Behavioural Processes 82 (2009) 178–183

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Coyotes (*Canis latrans*) and the matching law

Lynne B. Gilbert-Norton[a,*], Timothy A. Shahan[b], John A. Shivik[c]

[a] Department of Wildland Resources, 2810 Old Main Hill, Utah State University, Logan, UT 84322, United States
[b] Department of Psychology, 2810 Old Main Hill, Utah State University, Logan, UT 84322, United States
[c] USDA Wildlife Services National Wildlife Research Center, 2810 Old Main Hill, Utah State University, Logan, UT 84322, United States

ARTICLE INFO

Article history:
Received 11 March 2009
Received in revised form 10 June 2009
Accepted 13 June 2009

Keywords:
Behavioral flexibility
Coyotes
Canis latrans
Foraging strategy
Matching law
Resource tracking

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. We tested eight wild-born, captive coyotes individually on an operant two-choice test using concurrent variable interval (VI) schedules. We held the overall rate of reinforcement constant but manipulated the ratio of reinforcement available from the two choices. We 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. We 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

* Corresponding author. Tel.: +1 435 881 9619.
E-mail address: lgilbertnorton@gmail.com (L.B. Gilbert-Norton).

0376-6357/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.beproc.2009.06.005

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, we 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, we 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 we 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. We 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 × 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 × 15 cm^2 wooden box, and a 1 cm × 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, USA), 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, USA). 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, USA).

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). We 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 we 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. We 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 ($T_L/[T_L + T_R]$) across sessions as a function of the VI condition was plotted on a graph for each subject (Fig. 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 ≤.05 percent.

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

$$\log\left(\frac{T_1}{T_2}\right) = a\log\left(\frac{R_1}{R_2}\right) + \log b \quad (1)$$

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.

We 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. We used t-tests to analyze if coyote sensitivity in changes of relative