that foraged in groups were re-analyzed and found to follow the parameters of the matching law (Kennedy and Gray, 1993). For coyotes, voles and pocket gophers are often simultaneously available in differing habitat patches throughout the year. At a localized scale, Gese et al. (1996) found that small mammal capture rates within a habitat patch explained 84% of the variation of time that coyotes spent hunting in that patch, which is indicative of matching. Furthermore, the amount of time coyotes spent hunting in each habitat increased proportionally as capture rate increased. Therefore, my results suggest matching provides a good explanation of coyote foraging choice at the local scale, and could provide a good foundation from which to explore more complex foraging patterns in coyotes.

If, as I believe, the matching paradigm can be successfully implemented in exploring behavioral flexibility and foraging strategies in coyotes, then it would seem appropriate to extend its application to other wildlife species. It is interesting to note that most, if not all, matching research to date has inadvertently been conducted on generalist or commensal species. Yet there is great variation across species in behavioral flexibility and ability to adapt to change. Specialist species are more adapted to stable environments (Futuyma and Moreno, 1988). Evidence has shown that of 47 mammalian species introduced in to new environments in Australia, only specialist species failed to adapt (Myers, 1986). Thus there is an urgent need to undertake comparative studies to determine whether matching, which is so firmly established in generalist species, also holds for specialist species. From that point, the description of rates of behavioral change during transition periods, perhaps via the generation of acquisition curves for individuals within a species, might provide a metric for comparing behavioral flexibility across species. Such research would be invaluable in understanding species' potential for range expansion and adaptation to new or altered habitats. Anthropogenic influence will continue to impact species. By determining how quickly or how accurately various species match, or understanding the strategies underlying their matching behavior, we may better understand how some species are more able to adapt to conditions of extreme environmental change imposed by humans, while others are not.

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CHAPTER 4

BRAIN OR BRAWN: THE FORAGING STRATEGIES OF CAPTIVE COYOTES (*CANIS LATRANS*) AND THE EFFECT OF DOMINANCE HIERARCHY ON FORAGING BEHAVIOR

Abstract

Efficient foragers often use previous experience to guide foraging strategies. However, individual strategies may be affected by social competition and group dynamics. My objectives were to explore individual and spatial foraging strategies in captive coyotes (*Canis latrans*) in order to determine how dominance influences foraging behavior. Eight male and female coyote pairs in 1-ha pens at the Millville Predator Research Facility were used. Prior to testing, I determined social rank within pairs using competitive food trials. I then explored coyote foraging strategies in individual and pair conditions. During both conditions, coyotes searched for food hidden in one in eight possible locations. I recorded the general area and number of feeders searched, the latency to find the correct feeder, and the frequency of scent-marking on feeders by dominant and subordinate coyotes. Results showed that subordinates increased efficiency by remembering and relocating food when foraging individually, but efficiency decreased when foraging in pairs despite prior location knowledge. Dominant coyotes did not follow subordinates to increase efficiency. Results suggest that coyotes may use olfactory cues and memory to find food, but that social status may overrule information use.

1. Introduction

When resources are clumped and relatively stable, an individual animal should return to an area where food was previously found, which is a foraging strategy called 'win-stay' (Levine, 1959; Olton et al., 1981; Gaffan and Davies, 1982). In contrast, when food resources are widely dispersed and replenished at variable rates, then an animal should search elsewhere once food has been found and consumed. That is, an animal should use a win-shift strategy (Levine, 1959; Olton et al., 1981). To be efficient at either strategy, an animal should remember the location of food and adapt foraging behavior appropriately (Olten et al., 1981). Spatial foraging strategy models have been described for Clark's nutcrackers (*Nucifraga Columbiana*; Olson et al., 1993), pigeons (*Columba livia*; Olton and Samuelson, 1976; Olton and Schlosberg, 1978), rats (*Rattus norvegicus;* Olton et al., 1981), common marmosets (*Callithrix jacchus jacchus;* Menzel and Juno, 1985; MacDonald et al., 1994), sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos taurus*; Hosoi et al., 1995a, b), pigs (*Sus scrofa*; Laughlin and Mendl, 2000), wolves (*Canis lupus*), red foxes (*Vulpes vulpes*) and coyotes (Loether, 1978; Cheney, 1982).

In social species however, social interactions may complicate foraging strategies. Indirectly, cues and signs from conspecifics can provide information about resources that can affect foraging behavior (Box and Gibson, 1999; Galef and Laland, 2005). Directly, some individuals may exploit food resources found by conspecifics (e.g., by stealing) and thus force them to adopt alternative foraging strategies (Barnard and Sibly, 1981; Barta and Giraldeau, 1998; Giraldeau and Caraco, 2000).

In social species with dominance hierarchies, the choice to find or steal food may depend upon an individual's social status. Dominant animals are more likely to steal because they can rely on their competitive ability and aggression to do so (Barta and Giraldeau 1998; Giraldeau and Caraco, 2000; Liker and Barta, 2002; Lendvai et al., 2006). Dominant pigs naïve to the location of food can increase their foraging efficiency by following and displacing subordinate pigs (Held et al., 2000). In contrast, subordinate animals may specialize in finding their own food because they lack competitive ability to steal (Lendvai et al., 2006), and learning cues associated with food or remembering food locations may increase their foraging advantage. Subordinate green anole lizards (*Anolis carolinensis*) and firemouth cichlid fish (*Thorichthys meeki*) were able to steal food more effectively from naïve dominants after learning food cues (Hollis et al., 2004), and subordinate pigs increased advantage over naïve dominant pigs by relocating food (Menzel, 1974; Held et al., 2000).

The aim of my study was to extend foraging strategy research to canids, specifically to coyotes. Coyotes forage both individually and in the company of conspecifics and have a well defined social structure (Gese, 2004). Dominant individuals enjoy preferential access to resources: food, territory and breeding (Bekoff and Gese, 2003). Coyotes of lower social rank may alter foraging behavior to circumvent dominant resource holding power (Séquin et al., 2003). Assumptions on coyote foraging strategies and efficiency have been indirectly based upon scat analysis (i.e., MacCracken, 1984; MacCracken and Hansen, 1987; Hernández et al., 2002; Sacks and Neale, 2002), field observations of packs (Bekoff and Wells, 1981; Gese et al., 1996a, b) and captive studies of individual animals (Loether, 1978, Cheney, 1982). To my knowledge, there have been no controlled studies that determine how individuals make foraging choices and how dominance affects those choices in social situations.

My objectives were to explore coyote foraging behavior, and determine how social status impacts coyotes when they forage socially. I used an experimental analogue of a semi-naturalistic foraging scenario in which one member (the 'informed' animal) of a group of chimpanzees was given privileged information of the location of a monopolizable food resource, and then the group was allowed to forage together. Interactions within the group revealed individual strategies and flexibility in adjusting behavior according to social and hierarchical competition, and as a function of prior information on the food resource (Menzel, 1974). The same procedure was used in pairs of pigs to determine how dominance impacted upon individual foraging behavior when a subordinate was given prior location knowledge (Held et al., 2000). In the present study, I gave a subordinate animal prior access to, and thus prior knowledge of, a food source and then allowed coyote pairs to forage together. I expected that given prior information on food location, subordinate coyotes could relocate a food resource when foraging alone as they have been observed returning to specific areas to hunt or forage (Gese et al., 1996a). I expected that coyotes to use olfaction, rather than vision to search, as canids mark food caches (Henry, 1977; Harrington, 1981a, b) which may aid orientation (Johnson, 1973). I predicted that dominant coyotes would follow and displace subordinates coyotes when foraging in pairs.

2. Materials and methods

2.1 Subjects

Sixteen captive coyotes (eight male and female breeding pairs) at the National Wildlife Research Center Predator Research Facility in Logan, Utah were tested in two successive groups of four pairs. Group 1 was trained and tested from October 2007 – June 2008, and Group 2 from July 2008 – December 2008. By keeping coyotes in established pairs I maintained a natural social order and could explore dominance effects on foraging behavior. All research protocols were approved by the USDA/National Wildlife Research Center's and Utah State University's Institutional Animal Care and Use Committees.

2.2 Apparatus

I tested each pair of coyotes separately in one of four adjacent 1-ha wedge-shaped experimental pens. Each pen contained natural vegetation (grass), two shade shelters and two adjoining kennels under an observation building. I divided each pen into a test area and a holding area using an opaque fence, with a 60-cm^2 guillotine door that allowed coyote access but restricted visual contact between the two areas (Fig. 4-1).

The coyotes' normal mink food was used throughout the experiment. I constructed eight feeders using 7.5-cm x 30-cm plastic pipes, divided in to two compartments. One compartment was open and allowed coyote access to food. Food in the other compartment was inaccessible and could be smelled through holes drilled in the pipe wall, which controlled for olfactory cues. Feeders were secured to the ground using a metal stake. I positioned eight feeders in four pairs (two feeders 7-m apart, and 14-m between pairs) along a test arc that was 90-m from the dividing fence and paralleled the outer perimeter of the pen (Fig. 4-1).

I installed four cameras on 3.5-m poles in front of the test arc so that one camera observed two feeders (Fig. 4-1). Two additional cameras on the observation building recorded coyote approaches to the test arc. I used video tapes and digital recorders to

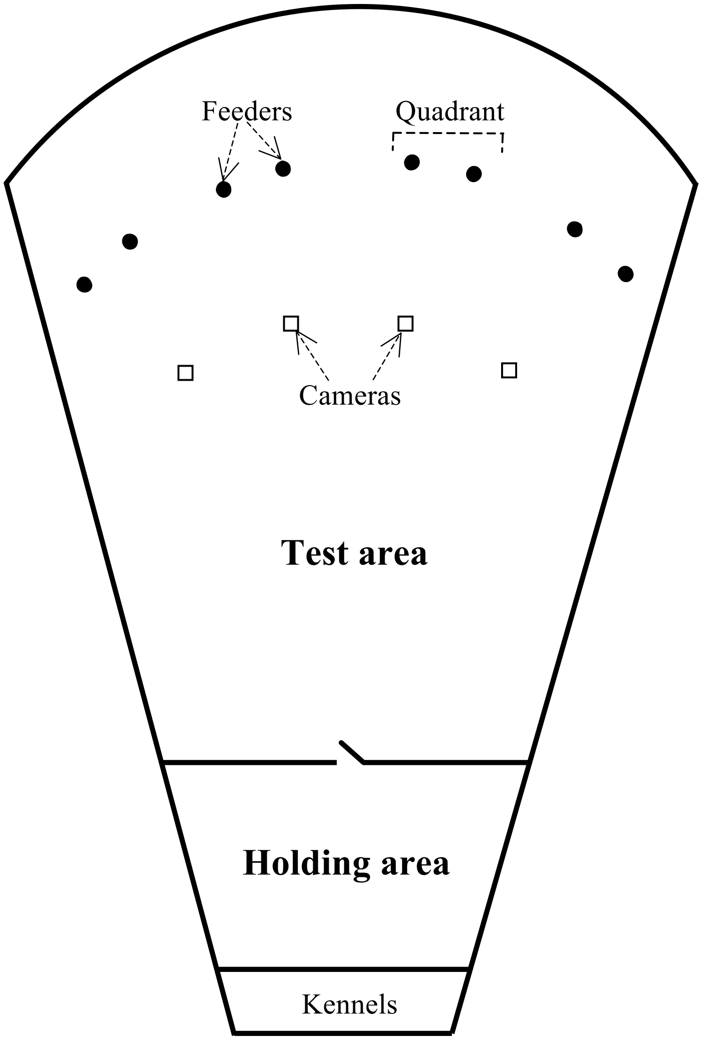

Fig. 4-1. Division of each 1-ha experimental pen in to a holding area and a test area. The test area contained eight feeders placed in four quadrants, and four cameras with one camera observing each quadrant (not to scale).

continuously record all behavior during trials, which was subsequently coded using Noldus Observer® (Noldus, Leesburg, VA, USA).

2.3 Procedure

2.3.1. Dominance

Prior to spatial foraging trials, I tested pairs for dominance. Group 1 was tested for dominance during October and Group 2 was tested during August. I gave each group of coyotes four weeks to adjust to the pens and then tested pairs for dominance over four competitive food trials. For each trial, I broke five hotdogs in pieces and placed them in a pile. Trials began when the first coyote ate, and ended when all food was eaten. I measured dominance using asymmetric outcomes of dyadic conflicts (Drews, 1993). I defined the animal that displaced the other coyote from the food more often as the food dominant coyote, and the subordinate as the animal that was displaced from the food more often.

2.3.2. Individual and pair trials

I trained the coyotes to search for food over five successive days. Specifically, on day one, I placed food at each of the eight feeder locations and gave coyote's access to the test area. On day two, I kept pairs in the holding area while I put accessible feeders at all eight locations. I released both coyotes individually and then in pairs, to search the eight sites. Over the next three days I reduced the number of feeders with accessible food from eight to four, four to two, and then two to one. No behavioral observations were recorded during the training phase.

For testing, I used a two factor repeated measures design, with social status and condition as factors. Each coyote was tested individually (in individual search and individual relocation trials) and then as a pair (in pair search and pair trials). Coyotes proceeded to the pair trials once the subordinate coyote had reached a performance criterion: when the first feeder searched in three consecutive relocation trials was the correct feeder (i.e., no investigation errors).

During the individual trials, subordinates were given a search trial followed by a relocation trial each day, with the accessible feeder in the same location for both trials. This ensured that subordinate coyotes learned to expect food in the same location (i.e., have privileged information on the location when foraging as a pair). In contrast, dominant coyotes were given two search trials per day with the accessible feeder in a different location for each trial to ensure they did expect food in the same location (i.e., no prior information on food location in the pair trials). I put both coyotes in the holding area before trials began each day. I then entered the pen from a central back gate, walked along the test arc setting each feeder in position and then left through the same gate. I visited each location for the same length of time to control for human scent cues. I randomized the feeder location without replacement each day (i.e., pair of trials) for the subordinate, but for every trial for the dominant. I counterbalanced the trial order for the two animals daily to control for coyote scent marking during trials.

For subordinate trials, I released the subordinate in to the test area while the dominant coyote remained in the holding area, and both animals received the same amount of food to control for food motivation. When the trial ended, I returned the subordinate to the holding area, wiped down the feeders and re-baited the same feeder as in the first trial. I then released the subordinate for a second trial. After the second trial ended, both coyotes were placed back in the holding area and a new set of feeders were set in position. I then tested the dominant animal while the subordinate remained in the holding area. Both dominant trials were conducted in the same way as previously except that the feeder was placed in a different location in the second trial. I gave the coyotes access to all pen areas once both sets of trials were completed. All individual trials lasted 6 min or less if the coyote left the test arc.

For the pair trials, I conducted two trials per day using the same procedure as before, except that an individual search trial for the subordinate (henceforth pair-search trial) was followed by a pair trial, in which both animals were tested together. The feeder remained in the same location for both trials but was randomized without replacement each day. Thus the pair trial was a relocation trial for the subordinate but a search trial for the dominant. Pair trials ended after 10 min and coyotes were given access to all pen areas. Animals received 50% of their daily food ration during daily trials and the remaining 50% 1 h after trials ended.

2.4. Data collection and analyses

2.4.1. Dominance

I recorded the total number of displacements within pairs. Displacements were reciprocal such that a win by one animal equaled a loss by the other. I also recorded the amount of time (min) each animal had access to the food (resource holding power). I analyzed correlations between displacements and time using non-parametric Spearman's rho. Differences in behavior between the two groups as a function of seasonal effects were analyzed using Mann Whitney U test (displacements) and paired *t*-test (resource holding power).

2.4.2. Individual and pair trials

I recorded the number of feeders each coyote searched (before and including the correct feeder location) within individual search, individual relocation, pair-search and pair trials. To determine if coyotes increased efficiency as a function of prior location knowledge when foraging individually, I compared the mean number of locations in search vs. relocation trials for the subordinate, and search-1 vs. search-2 trials for the dominant with Wilcoxon signed ranks tests. To determine if foraging performance differed when alone compared to foraging in pairs, I compared individual relocation and pair trials for subordinates, and individual search-1 and pair trials for dominants using Wilcoxon signed ranks tests. I compared subordinate and dominant performances within the pair trial using a Mann-Whitney U test.

I recorded the time (in seconds) it took coyotes of either status to find the correct feeder, recorded as the time the animal left the holding area to the time it started eating food. I compared subordinates in individual search and individual relocation trials, and individual relocation and pair trials, and dominants in individual search-1 and individual search-2 trials, and individual search-1 to pair trials using Wilcoxon matched-pairs signed-rank tests. I compared latencies between subordinate and dominant coyotes within each condition using Mann-Whitney U tests.

To determine whether search was general rather than specific (i.e., if the coyotes' entry into the test arc was at the correct feeder location or within 7 m of the correct feeder), I divided the test arc in to quadrants (Fig. 4-1). I recorded the first quadrant the coyote entered and compared it to the one that contained the correct feeder. I calculated a mean percent correct and compared individual search and relocation trials, and in pair-search and pair trials for subordinates, and individual search-1 to individual search-2 trials for dominants using Wilcoxon signed ranks tests. I compared subordinate and dominant performance in the pair trial using a Mann-Whitney U test.

To determine if marking differed by social status, I recorded the frequency of urinations by subordinate and dominant coyotes and compared frequencies across conditions using a Chi-square test of independence. To determine if coyotes marked the correct feeder more frequently than other feeders, I categorized feeders according to their position in relation to the correct feeder. Proximal feeders were immediately adjacent to the correct feeder, and distal feeders were any other feeder on the test arc. I recorded the frequency of marks made to the three feeder types and compared observed proportions to expected proportions using Chi-square goodness of fit tests.

Potential differences in behavior (for the number of feeders searched, latency to find the correct feeder, quadrant approached and marking frequency) between the two groups due to seasonal effects were analyzed using Mann Whitney U tests.

3. Results

3.1. Dominance status

Results of the dominance hierarchy trials showed that there was a significant positive correlation between the number of agonistic displacements and resource holding power (rho = .623, $N = 16$, $P = .01$), although the number of displacements varied within pairs, as did the mean resource holding power (Fig. 4-2).

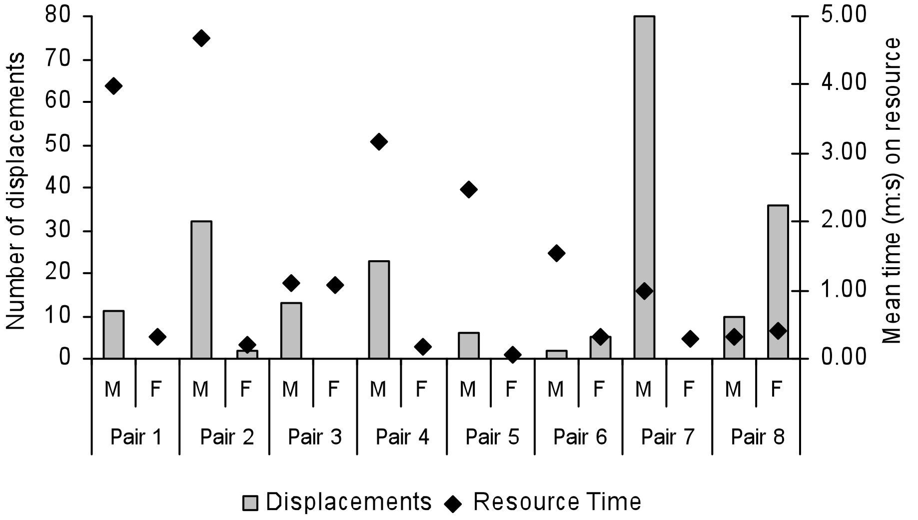

Fig. 4-2. Total number of displacements by males (M) and females (F) within established pairs, and the average access time (min) to food that each coyote had during competitive food trials, ($N = 8$ pairs).

Six males and two females were food dominant within the eight pairs; four males in Group 1 and two males and two females in Group 2. However, there was no statistical difference in number of displacements ($U = 29.5$, $P > .790$) or resource holding power ($t_{14} = 1.457$, $P = .167$) between the two groups.

3.2. Individual and pair conditions

Subordinates searched fewer feeders during relocation trials than during search trials in the individual condition ($Z = -2.533$, $P = .01$; Fig. 4-3). There was little difference in the number of feeders searched by dominant coyotes in individual search-1 and search-2 trials (*Z* = -0.507, *P* = .61). Subordinates searched more feeders in the pair trials compared to individual relocation trials, but the difference was not significant (*Z* = -1.120, *P* = .26). There was little difference in the number of feeders searched by dominant coyotes in the individual search-1 and pair trials (*Z* = -1.014, *P* = .31). Furthermore, there was no statistical difference in the number of feeders searched by subordinate and dominant coyotes in the pair trials (*U* = 24, *P* = .40). There was no statistical difference in the number of feeders searched by the two groups in search (*U* = 2, *P* = .083), relocation (*U* = 26, *P* = .564) and pair trials (*U* = 6, *P* = .564) by subordinates. Similarly there was no statistical difference between the two groups in the number of feeders searched by dominants in search-1 (*U* = 6, *P* = .561) or pair trials (*U* = 3.5, *P* = .191). There was a significant difference in the number of feeders searched by dominants in the two groups in search-2 trials (*U* = 6, *P* = .561), with a median Group 1 = 4.2 feeders (range = 3.1 – 4.9 feeders) and Group 2 = 2.5 feeders (range = 1.8 – 3.5 feeders).

I found little difference in the time subordinate coyotes took to approach the correct feeder in individual search and relocation trials (*Z* = .0, *P* = 1.0), or in individual relocation and pair trials (*Z* = -1.352, *P* = .176). There was little difference in approach time by dominants in individual search-1 and search-2 trials (*Z* = -.911, *P* = .36), or in individual search-1 and pair trials (*Z* = -.140, *P* = .89). I found that subordinates were faster than dominants at locating the correct feeder in the first individual search trials (*U* = 9.0, *P* = .016). Similarly, subordinates were faster in the relocation condition than dominant coyotes were in the search-2 condition (*U* = 7.0, *P* = .009).

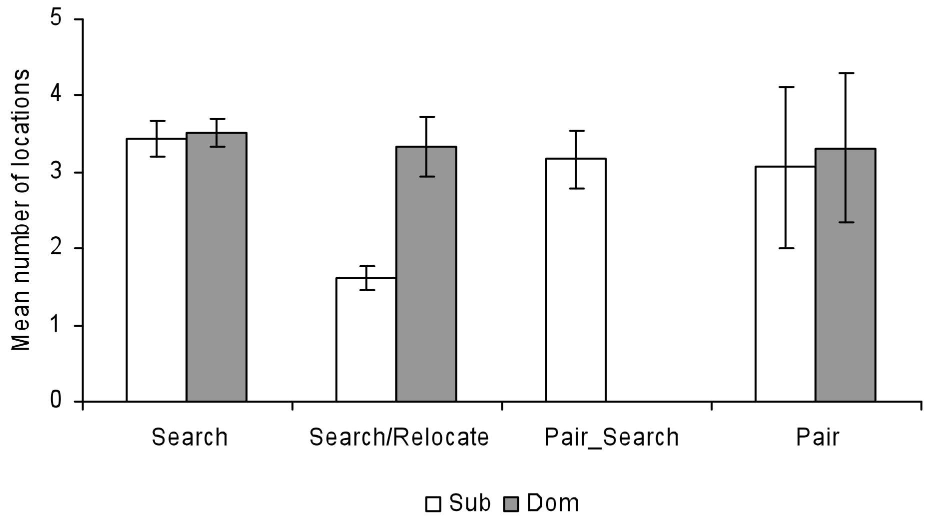

Fig. 4-3. Average number of locations (± *SE*) searched (before and including the correct location) by subordinate and dominant coyotes in individual and paired conditions.

There was no statistical difference in approach time by status in the pair condition (*U* = 26.0, *P* = .53). There was a significant difference in the latency to the correct feeder between subordinates in the two groups in individual search trials (*U* = 1, *P* = .043), with a median Group 1 = .40 sec (range = .33 – .54 sec) and Group 2 = .29 sec (range = .14 – .37 sec). But no statistical difference in the latency to the correct feeder by subordinates in the two groups in relocation (*U* = 4, *P* = .248) or pair trials (*U* = 7, *P* = .773).

The percentage of approaches to the correct quadrant increased in individual relocation trials compared to the individual search trials for subordinate coyotes (*Z* = -2.366, *P* = .02*;* Fig. 4-4). Subordinates approached the correct quadrant more frequently in pair trials compared to pair-search trials (*Z* = -2.527, *P* = .01). There was little difference in the percentage of correct approaches in individual search trials by dominants (*Z* = -0.674, *P* = .5), or in pair trials compared to individual search trials (*Z* = -0.423, *P* = .67).

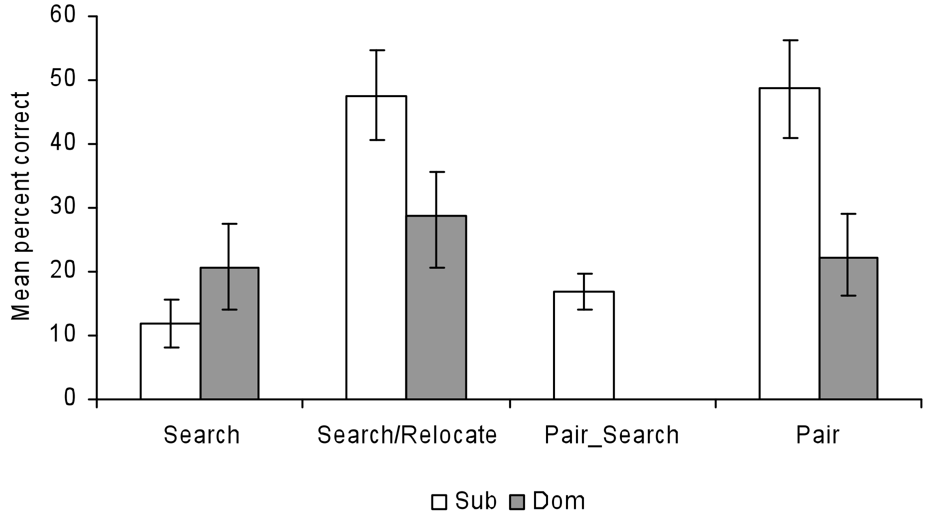

Fig. 4-4. Mean percentage (± *SE*) of approaches to the correct quadrant by subordinate and dominant coyotes in individual and pair conditions.

Subordinates approached the correct quadrant more frequently than dominant coyotes in the pair condition (*U* = 8, *P* = .02). There was no statistical difference in approaches to the correct quadrant by subordinates in the two groups in search (*U* = 2.5, *P* = .102), relocation (*U* = 7, *P* = .767) or pair trials (*U* = 6.5, *P* = .663). Similarly there was no statistical difference in approaches to the correct quadrant by dominants in the two groups in search-1 (*U* = 4.5, *P* = .593), search-2 (*U* = 3, *P* = .289) or pair trials (*U* = 3, *P* = .289).

Subordinates marked feeders more frequently that dominant coyotes during individual trials (totals 335 and 153 respectively). However, there was little difference in frequencies between subordinate and dominant coyotes in initial search trials (*U* = 22.0, *P* = .293), or in search-2 and relocation trials (*U* = 21.5, *P* = .270), or in pair trials (*U* = 27.5, *P* = .636). There was a significant difference in marking frequency between the two groups in individual search trials (*U* = 13, *P* = .05), median Group 1 = 19 events (range = 2 – 80) and Group 2 = 6.5 events (range = 0 – 21), and in pair trials (*U* = 8, *P* = .01), median Group 1 = 64 events (range = 15– 91) and Group 2 = 24.5 events (range = 0 – 40). There was no statistical difference in marking frequency between the two groups in search-2/relocation trials (*U* = 19, *P* = .172).

I combined the frequency of marking by subordinate and dominant coyotes across all conditions and found a difference in observed frequency of marking to correct, proximal and distal feeders compared to expected frequencies: 1/8 feeders = correct, 1/4 = proximal, 5/8 = distal ($X^2 = 115.26$, df = 2, $P < .001$). Coyotes marked the correct feeder more than expected and marked proximal and distal feeders less than expected across trials (Fig. 4-5).

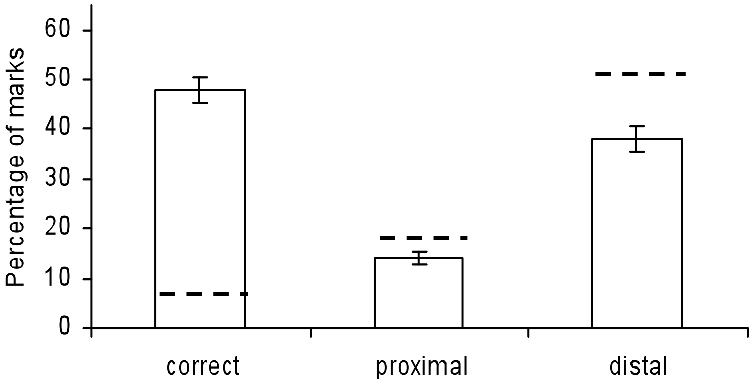

Fig. 4-5. Percentage of observed marks (± *SE*) compared with percentage of expected marks (- -) to correct, proximal (adjacent) and distal (other) feeders, by all coyotes (*N* = 16) across all conditions.

4. Discussion

I investigated the spatial foraging strategies of captive coyotes when foraging alone and in pairs. When foraging individually, subordinates used prior information on food location to increase foraging efficiency. However, foraging was affected by social dynamics in that subordinate foraging efficiency decreased and dominant efficiency failed to increase during the pair condition.

Many animals use strategies to improve foraging efficiency e.g., bees (*Bombus terrestris*) restrict search areas to reduce flight distances (Keaser et al., 1996), nectar feeding birds (*Loxops virens*) avoid repeating visits to empty patches (Kamil, 1978), and marmosets (MacDonald, 1994) and pigs (Held et al., 2000) remember food locations and minimize travel distances. My results support findings that show canids have the ability to forage strategically (Loether, 1978; Cheney, 1982). Loether (1978) showed coyotes and red fox will use win-shift and win-stay strategies to increase foraging efficiency in a task where the probabilities of finding food in three locations vary over time. I found subordinate coyotes learned to relocate (win-stay) when foraging independently and increased their efficiency by using prior information on the location of food. Win-stay is an efficient strategy when resources are clumped and fairly stable (Olton et al., 1981).

Coyotes may use memory and olfactory cues to relocate spatially distributed food. That is, subordinates approached the correct quadrant in the second individual trial which suggests they remembered the general area in which they previously found food. From there they may have used odor cues to find the exact location. My results support findings which show pigs use memory to home in on a foraging patch and then use olfactory cues to find the food within the patch (Mendl et al., 1997; Held et al., 2000).

Possible odors that coyotes used were human and food odors. However, I controlled for human scent cues by visiting every location, and food cues by filling every feeder with food. Research has shown that coyotes are unable to discriminate resource quantity by food odor (J. Baker, Department of Psychology, Utah State University, pers comm.). Thus it is likely that coyotes in my study were unable to distinguish the correct feeder through food odor alone.

Coyotes may use scent marking to relocate food. Scent marking has various functions for mammals including aiding spatial orientation (Johnson, 1973). Canids mark food caches which researchers suggest may improve foraging efficiency (Henry, 1977; Harrington, 1981a, b). I found that coyotes scent-marked all the feeders but marked the correct feeder more, which could suggest that they use scent marking to discriminate correct from incorrect feeders. Furthermore, research suggests canids mark empty caches in order to 'book-keep' locations and avoid revisiting empty sites (Henry, 1977; Harrington, 1981b). When foraging individually, approximately 93% of marks that coyotes made were to the correct feeder once it was empty. However, coyotes often returned to the empty feeder during the same trial which does not support the book-keeping hypothesis, nor is the behavior particularly efficient. I suggest that marking may function as a location cue when coyotes expect food to replenish in the same location, which may be why subordinates marked more often than dominant coyotes. However, further investigation is needed to determine of the function of marking food sites in canids.

Dominant coyotes used a win-shift strategy because food location varied in every trial, and thus foraged as efficiently as they were able given the variable environmental conditions and lack of prior information of food location (Olton et al., 1981). Animals often use both strategies but show a preference for one over the other, which suggests a species specific adaptation to foraging (Olton et al., 1981). Marmosets (Menzel and Juno, 1985; MacDonald et al., 1994), sheep, goats and cattle (Hosoi et al., 1995a, b) show a preference to win-stay. In contrast, pigs (Laughlin and Mendl, 2000), rats (Olton et al., 1981), pigeons and Clark's nutcrackers (Olton and Samuelson, 1976; Olton and Schlosberg, 1978; Olson et al., 1993), wolves, foxes and coyotes (Loether, 1978; Cheney, 1982) show a preference to win-shift. I observed that subordinates often left the correct feeder to explore other feeders which suggest a preference for a win-shift strategy despite learning to win-stay. Research suggests animals that search empty food sites in foraging experiments may be sampling rather than making location errors (Bednekoff and Balda, 1997). The better informed an animal is about its environment, the more adaptable its foraging behavior can be (Clark and Mangel, 1984; Dall et al., 2005). Thus coyotes could have adapted to explore and gather information in fluctuating environments (Gaffan and Davies, 1982; Maki, 1987; Laughlin and Mendl, 2000; Inglis et al., 2001; Gibson et al., 2006), which may contribute to the success of coyote expansion across diverse habitat (Bekoff and Gese, 2003; Gehrt, 2007).

In a social situation, I found subordinate behavior was affected by conspecifics. The amount of time to find the correct location was similar for dominant and subordinate coyotes in company, even though subordinates were faster when foraging alone. Subordinates also searched more locations during the pair trial despite knowing the correct location and making approaches to the general area. One explanation for the reduction in efficiency and accuracy by subordinates is that their foraging behavior suffered from interference or interruption. Pigs make more relocation errors when subjected to mild environmental disturbance (Mendl et al., 1997). Disturbance can be socially mediated i.e., from the presence of conspecifics (Rands et al., 2006). Moreover, social hierarchies can impact upon individuals depending upon their position within the hierarchy. Subordinate rhesus monkeys (*Macaca mulatta*) successfully learn a discrimination task when alone, but fail to express a previously learned behavior when dominant monkeys are present (Drea and Wallen, 1999). Thus any potential advantage subordinate coyotes gained by knowing the food location appeared to be negated by the presence of the dominant animal.

In general, I found that dominant coyotes did not follow subordinates, but searched the same number of locations when in company as when they foraged alone. In social situations, dominant animals can reap greater net rewards by following and stealing (scrounging) food from conspecifics (Barnard and Sibly, 1981; Barta and Giraldeau, 1998; Giraldeau and Caraco, 2000; Held et al., 2000), relying on status and aggression to do so (Richards, 2002). A scrounger is defined as an animal that obtains a limited resource by exploiting the foraging effort of a conspecific that initially gained (produced) the resource (Barnard and Sibley, 1981). However, because subordinates did not express their location knowledge and relocate the correct feeder when foraging in company, dominant animals were unable to increase efficiency by following. Yet on the few occasions when subordinates did locate the correct feeder first, they were very swiftly and aggressively displaced by the dominant animal.

An alternative explanation for lack of following by dominant coyotes is that foraging strategies are not a function of social status (Giraldeau and Lefebvre, 1986; Ha and Ha, 2003; Beauchamp, 2006). Research has shown that dominant and subordinate animals both scrounge and produce in social foraging situations (Lendvai et al., 2006). Dominant coyotes in the wild initiate hunts and consume higher-quality food items (organ and large muscle tissue) before subordinates have an opportunity to feed (Atwood and Gese, 2008), and coyotes of lower social status access carcasses once dominant animals have finished, i.e., scrounge (Gese et al., 1996a). My study corroborates field observations in that dominant coyotes favored their own search strategy to find food and subordinates often returned to the correct feeder once the dominant animal had consumed the food and left the area.

Although the majority of behaviors measured in the study were similar, I did detect potential seasonal effects in both dominance and foraging behavior in captive coyotes. The two groups of coyotes were tested in succession at different times of the year. Research shows that dominance and foraging behavior can be affected by seasonal changes, particularly the breeding season (Gese and Ruff, 1997; Gese, 2004). The performance of Group 1 may have been affected by the approach of the coyote breeding season. That is, all males in that group were dominant (as opposed to two females in Group 2), but there were no differences in number of displacements or resource holding power compared to Group 2. Similarly, Group 1 searched more feeders and took longer to find the correct feeder, suggesting perhaps, that food motivation had decreased. They also engaged in a greater frequency of marking when foraging individually and in pairs, and increased scent marking during the breeding season has been noted in wild populations (Gese and Ruff, 1997).

Further research is warranted to determine the relationship between social status and foraging strategies in coyotes. My study was a simplified foraging scenario based upon a relatively small sample size. Therefore I suggest that an extension of our design, in which both dominant and subordinates have prior knowledge of more that one food location (as in Caraco et al., 1989), may provide more conclusive and generalizable results on whether specific strategies are associated with social status in coyotes.

I also suggest two further improvements that might improve effect size. Increase the value of the food reward, which would give subordinate coyotes more incentive to relocate during pair conditions. Also, increase the effort required to search for food as coyotes in the wild often travel large distances to forage, and increased effort has been shown to reduce location errors in spatial memory tasks (Laughlin and Mendel, 2004). If coyotes continue to visit incorrect feeders after increasing search effort, results may add further support that coyotes are sampling as I suspect they may be. Although foraging strategies have been explored in the wild (Bekoff and Wells, 1981; MacCracken and Hansen, 1987; Gese et al., 1996a, b; Hernández et al., 2002; Sacks and Neale, 2002), the next logical step is to attempt to replicate my research in the field. Comparing the behavior of individuals when foraging alone and when foraging in a group may prove a challenge in the field, however my experimental paradigm originated from observations of a hierarchical social group in a natural setting (Menzel, 1974).

In conclusion, we showed that coyotes remembered the location of food and increased foraging efficiency by relocating when foraging individually. In a social context however, we found that dominance hierarchy overruled information use and impacted upon individual behavior and efficiency. In a real world setting, strategy choice and foraging efficiency may also be affected by resource distribution, prey behavior, environmental conditions, behavioral adaptations to foraging, past experience, learning and group dynamics. With such social and environmental constraints, coyotes may not be able to forage optimally as past research suggests (MacCracken and Hansen, 1987; Hernández et al., 2002). Instead coyotes may be forced to adopt less efficient strategies as a function of current conditions, but that nonetheless, provide the best option available at the time. Only by exploring how social and environmental constraints affect individual choice can we gain a better understanding of how groups of coyotes in the wild allocate their time to spatially distributed resources.

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CHAPTER 5

CONCLUSIONS

Animals can increase individual fitness in the face of social competition through phenotypic traits or behavioral traits (Drews, 1993), or via behavioral strategies based on individual experience and learning (Krebs and Inman, 1992). Learning may occur through a combination of individual and social mechanisms (Skinner, 1938; Heyes, 1994; Galef and Laland, 2005), and many canids live in social systems that could enhance learning between conspecifics. However within social groups, dominance status may affect learning ability or the expression of learned behavior between ranked individuals (Nicol and Pope, 1994; Drea and Wallen, 1999; Held et al., 2000; Barnard and Luo, 2002).

One of the most adaptable canids is the coyote (*Canis latrans*), which thrives in deserts, woodland, mountains, grasslands and metropolitan areas (Bekoff and Gese, 2003; Gehrt, 2007). Behavioral differences between ranked coyotes may be a function of social status or of learning ability. That is, dominant animals are the principal hunters within coyote packs (Conner et al., 1998; Sacks et al., 1999a; Blewjas et al., 2002; Mitchell et al., 2004), and primarily enforce territorial boundaries (Bowen and Cowan, 1980; Bekoff and Wells, 1986; Gese and Ruff, 1997; Gese, 2001). However, dominant coyotes may be less susceptible to capture in traps and snares than low ranking animals (Sacks et al., 1999b; Jaeger et al., 2001; Séquin et al., 2003; Mitchell et al., 2004). To date there have been no controlled studies of coyote behavior that take learning into account. Moreover, no studies have manipulated both resources and social dynamics. Therefore I explored the effects of social status and learning on the foraging and territorial behavior of coyotes under controlled conditions, as behavioral mechanisms are similar in captivity and in the field (Shettleworth, 1998).

I first determined social status within coyote pairs using competitive food trials. I defined the animal that displaced the other more often from the food source as the food dominant animal (Drews, 1993) as research shows dominant coyotes have preferential access to food (Bekoff and Gese, 2003). My justification for exploring rank within pairs was based upon research that shows one coyote within a pair will often instigate hunts or depredation attacks (Conner et al., 1998; Sacks et al., 1999a; Blewjas et al., 2002; Mitchell et al., 2004). My results showed that six males and two females were food dominant animals within established pairs, which supports findings that dominance is not perfectly correlated with sex in coyotes (Mettler and Shivik, 2007). However, differences in status according to sex in either group of coyotes in my study may be a function of seasonal effects and warrants further investigation. I found that dominance was positively correlated with resource holding power, but that the number of agonistic displacements required to maintain a resource differed markedly between pairs (range 5 to 80 displacements). The severity of aggression and the number of displacements needed to maintain a resource may depend upon the persistence of the subordinate animal to gain access. That is, the more persistent the subordinate, the more displacements may be necessary for the dominant animal to maintain control of the food. Research has shown that individual coyotes can be stratified (i.e., bold, persistent or shy) by their persistence to gain access to a resource in the face of threat (Darrow and Shivik, 2009).

Next I investigated the behavior of established coyote pairs in response to a simulated scent boundary to determine whether coyotes altered space use and avoided areas surrounded by an artificial boundary, and whether response differed by social status. I found that all coyotes (dominant and subordinate) trespassed in to the protected area and concluded that scent boundaries are likely to be ineffective as a management tool. My findings correlate with research in the wild that shows canids will often intrude in to scent marked territories (MacDonald, 1980; Mills et al., 1980; Wells and Bekoff, 1981; Sillero-Zubiri and MacDonald, 1998; Shivik et al., 1996; Gese and Ruff, 1997; Allen et al., 1999). The lack of repellency effect may be a function of the frequency with which I distributed scent marks compared to scent marking rates in the wild (Gese and Ruff, 1997), or it may be a function of my sample size.

Moreover, the lack of observed effects highlights a lack of understanding on the chemical properties of marks and the information they potentially convey, and of the mechanisms by which animals learn. That is, scent marks may take on aversive properties only after an animal experiences repeated direct or indirect threat at territorial boundaries. I found the scent boundary reduced coyote presence slightly compared to the pre-treatment baseline phase but the effect was not significant. Indeed, coyotes were more effectively repelled by human presence alone. That is, coyotes were attracted to the area when a human walked the boundary and laid scent, but avoided the area when a human just walked the boundary. Research shows that coyotes will approach scent lures (Windberg and Knowlton, 1990) but avoid areas of human disturbance (Kitchen et al., 2000; Mech et al., 2000; Gehrt, 2007). The differential response to the boundary that I observed is indicative of the approach-avoidance response, in which animals move toward potentially beneficial stimuli but away from potentially harmful ones (Elliot and Covington, 2001; Elliot, 2006).

I found subordinates investigated and marked the boundary more than dominant coyotes. One possible reason is that subordinates are less neophobic and take greater risks under novel situations because dominant animals control resources in familiar environments (Katzir, 1982; Johnson and Balph, 1990; Darrow and Shivik, 2009). My results may help to explain why coyotes of lower status are more likely to be caught in traps and snares (Sacks et al., 1999b; Jaeger et al., 2001; Séquin et al., 2003) in that they may be more likely to approach lures.

Alternatively, results may suggest that defining status within coyote pairs requires greater clarity, particularly when there is a lack of consensus of what factors define dominance. Currently there are over 13 definitions of dominance which are based upon the role, behavior or property of an individual (Drews, 1993). Consequently there is great debate as to the usefulness and appropriateness of each definition. Two definitions are used in the coyote literature. Alpha coyotes in the wild are usually classified via preferential access to food, territorial holding power and breeding status (Gese, 2004). However, I established dominance via competitive food trials (as in Johnson and Balph, 1990; Mettler and Shivik, 2007). I believe the first definition is useful in defining a pair within a larger group, while the latter is useful to define a relationship between an established pair.

My next objective was to investigate foraging behavior in coyotes. Specifically, I was interested in the ability of individual coyotes to track temporal resource change in a simultaneous two choice test. I found that coyotes efficiently tracked variation in resource distributions and matched their relative time (output) to relative rates of available resources (input). Moreover, coyotes adjusted their behavior within the first few sessions of distribution change. In the wild, small mammal capture rates within a specific patch explained 84% of the variation in time that coyotes spent in the patch (Gese et al., 1996a). My results showed that the generalized matching law described data accurately (Herrnstein, 1961; Baum, 1974). In general, I found coyotes were less sensitive to change than perfect matching suggests, but my data are comparable to the performance of other species tested under the matching paradigm (Baum, 1979). Undermatching could indicate a procedural effect (Baum, 1982), which further research may eliminate. Alternatively, undermatching may be indicative that coyotes were losing efficiency by spending time sampling potential resources. Sampling may be sub-optimal in the short term but may be adaptive in variable environments, which may help coyotes adapt to a wide variety of habitats. My results suggest the matching paradigm provides a direct measure of individual coyote foraging behavior, and an alternative methodology to traditional field methods. That is, matching research has been used to tease apart optimal and sub-optimal foraging strategies and could help determine whether coyotes use optimal or opportunistic strategies. Furthermore, matching may provide the tools to determine how flexible coyotes are as a species, while equation parameters would allow comparisons of coyote behavior to that of other species. Comparisons may shed light on which species are more likely to adapt under variable environmental conditions.

My final objectives were to explore individual coyote foraging strategies during a spatial task, and determine how social status impacts upon behavior when foraging in pairs. When foraging alone, I found subordinate coyotes increased foraging efficiency by relocating food and using prior location knowledge. Relocating a replenishing food source suggests coyotes are able to use a win-stay strategy in situations where resources are clumped and relatively stable (Levine, 1959; Olton et al., 1981; Gaffan and Davies, 1982). In contrast, I found that dominant coyotes searched alternative feeders to previously visited ones because they learned that food location varied in every trial. Behavior of dominant coyotes is indicative of a win-shift strategy, which is an efficient strategy to use when food resources constantly vary (Levine, 1959; Olton et al., 1981; Gaffan and Davies, 1982). Interestingly, subordinates often left the correct feeder to search alternative feeders, and my observations suggest coyotes may have a preference for a win-shift strategy which supports previous findings in canids (Loether, 1978; Cheney, 1982). Many species use both strategies but often rely on one, which may be a function of species specific foraging adaptations or of resource distribution (Olton et al., 1981). My results suggest that coyotes are flexible enough to use either strategy, but may have adapted to explore and gather information as a function of variable food resources and fluctuating prey abundance.

During relocation, I found that subordinate coyotes increased approaches to the correct quadrant which suggests they may use memory to return to the general area in which food was previously found. From there, coyotes might rely on odor cues to locate the exact location of food. I controlled for human scent cues and food cues, however coyotes scent marked all feeders but marked the correct feeder more. Researchers have suggested that marking empty food sites serves to ‘book keep’ so that an animal avoids revisiting empty caches (Henry, 1977; Harrington, 1981). Interestingly, I observed that coyotes often returned to an empty scent marked feeder and thus marking did not appear to deter revisits. Instead, I suggest coyotes may use differential marking rates to discriminate between feeder types and as a location cue when resources are likely to replenish over time. However, further research is warranted to determine the exact function of marking food sites, and its potential role in increasing foraging efficiency in coyotes.

When foraging in a social context, I found coyote foraging behavior was affected by social dynamics. I found that subordinates were faster at finding food when foraging alone compared to their performance when foraging in company. Specifically their performance decreased and was similar to that of dominant coyotes. Interestingly, subordinates did increase approaches to the correct quadrant (general area), which suggests they remembered the location. However, from that general area, subordinates searched more locations and failed to locate the correct feeder. One explanation is that they suffered from socially mediated disturbance i.e., from the presence of the dominant animal (Rands et al., 2006). My results support research that shows social hierarchies can affect the expression of learned behavior (Drea and Wallen, 1999). Thus any advantage that subordinates had by implementing previous information appeared to be negated by social hierarchy.

Contrary to my expectation that dominant coyotes would increase their efficiency in a social foraging situation, I found dominants searched as many locations in company as when they foraged alone. Some authors suggest that dominant animals increase efficiency by following and stealing food from conspecifics (Barnard and Sibly, 1981; Barta and Giraldeau, 1998; Giraldeau and Caraco, 2000; Held et al., 2000). Others suggest that foraging strategies are not a function of social status (Giraldeau and

Lefebvre, 1986; Ha and Ha, 2003; Beauchamp, 2006). My findings show that on average, dominant coyotes did not follow and displace subordinates from the resource. One explanation is that because subordinates did not relocate the correct feeder, dominant animals were unable to follow them and so relied upon their own behavior to find food. On a few occasions when subordinates did arrive first however, they were quickly and aggressively displaced by the dominant animal. To determine whether specific strategies are a function of social status in coyotes, future research may extend my design by giving both dominant and subordinate coyotes prior knowledge of two food locations (as in Caraco et al., 1989). That said, my results suggest that coyotes are flexible enough in the company of conspecifics to implement more than one foraging strategy to gain an advantage. In the wild, coyotes of either status both produce and scrounge resources (Gese et al., 1996a; Atwood and Gese, 2008), and strategy choice may be affected by the context, social competition, resource availability and value. Therefore, increasing the value of food may give subordinate coyotes more incentive to relocate during social conditions, while increasing the effort required to search may reduce location errors and add further support that coyotes are using win-shift strategies to explore potential resources.

My research was based upon simplified territorial and foraging scenarios with a relatively small sample size by ecological research standards. However, many underlying behavioral patterns obscured by the complexity of the natural world have been highlighted in controlled conditions with relatively few individuals. Because I recognize that factors such as nutritional state and energetic costs, competition, predation risk, parasitism, prey availability and preference, and prey behavior can affect foraging decisions (Sih, 1993), I suggest that replicating our research in the field could begin to increase the relevance of my findings to natural coyote populations. Although replication would present a challenge, each of my areas of study has been conducted in natural contexts. Simulated territorial boundaries and their effect on coyote behavior are currently being explored in the wild (Wilson, 2009, Department of Psychology, Utah State University, pers. comm.), and matching has been explored in a territorial species in the wild (Houston, 1986). My competitive spatial test originated from observations of a hierarchical social group in natural setting (Menzel, 1974). I believe that understanding the behavior of any species would greatly benefit from the collaboration of ecological and psychological approaches and research methods. Because only when '...behavioral science develops the tools for studying organismic 'events as a whole' in a really adequate fashion, [will] the old controversies between laboratory versus field, experiment versus observation, and various 'schools' of behavior theory truly fade in to oblivion' (Menzel, 1974, p149).

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CURRICULUM VITAE

Lynne B. Gilbert-Norton
(October 2009)

CAREER OBJECTIVE

To be certified as a CAAB and provide a behavioral consultancy service, specializing in canid behavior. Special areas of interest: application of scientific theory and behavioral analytical techniques to provide applicable solutions to behavioral problems.

EDUCATION

BSc in Psychology, University of Plymouth, Devon, UK. (7/02) Emphasis on social, behavioral, cognitive and physiological approaches with specialization in captive avian foraging behavior, 1st Class Honors. MSc in Psychology, University of Exeter, Devon, UK. (7/04) Emphasis on canid ecology and cognition, Distinction. PhD in Wildlife Biology, Utah State University, Logan, Utah (expected 12/09) Grad GPA: 3.96. Emphasis on canid foraging behavior and cognition. Dissertation research conducted at the National Wildlife Research Center's Predator Ecology Facility in Millville, Utah.

EXPERIENCE

RESEARCH ASSISTANT, Utah State University and USDA, Logan, Utah. (2005-present).

Generation of innovative and sophisticated computer-based lab experiments to provide applicable behavioral solutions to predator management problems.

Unique operant and positive reinforcement training of canids for behavioral research. Successful collaboration on research projects and publications with USDA biologists, academic colleagues and graduate students. Initiated links between US and UK research institutions. Scientific publishing and public speaking experience. Extensive and proficient use of SPSS and SAS statistical packages, MED-PC and NOLDUS Observer, Microsoft Office: Word, Excel and Powerpoint. Ability with GIS: ArcView v.8.

BUSINESS MANAGER, Smart Art, Bristol, UK

GRAPHIC DESIGNER, the Artwork Factory, Bournemouth, UK and Dorset County Council, Ringwood, UK. (1988 – 1994).

Generation and management of media business with progressive expansion of corporate client base. Innovative design of both independent and collaborative marketing projects from initial concept to finished production.

PRESENTATIONS AND PUBLICATIONS

Gilbert-Norton, L., Shahan, T. A., and Shivik, J.A. (2009). Coyotes (*Canis latrans*) and the matching law. Behavioural Processes, 82, 178-183.

Gilbert-Norton, L., Leaver, L.A., and Shivik, J.A. (2009). The effect of randomly altering the time and location of feeding on the behavior of captive coyotes *(Canis latrans)*. Applied Animal Behaviour Science, doi:10.1016/j.applanim.2009.06.007

Gilbert-Norton, L., and Shivik, J.A. (2008). Matching: How coyotes *(Canis latrans)* track resources in a stochastic environment. 45th Annual Meeting of Animal Behavior Society, Snowbird, Utah.

Gilbert-Norton, L., and Shivik, J.A. (2005). Coyotes *(Canis latrans)*, voice of the wilderness. Presentation at Utah State University 8th Annual Graduate Symposium, Logan, Utah.

Gilbert-Norton, L. and Gee. P. (2005). Captive birds and contrafreeloading: the choice to work. Presentation at the 7th International Conference of Environment Enrichment, Columbia University, New York.

Gilbert-Norton, L., Jule, K., Richards, G., and Goto, K. (2004). Social structure of pony *(Equus caballus)* mares in an all female herd on Lundy: analysis of dominance relationship and preferred associate. Lundy Field Society, Annual Report, 54, p71-88.

Gilbert-Norton, L., and Gee. P. (2002). Captive birds and contrafreeloading: the choice to work. Presentation at the South West Undergraduate Conference, University of Plymouth, United Kingdom. 2002.

PUBLICATIONS IN PREPARATION

Gilbert-Norton, L., and Shivik, J.A. (2009). Will a simulated territory boundary prevent coyote intrusion? The Journal of Wildlife Management.

Gilbert-Norton, L. (2009). Brain or brawn: the foraging strategies of captive coyotes (*Canis latrans*) and the effect of dominance hierarchy on foraging behavior. Behavioural Processes

Gilbert-Norton, L., Wilson, R. R., Stevens, J.R., and Beard, K.H. (2009). Corridors increase movement: A meta-analytical review. Conservation Biology (in review)

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Travel Grant Graduate Student Senate, Utah State University	(2008)	$ 300
Travel Grant Graduate Student Senate, Utah State University	(2005)	$ 300
University of Exeter, Masters Degree Scholarship	(2003)	£1500
Richard Stapley Trust Fund	(2003)	£ 500

INTERESTS AND EXPERIENCE

Dog handling, training and UK competition: obedience, flyball and agility

Wildlife capture and handling certification: chemical and physical immobilization, biological sampling, euthanasia and field necropsy of canid and felid predators. Assisted helicopter capture, immobilization, biological sampling, and deployment of GPS collars on coyotes in Valles Caldera National Preserve, New Mexico. Coordinator of Inner City Youth Sports Project, UK. Committee Member of University of Plymouth Student Union Sports and Societies, UK. Trans-Atlantic ocean yacht delivery. National yacht and dinghy racing (UK and Europe). Yachtmaster Navigation, Coastal Skipper and PADI Open Water Diver certifications.