

The Canadian Field-Naturalist

Volume 120, Number 3

July–September 2006

An Ethogram Developed on Captive Eastern Coyotes *Canis latrans*

JONATHAN G. WAY¹, DEAN-LORENZ M. SZUMYLO², and ERIC G. STRAUSS³

¹Boston College, Environmental Studies Program and Lynch School of Education, Higgins Hall, Chestnut Hill, Massachusetts 02467 USA; e-mail: jw9802@yahoo.com

²Urban Ecology Institute and Environmental Studies Program, Higgins Hall, Chestnut Hill, Massachusetts 02467 USA

³Boston College, Biology Department and Urban Ecology Institute, Higgins Hall, Chestnut Hill, Massachusetts 02467 USA; e-mail: strausse@bc.edu

⁴Present address: 64 Cranberry Road, Marstons Mills, Massachusetts 02648 USA; Corresponding author: e-mail: szumylo@bc.edu

Way, Jonathan G., Dean-Lorenz M. Szumylo, and Eric G. Strauss. 2006. An ethogram developed on captive eastern Coyotes *Canis latrans*. *Canadian Field-Naturalist* 120(3): 263-288.

We studied capture Eastern Coyotes (*Canis latrans*) from 27-585 days of age and compiled an ethogram on them. A total of 72247 15-sec samples were taken, amounting to 301 h of field time varying between 59.4–61.3 h per Coyote. A total of 540 behavioral patterns was observed amongst the 16 behaviour categories ranging from 9 (miscellaneous) to 72 (explore/investigate) action patterns per parent category. The 16 parent categories that we believed best described and appropriately sorted the behavioural actions were resting, sitting, sitting1, sitting2, standing, traveling, explore/investigating, hunting, feeding, infantile, greeting, self play, play initiating, playing, agonistic, and miscellaneous. Exploring accounted for >31% of all of the behaviours observed with resting and sitting (combined), standing, traveling, and play as categories decreasing in order of most to least frequent. Despite some omissions in our ethogram and drift associated with its ongoing development, we believe that the large amount of data collected made it rigorous enough to be a useful guide for the species. We argue that although future research will no doubt add to and/or modify components of it, its ease of use in the field (in captivity or in the wild) and it being the first complete ethogram described for the species, make it a useful tool for future researchers.

Key Words: canid, *Canis latrans*, eastern Coyote, ethogram, behavioural study.

The concept of an ethogram, also called action system (Makkink 1936), behavioural inventory (Bekoff 1972a, 1978), or behaviour pattern (Scott and Fuller 1965), is a durable tool for analyzing vertebrate behaviour and dates back to Jennings (1906), Makkink (1936), Tinbergen (1959), and Lorenz (1971). Although there have been direct observation behavioural studies of Coyotes (*Canis latrans*) in captivity (Snow 1967; Silver and Silver 1969; Bekoff 1972a, 1978; Parks 1979; Ryon 1986) and in the wild (Camenzind 1978; Bekoff and Wells 1981; Gese et al. 1996), there has yet to be a standardized and complete ethogram published for the species. Except for Goodmann and Klinghammer's (1990) non-peer reviewed but detailed manual which presents a Wolf (*Canis lupus*) ethogram and Scott and Fuller's (1965) ethogram on Domestic Dogs (*Canis familiaris*) (which they compared with literature on Wolves, Coyotes and Red Foxes [*Vulpes vulpes*]), we could not find any other study that described a full behavioural repertoire of any other of the approximately 35 canid species (Ewer 1973; Wozencraft 1989). Most studies examining behavioural data have focused on specific time periods (e.g., young pups/behavioural development – Bekoff 1972a, 1978, 1989), specific

actions (e.g., social interactions – Fox 1970; Bekoff 1974; Zimen 1982), lumping behaviours into general categories (Silver and Silver 1969; Parks 1979; Gese et al. 1996), or describing many behavioural patterns but providing no summary or chart showing a complete ethogram (Mech 1970; Lehner 1978). Schleidt et al. (1984) termed these "partial ethograms" and stated the importance of publishing complete ethograms on as many species as possible. In addition, Macdonald et al. (2000) underscored the significance of developing ethograms on different species by stating that without one, meaning is not fixed. As such, ethograms are vital reference material for assessing a study's conclusions (Macdonald et al. 2000).

The objective of this paper is to describe, in detail, the full range of behavioural acts that we have observed in a captive group of five Eastern Coyotes. This ethogram is intended to be: (1) reader-friendly in format and applied and used in future direct observation behavioural studies of wild and captive Coyotes; and (2) compared with ethograms of closely related species (e.g., Wolves, Jackals [*Canis sp.*] and foxes) and taxa (e.g., ursids, procyonids, and mustelids: Ewer 1973).

Methods

On 12 April 2002, five (2 M; 3 F) of an original litter of nine (3 M; 6 F) estimated 25 day old (Parks 1979), wild-born sibling Coyote pups were removed from under a shed in a residential area in Falmouth (Cape Cod), Massachusetts, and were reared at JGW's house (note: the other four pups [1M; 3F] were placed back underneath the shed for the wild parents to raise). The five Coyotes taken into captivity were contained within a 53 m² area both inside and outside of JGW's house until 13 May 2002, when the Coyotes were transferred to a 16 m² quarantine facility for one month at the Franklin Park Zoo, Boston, Massachusetts. On 13 June 2002 the five Coyotes were moved to their permanent 403 m² public viewable exhibit at the Stone Zoo located in Stoneham, Massachusetts, and remained there for the duration of this study until late October 2003 – pup age 585 days). We chose the endpoint of our study as the last day of data collection prior to the Coyotes being permanently separated due to intrapack aggression (Late and Trans [See Table 1] were removed). The area of their exhibit was described by Frank (1987) as a suitable size for a long-term study of canid behaviour. Although the Coyotes were hand-raised, we made no attempt to interfere with or discipline their activities and therefore gave the Coyotes free access, at all times, to their exhibit/living facilities. The Coyotes were provided with puppy milk (Esbilac, PetAg, Inc., Hampshire, Illinois) via bottle or bowl up until 15 May and were given access to water and dry dog chow (commercially available dog foods until March 2003 then Mazuri exotic canine chow/diet [PMI Nutrition International, LLC., Brentwood, Missouri] thereafter) at all times. They were group fed (i.e., all five at once) 0.75 – 1.6 kg (varying with their age) of Nebraska Brand chopped frozen canine meat (Central Nebraska Packing Co., North Platte, Nebraska) mixed with dog chow on a daily basis and were given frozen or thawed laboratory rats, guinea pigs and mice (donated from a rodent breeding facility), and/or bones 2-4 times per week. Within their exhibit, the Coyotes commonly hunted (at least 1 prey item 2-3 times daily) and captured (about 1-2 prey items per week) Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), Chipmunks (*Tamias striatus*), Brown/Norway Rats (*Rattus norvegicus*), Meadow Voles (*Microtus pennsylvanicus*), and Gray Squirrels (*Sciurus carolinensis*), but did not appear to eat much or any of these prey items. Care and use of animal subjects was approved by Zoo New England's Institutional Animal Use and Care Committee (letter dated 23 January 2002 to JGW), by Boston College's Institutional Animal Care and Use Committee Protocol Number 01-03, and by the Massachusetts Division of Fisheries and Wildlife Permit #052.02LP.

We developed an ethogram that noted basic behavioural patterns (Scott and Fuller 1965; Bekoff 1972a, 1972b, 1978; Parks 1979). To avoid influencing Coy-

ote behaviour with different observers only JGW interacted with and conducted activity budgets on them. Using this technique, we acknowledge that we did not have interobserver reliability as described by Bekoff (1974) but the large amount of data collected attempted to offset intraobserver reliability. We used focal individual animal sampling (i.e., one Coyote per 30 min bout of data collection), took instantaneous point or scan samples (Martin and Bateson 1986; Macdonald et al. 2000) every 15 sec for 30 min on the target Coyote, recorded the date, time, and weather before each observation bout took place, and noted important contextual information in between each 15 sec sampling period. By using frequent (i.e., every 15 sec) instantaneous samples, we tried to obtain an accurate approximation from continuous recording (Martin and Bateson 1986). Thus, 120 samples per 30 min behavioural bout on a Coyote were ideally recovered. However, there were two reasons why we occasionally did not obtain 120 samples per bout: (1) a Coyote was momentarily out of sight during a particular 15 sec sampling period (usually this happened at most, once per 30 min bout); and (2) we had to stop a sampling bout earlier (e.g., rain, darkness, or some kind of disturbance that forced JGW to abandon an activity budget). We randomly chose which Coyote to conduct observations on before entering the field but attempted to evenly sample all Coyotes (i.e., each Coyote was scored every fifth time) during the study. We typically recorded behavioural data about 5 days/week and took between 1 and 4 (usually 1-2) 30 min behavioural bouts/day during daylight hours. Behaviours were also recorded on digital still and videocameras and 35-mm film cameras weekly for the duration of the juvenile period of the pups (Parks 1979) then *ad lib* after pups reached adulthood (one yr of age – Bekoff and Jamieson 1975). We conducted most of the behavioural bouts during early to mid-morning (ca. 07:00-11:00 h) or between late-afternoon to early-evening hours (ca. 16:00-19:30 h); these were the times with the fewest number of people around the zoo (the zoo opened at 10:00 and closed at 16:30-1800 h depending on the time of year). Because the Coyotes were habituated to and did not react negatively to JGW's presence, he followed them around the exhibit similar to the description of Goodall's (1986) "follows" of wild Chimpanzees (*Pan troglodytes*) in Gombe, Tanzania. JGW made an effort not to influence the movements and/or behaviour of Coyotes by minimizing his movement in the exhibit. This was especially important because the Coyotes would follow him around the exhibit when he interacted with them but would generally ignore him when he was standing erect and writing on a clipboard (J. Way, unpublished data). "Following" was a necessary technique to use on the Coyotes because there was not a single observation spot outside the exhibit where the Coyotes could reliably be seen all of the time (i.e., many times trees and shrubs concealed the Coyote under observa-

tion). B
contact
samplin
behavio
to the C
ample, t
on the p
at staff
of the p
or appr
did not
interact
were no
their ac
presenc
walked
otes shi
of peop
Coyotes
tempted
size of
We e
First, w
Then w
ilar beh
frequen
we ente
(for eac
Due to
quences
and con
creation
subcate
ler (196
behavio
(1984),
Fuller (1
ity obse
In ou
the beh
general
an activ
ities. N
groupe
play, w
of a sol
believe
behavio
ting2, s
ing, fee
ing, pla
instanc
working
tions) w
we coul
what th
when a
tially of
its pare

tion). Besides the senior author's presence, other human contact was kept to a minimum before and after each sampling period to avoid humans affecting Coyote behaviour. Context was a critical variable with respect to the Coyotes' response to human behaviour. For example, they generally ignored people (unless very loud) on the public path but would intently watch and/or bark at staff members that were behind (i.e., the opposite side of the public path that was off-limits to non-employees) or approaching their exhibit. Accordingly, zookeepers did not enter the exhibit to feed the Coyotes when JGW interacted with them. Despite these precautions there were no doubt many instances where Coyotes changed their activity in response to a person's (public or staff) presence – sometimes even when a person simply walked by their exhibit area. Similar instances of Coyotes shifting their behaviour because of the presence of people have been documented in areas where wild Coyotes inhabit urbanized areas (Way 2001). We attempted to mitigate these factors by increasing the total size of the pool of sample bouts.

We entered all of the data into an excel spreadsheet. First, we entered the raw data into the spreadsheet. Then we alphabetized that data in order to group similar behaviours for each budget. Next we summed the frequency of each distinct behaviour observed. Finally we entered those summed values into a separate file (for each Coyote) that had our developing ethogram. Due to the large amount of data and behaviour sequences in our ethogram (Table 1), properly entering and compiling data were critical parts of this ethogram's creation. Behavioural actions or patterns (denoted as subcategories in Table 1), as defined by Scott and Fuller (1965), were grouped into "parent" categories, or behavioural complexes as described by Schleidt et al. (1984), or behavioural systems, as noted by Scott and Fuller (1965), based on motivational context and activity observed (Parks 1979).

In our ethogram, we organized the categories and the behavioural actions within each of the complexes generally on a scale from less to more active or intense an activity, then from solitary to group-oriented activities. Notable exceptions were feeding, which was grouped next to hunting for obvious reasons, and self play, which was grouped close to social play but was of a solitary endeavor. The 16 parent categories that we believed best described and appropriately sorted the behavioural actions were resting, sitting, sitting1, sitting2, standing, traveling, explore/investigating, hunting, feeding, infantile, greeting, self play, play initiating, playing, agonistic, and miscellaneous. There were instances (especially early in our study when we were working on differentiating different behavioural actions) where a Coyote was engaged in an activity but we could not describe, other than in a general category, what the Coyote was doing. When this occurred (e.g., when a Coyote was behind trees and was only partially observed) we simply classified the behaviour in its parent category, so that we could at least provide a

coarse description of a Coyote's behaviour at a given 15 sec interval (Table 1).

We calculated the percentage that each behaviour pattern was observed and added all within a parent category to examine the relative frequency that each behavioural complex/system occurred (Table 1). In addition, we used the ages (in days) of the Coyotes to denote the first time that each behaviour was observed, with day 27 (14 April 2002) being the beginning point – i.e., the date we first did an ethogram on a Coyote. We want to stress here that although we report both the percentage of each behaviour observed and the age that each behaviour was first recorded for comparison purposes (Table 1), the purpose of this manuscript is to describe the ethogram that we developed. We will more thoroughly analyze these data in future manuscripts.

Results and Discussion

The ethogram that we developed on the Eastern Coyote is presented as Table 1. A total of 72247 15-sec samples were taken amounting to 301 h of field time, varying between 59.4-61.3 h per Coyote. A total of 540 behavioural patterns were observed amongst the 16 behaviour categories ranging from 9 (Miscellaneous) to 72 (Explore and Investigate) acts per parent category (Table 1; Figures 1-25).

Resting (RE) occurred when a Coyote was lying down with its head on the ground. Sitting (SIT) was classified as sitting down either on rear or all four legs; this category was subsequently divided into sit1 (SIT1) and 2 (SIT2). SIT1 was noted when a Coyote was sitting down on all four legs; in other words, it was almost lying down but it had its head up. SIT2 was when a Coyote sat on its rear legs but its front legs were up in standing-like position. It was difficult to always reliably determine what the motivation was for a Coyote in the aforementioned positions. For example, a Coyote frequently sat in SIT1 position to sniff the ground. Because the animal was in a resting-like position we believed that it was important to separate these activities from explore/investigate activities where the animal was active (i.e., at least in a standing position). Similarly, it was sometimes difficult to understand the motivational context when an animal was just standing (ST) and performing routine activities. Thus, we developed a category for just standing activities.

Any of these categories could always be lumped together or put into different or new categories if the need arose – but the opposite cannot occur if the behaviours are not split into discrete actions at the outset (Bekoff 1972b). For example, SIT1 Alt and SIT1 Alt Pt were very similar except for the panting involved. Although we could have easily combined these categories we thought that keeping them separated would allow us to potentially analyze this difference in the future (e.g., the level of panting on hot versus cold days).

Resting and sitting behaviours were observed quite frequently and accounted for >23% of all of the ethogram despite the Coyotes generally being much more

TABLE 1. Ethogram on eastern Coyotes: "Age" refers to the age of the Coyotes (in days) when a behavior was first observed (data collection began on day 27 for Lupe and day 33 for others); "%" refers to the percentage of each behavioral pattern observed relative to the total number of samples (spot fixes) taken; a zero signifies that the behavior was either never recorded for a Coyote(s) or was <0.0049% (i.e., not rounded up to 0.01%); and letters in parentheses refer to abbreviations from the previous word(s) or phrase(s).

Parent Subcategory	Description	Age		%		Age		%		Age		%	
		All 5	All 5	All 5	All 5	Cane	Late	Lupe	Trans	Cane	Late	Lupe	Trans
Resting (RE)	Coyote lying down with its head on the ground	27	1.49	39	34	34	34	33	1.18	2.08	2.11	1.36	0.74
Sniff (sn)	Sniffing ground or air while lying	54	0.03	54	0	67	147	55	0.12	0.00	0.01	0.01	0.01
Alert (alt)	Eyes open and alert (focused) while lying	39	0.88	39	43	48	58	48	1.26	1.19	0.48	0.92	0.54
Pant (pt)	Panting with no comment on eye activity	99	0.01	0	0	108	99	0	0.00	0.00	0.05	0.01	0.00
Alt pt	Alert and panting while lying	99	0.02	149	464	0	99	0	0.01	0.01	0.00	0.07	0.00
Yawn	Yawning while lying	121	0.00	0	121	0	0	0	0.00	0.01	0.00	0.00	0.00
Lick self	Licking itself, usually paws while lying	40	0.06	40	50	57	58	43	0.13	0.05	0.05	0.03	0.05
Stretch	Lying and stretch body	75	0.04	122	100	147	75	85	0.04	0.03	0.03	0.07	0.04
Rub head	Rubbing head against object (e.g., tree) or the ground while lying down	94	0.02	148	0	394	97	94	0.01	0.00	0.01	0.03	0.04
Scratch	Lying down and scratching part of body	38	0.04	38	47	53	42	39	0.08	0.02	0.01	0.06	0.03
Eyes (I) open	Eyes open but not focused on anything	49	0.79	57	58	60	58	49	0.78	0.76	0.96	0.65	0.78
I open & stretch	Stretching while staring and lying down	150	0.00	0	0	150	0	0	0.00	0.00	0.01	0.00	0.00
I open pt	Panting while eyes are open	108	0.03	0	0	108	147	0	0.00	0.00	0.10	0.05	0.00
Move head I open	Moving head quickly while lying down; eyes open in the process	542	0.00	0	542	0	0	0	0.00	0.01	0.00	0.00	0.00
I closed (cl)	Eyes closed while lying; does not appear to be sleeping	39	0.89	39	58	67	58	73	0.82	0.76	0.94	0.96	0.97
I cl pt	Same as above with panting	108	0.08	122	108	108	147	149	0.01	0.01	0.21	0.13	0.04
I cl licking motion	Making a licking motion while eyes are closed	541	0.00	0	0	541	0	0	0.00	0.00	0.01	0.00	0.00
I cl & scratch	Scratching self while eyes are closed	148	0.00	148	0	0	0	0	0.01	0.00	0.00	0.00	0.00
I cl & stretch	Stretching while eyes are closed	121	0.00	148	121	177	0	0	0.01	0.01	0.01	0.00	0.00
Blink	Blinking eyes while lying	123	0.26	148	161	157	123	143	0.27	0.11	0.20	0.37	0.34
Blink I pt	Blinking eyes while lying down and panting	121	0.01	0	121	477	464	0	0.00	0.01	0.01	0.01	0.00
Doze	Head nodding back and forth and eyes blinking while lying	75	0.33	82	86	98	87	75	1.06	0.19	0.09	0.22	0.09
Doze pt	Same as above while panting	108	0.01	149	108	0	135	0	0.01	0.01	0.00	0.01	0.00
Roll (to side)	Side-to-side maneuvering while lying down	150	0.00	0	0	150	0	0	0.00	0.00	0.01	0.00	0.00
Twitch I	Quick flickering of eyes while lying down and sleeping	35	0.02	106	0	150	0	35	0.07	0.00	0.03	0.00	0.01
Sleep (SI)	Eyes closed for >15 sec	42	4.41	57	42	49	42	62	4.15	5.36	5.43	5.10	2.00
SI pt	Sleeping and panting while lying	108	0.14	149	108	394	111	0	0.01	0.05	0.01	0.14	0.00
Whine	Whining while resting; eyes open	43	0.00	0	0	43	0	0	0.00	0.00	0.01	0.00	0.00
RE	Total percentage for RE	N = 28	9.58						10.02	11.17	10.79	10.21	5.66
Sitting (SIT)	Sitting down either on rear or all 4 legs; subsequently divided into sit 1 and 2	34	0.02	0	0	34	34	0	0.00	0.00	0.04	0.05	0.00
Doze	Head nodding side to side while sitting	177	0.00	0	0	177	0	0	0.00	0.00	0.01	0.00	0.00
Alt	Eyes open and alert while sitting	60	0.23	64	62	60	60	60	0.10	0.13	0.36	0.35	0.22
Pant I open	Panting while eyes are open but not focused on anything	94	0.00	0	0	0	0	94	0.00	0.00	0.00	0.00	0.01
Sn	Sniffing object while sitting	67	0.14	75	73	67	67	68	0.27	0.09	0.08	0.16	0.08
Sn & alt	Sniffing (usually the air) while alert	85	0.03	85	134	150	111	185	0.09	0.04	0.01	0.01	0.01
Alt pt	Alert and panting while sitting	73	0.00	73	0	0	0	0	0.01	0.00	0.00	0.00	0.00

SIT	N = 21	0.95	0.71	0.45	1.01	1.69	0.89						
Sitting (SIT)		34	0.02	0	0	34	34	0	0.00	0.00	0.04	0.05	0.00
sit1 and 2		177	0.00	0	0	177	0	0	0.00	0.00	0.01	0.00	0.00
Head nodding side to side while sitting		60	0.23	64	62	60	60	60	0.10	0.13	0.36	0.35	0.22
Eyes open and alert while sitting		94	0.00	0	0	0	0	94	0.00	0.00	0.00	0.00	0.01
Panting while eyes are open but not focused on anything		67	0.14	75	73	67	67	68	0.27	0.09	0.08	0.16	0.08
Sniffing object while sitting													
Sn & alt		85	0.03	85	134	150	111	185	0.09	0.04	0.01	0.01	0.01
Alert and panting while sitting		73	0.00	73	0	0	0	0	0.01	0.00	0.00	0.00	0.00
Sniffing something while panting		464	0.00	0	0	0	464	0	0.00	0.00	0.00	0.01	0.00
Whining while sitting		85	0.00	0	0	85	0	0	0.00	0.00	0.01	0.00	0.00
Squeal-like sound done when a more dominant Coyote approached		82	0.00	0	0	0	0	82	0.00	0.00	0.00	0.00	0.01
Licking self while sitting		49	0.02	75	161	0	64	49	0.02	0.01	0.00	0.05	0.01
Sniffing and licking self		77	0.00	0	0	0	77	0	0.00	0.00	0.00	0.01	0.00
Looking around while sitting; not focusing on anything specifically		85	0.00	0	0	0	85	0	0.00	0.00	0.00	0.01	0.00
Quickly moving head while sitting; e.g., the movement between being alert and licking self		64	0.00	0	0	64	0	0	0.00	0.00	0.01	0.00	0.00
Rubbing head against object or ground in a sitting position		94	0.00	0	0	0	94	0	0.00	0.00	0.00	0.00	0.01
Scratch and lick self while sitting		71	0.00	0	71	71	0	0	0.00	0.01	0.01	0.00	0.00
Scratch self while sitting		60	0.04	64	80	60	60	75	0.03	0.01	0.08	0.05	0.03
Stretch		78	0.00	93	0	78	0	0	0.01	0.00	0.01	0.00	0.00
Bite obj		64	0.08	79	80	64	70	81	0.10	0.05	0.07	0.16	0.04
Chewing on an object while sitting		60	0.36	75	62	64	62	60	0.09	0.11	0.30	0.82	0.48
Tug/pull obj		62	0.01	0	0	72	62	0	0.00	0.00	0.02	0.01	0.00
Total percentage for SIT:			0.95						0.71	0.45	1.01	1.69	0.89
SIT1		65	0.09	65	96	67	93	97	0.05	0.11	0.10	0.17	0.04
Sleep		177	0.00	0	0	177	324	0	0.00	0.00	0.01	0.01	0.00
Doze		169	0.40	324	179	171	169	345	0.18	0.25	0.20	0.53	0.83
Doze pant (pt)		394	0.01	0	464	394	0	0	0.00	0.01	0.02	0.00	0.00
I closed (cl)		292	0.04	0	547	292	514	373	0.00	0.01	0.08	0.01	0.08
I cl pt		108	0.03	0	108	464	476	0	0.00	0.00	0.08	0.07	0.01
I cl lick motion		527	0.00	0	547	0	0	527	0.00	0.01	0.00	0.00	0.01
I blinking		58	0.06	324	337	311	58	445	0.07	0.03	0.03	0.11	0.08
Blink I pt		465	0.01	0	0	0	0	465	0.00	0.00	0.00	0.00	0.04
I open		102	0.06	102	362	311	445	103	0.08	0.01	0.06	0.03	0.11
I open pt		98	0.02	98	464	100	106	465	0.01	0.01	0.04	0.03	0.01
Yawn		37	0.07	126	134	98	37	185	0.04	0.06	0.07	0.08	0.09
Yawn pt		339	0.00	0	0	339	0	0	0.00	0.00	0.01	0.00	0.00
Cough		486	0.00	0	0	0	486	0	0.00	0.00	0.00	0.01	0.00
Sneeze		526	0.00	0	0	0	526	0	0.00	0.00	0.00	0.01	0.00
Sniff (sn)		57	1.16	57	80	78	85	62	1.36	0.67	0.72	2.20	0.80
Sn pt		464	0.01	0	0	466	464	465	0.00	0.00	0.01	0.03	0.01
Sn growl		174	0.00	0	0	0	174	0	0.00	0.00	0.00	0.01	0.00
Sn self		145	0.00	145	0	0	0	0	0.01	0.00	0.00	0.00	0.00
Sn coy		122	0.05	122	0	0	514	0	0.04	0.00	0.00	0.21	0.00
Alert (alt)		37	4.95	38	37	40	37	39	4.59	4.10	2.90	7.27	5.83
Alt pt		94	0.78	102	108	100	106	94	0.65	0.31	0.89	1.18	0.85

TABLE 1. Ethogram on eastern Coyotes (*continued*)

Parent Subcategory	Description	Age		%																	
		All 5	All 5	Cane	Caon	Late	Lupe	Trans	Cane	Caon	Late	Lupe	Trans								
Alt yawn	Focused on something while yawning	134	0.00	0	134	339	0	368	0.00	0.01	0.01	0.00	0.01								
Alt & stretch	Focused on something while alert	119	0.01	126	119	177	0	0	0.01	0.01	0.01	0.00	0.00								
Alt & sn	Sniffing something (usually air) while focused on something	135	0.01	135	136	0	163	156	0.02	0.01	0.00	0.01	0.01								
Alt wag tail	Wag tail while sitting alert; a sign of excitement	559	0.00	559	0	0	0	0	0.01	0.00	0.00	0.00	0.00								
Lick object	Licking object (ground, tree/bush, toy, rock)	60	0.27	60	62	60	60	60	0.18	0.13	0.26	0.52	0.28								
Lick self	Licking self	62	1.17	82	80	72	80	62	1.40	1.01	0.94	1.26	1.22								
Alt licking motion	Making a licking motion with tongue while alert	554	0.00	0	0	0	554	0	0.00	0.00	0.00	0.01	0.00								
Lick self pt	Licking self while panting	464	0.00	0	0	0	464	0	0.00	0.00	0.00	0.01	0.00								
Sn & lick	Sniffing and licking an object	137	0.00	137	0	0	0	0	0.01	0.00	0.00	0.00	0.00								
Open mouth	Opening mouth but not yawning	339	0.01	507	491	339	0	0	0.01	0.01	0.01	0.00	0.00								
Chew obj	Chewing an object	48	1.77	52	48	49	77	49	1.14	1.79	1.81	2.79	1.30								
Alt chew obj	Chewing something while sitting (sit1) alert	105	0.01	150	0	105	0	136	0.01	0.00	0.03	0.00	0.01								
Sn & chew	Sniffing and chewing an object while in sit1	134	0.03	146	134	0	0	0	0.01	0.16	0.00	0.00	0.00								
Bite obj	Biting an object while sitting	59	0.09	96	108	59	93	59	0.16	0.01	0.15	0.09	0.04								
Bite at other	Bite at other; not Ag because there was no growl or other sign of Ag	99	0.01	106	485	108	99	0	0.03	0.01	0.01	0.02	0.00								
Bite other	Same as above but actually grabbing hold of another Coyote	42	0.01	42	0	0	97	0	0.02	0.00	0.00	0.03	0.00								
Sn & bite	Sniffing then biting something while sitting (e.g., grass/twigs)	100	0.01	0	100	0	0	0	0.00	0.04	0.00	0.00	0.00								
Stretch	Stretching while in sit1 position	118	0.02	126	542	118	133	0	0.01	0.01	0.01	0.04	0.00								
Stretch & yawn	Same as above with yawning	123	0.00	0	0	0	123	0	0.00	0.00	0.00	0.01	0.00								
Stretch chew obj	Stretch and chewing something while in sit1 position	137	0.00	0	0	137	0	0	0.00	0.00	0.01	0.00	0.00								
Stretch self	Stretching self in sit1 position	93	0.06	122	100	110	93	143	0.05	0.05	0.09	0.06	0.04								
Scratch lick self	Scratching and licking self in sit1 position	49	0.00	49	0	0	0	55	0.01	0.00	0.00	0.00	0.01								
Rub head	Rubbing head against ground or an object while sitting	150	0.01	150	0	157	158	415	0.01	0.00	0.01	0.01	0.02								
Head shake	Shaking head (e.g., if wet) while sitting	59	0.03	59	536	96	80	527	0.03	0.01	0.03	0.07	0.02								
Paw/dig	Paw or dig at ground while sitting	96	0.01	114	105	96	99	0	0.01	0.01	0.02	0.01	0.00								
Sn & paw obj	Sniffing and pawing at something while sitting	408	0.00	408	0	0	0	0	0.01	0.00	0.00	0.00	0.00								
Pull obj	Pulling something with mouth while sitting	59	0.00	59	0	0	0	0	0.02	0.00	0.00	0.00	0.00								
Look ar	Not focused on any object; moving head to see different things	49	0.59	59	59	74	73	49	0.62	0.22	0.41	0.78	0.93								
Look ar pt	Same as above while panting	108	0.07	490	464	108	410	410	0.03	0.03	0.11	0.03	0.13								
Whine	Whining/whimpering while sitting1	43	0.00	0	48	0	43	0	0.00	0.01	0.00	0.01	0.00								
Swat flies	Swatting bugs out of annoyance (e.g. not self play) while sitting	149	0.00	149	0	0	0	0	0.01	0.00	0.00	0.00	0.00								
Woof	Sit1 position and alertly making a warning woof-like call	85	0.00	0	0	85	0	0	0.00	0.00	0.01	0.00	0.00								
SIT1 N = 54	Total percentage for SIT1:	11.96		10.89						9.10						9.14		17.73		12.78	
SIT2	Sitting on back legs (rear haunches); front legs up in standing-like position	88	0.05	102	88	98	115	140	0.04	0.08	0.04	0.05	0.02								
Sniff	Sniffing in sit2 position	96	0.04	146	109	96	97	99	0.02	0.01	0.01	0.05	0.11								
Pant (pt)	Panting but not focused on anything (eyes open) while sitting	118	0.00	0	0	339	147	118	0.00	0.00	0.01	0.01	0.01								
Alt	Focused on something while sitting	96	0.67	96	105	100	97	97	0.31	0.64	0.59	0.71	1.12								

SIT1	N = 54	Total percentage tot. SIT1	88	0.05	102	88	98	115	140	0.04	0.08	0.04	0.05	0.02
SIT2		Sitting on back legs (rear haunches); front legs up in standing-like position	96	0.04	146	109	96	97	99	0.02	0.01	0.01	0.05	0.11
		Sniffing in sit2 position	118	0.00	0	0	339	147	118	0.00	0.00	0.01	0.01	0.01
		Panting but not focused on anything (eyes open) while sitting	96	0.67	96	105	100	97	97	0.31	0.64	0.59	0.71	1.12
		Focused on something while sitting												
		Same as above while panting	97	0.05	150	513	407	106	97	0.05	0.03	0.06	0.07	0.03
		Sniffing something (usually air) while alert in sit2 position	214	0.00	0	0	0	214	0	0.00	0.00	0.00	0.01	0.00
		Sitting and not focused on anything but eyes open	102	0.00	102	0	0	0	0	0.02	0.00	0.00	0.00	0.00
		Same as above while panting	551	0.00	0	551	0	0	0	0.00	0.01	0.00	0.00	0.00
		Licking self while sitting	103	0.16	114	134	113	129	103	0.05	0.10	0.13	0.10	0.41
		Licking an object while in sit2 position	99	0.01	102	0	0	99	0	0.01	0.00	0.00	0.02	0.00
		Quickly moving head while sitting	534	0.00	534	551	0	0	0	0.01	0.01	0.00	0.00	0.00
		Biting an object while sitting	97	0.00	0	0	0	99	97	0.00	0.00	0.00	0.01	0.01
		Chewing but not really feeding on something while sitting	99	0.08	146	388	110	120	99	0.05	0.01	0.16	0.13	0.04
		Scratch self; the typical dog-like scratch where a hindleg scratches the rib/shoulder region of body	45	0.13	135	45	108	99	103	0.16	0.08	0.13	0.11	0.18
		Looking around; not focused on a specific object; sometimes exaggerated head movement	97	0.10	332	337	331	97	314	0.10	0.09	0.03	0.04	0.22
		Same as above while panting	413	0.01	469	413	462	486	0	0.02	0.01	0.01	0.01	0.00
		Yawning in sit2 position	267	0.01	0	267	311	376	311	0.00	0.01	0.02	0.01	0.01
		Whining; looking down; not focused on anything in particular	492	0.00	0	0	0	0	492	0.00	0.00	0.00	0.00	0.01
		Giving a warning woof-like call/bark while sit2 position	304	0.00	0	0	304	0	0	0.00	0.00	0.01	0.00	0.00
		Howling in sit2 position	429	0.01	0	0	429	0	0	0.00	0.00	0.05	0.00	0.00
		Lifting head like howling but producing no sound	484	0.00	0	0	484	0	0	0.00	0.00	0.01	0.00	0.00
		Digging while in SIT2 position	519	0.00	0	0	0	519	0	0.00	0.00	0.00	0.01	0.00
		Sniffing and digging while in sit2 position	519	0.00	0	0	0	519	0	0.00	0.00	0.00	0.01	0.00
		Total percentage for sit2:		1.34						0.84	1.09	1.25	1.35	2.16

SIT2	N = 23	Total percentage for sit2:	33	0.42	33	34	34	34	33	0.43	0.33	0.44	0.48	0.45
Standing (ST)		Standing and performing behaviors that could not fit into other categories	301	0.00	0	0	0	0	301	0.00	0.00	0.00	0.00	0.01
Doze		Dozing while in a standing position	344	0.00	0	344	0	0	0	0.00	0.01	0.00	0.00	0.00
Eyes closed		Eyes closed while standing; often done in hot weather	361	0.00	361	0	0	0	396	0.01	0.00	0.00	0.00	0.01
Eyes open		Eyes open but not focused on anything in particular while standing	479	0.00	0	479	497	0	0	0.00	0.01	0.01	0.00	0.00
I open pt		Same as above while panting	466	0.00	0	0	466	0	0	0.00	0.00	0.01	0.00	0.00
Pt I open hd down		Head facing down while standing and panting	301	0.01	0	0	0	0	301	0.00	0.00	0.00	0.00	0.03
Blink		Blinking eyes while standing	174	0.07	272	267	177	174	234	0.06	0.15	0.06	0.04	0.06
Yawn		Yawning while standing	367	0.00	0	367	0	0	555	0.00	0.01	0.00	0.00	0.01
Yawn alt		Yawning while alert and standing	337	0.00	0	337	0	0	0	0.00	0.01	0.00	0.00	0.00
Yawn wag tail		Yawning and wagging tail implying excitement	78	0.01	0	149	561	531	78	0.00	0.01	0.01	0.01	0.01
Cough		Coughing while standing	94	0.01	0	380	108	102	94	0.00	0.01	0.01	0.01	0.04
Pant (pt)		Panting but not really focusing on anything	34	7.70	38	37	40	34	39	8.57	8.76	5.08	7.50	8.58
Alert (alt)		Focusing on something	92	0.75	114	92	100	102	94	0.52	0.95	0.95	0.42	0.92
Alert pant		Alert while panting												
Alert wag tail		Wagging tail while alert, implying some level of excitement; usually around other Coyotes	54	0.14	171	170	528	54	304	0.14	0.20	0.04	0.29	0.06
Alt wag tail pt		Same as above while panting	427	0.02	427	427	0	531	575	0.01	0.01	0.00	0.05	0.01
Alt pt tail up		Tail high while standing alert and panting	297	0.00	0	0	0	0	297	0.00	0.00	0.00	0.00	0.01
Alt tail tucked		Standing alert with tail tucked between legs; sign of submissiveness	582	0.00	0	582	0	0	0	0.00	0.01	0.00	0.00	0.00
Alt whine		Focused on something and whining	316	0.01	0	0	316	0	0	0.00	0.00	0.03	0.00	0.00

TABLE 1. Ethogram on eastern Coyotes (continued)

Parent Subcategory	Description	Age		%		%								
		All 5	All 5	All 5	All 5	Cane	Caon	Late	Lupe	Trans				
Alt whine wag tail	Same as above while wagging tail; Coyote appears anxious, socially related	380	0.00	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
Lick self	Grooming licking self	55	0.60	111	0.62	78	70	55	0	0	0.43	0.92	0.47	0.61
Lick coy	Briefly licking another Coyote but not grooming so not infantile behaviour	72	0.01	527	399	72	299	285	0.01	0.01	0.01	0.01	0.01	0.03
Lick object	Licking an object while standing	65	0.11	65	156	98	186	123	0.06	0.03	0.03	0.03	0.30	0.14
Chew obj	Chewing an object while standing	44	2.78	47	47	47	58	44	2.24	2.33	2.93	2.83	3.59	
Chew alt	Same as above while alert	122	0.01	177	290	122	0	0	0.01	0.01	0.01	0.00	0.00	
Chew wag tail	Chewing something while wagging tail; excitement evident	430	0.00	430	0	0	0	0	0.01	0.00	0.00	0.00	0.00	
Bite obj	Bite at an object, like a branch, while standing	43	0.48	50	45	67	43	45	0.44	0.49	0.35	0.51	0.60	
Bite obj hind legs	Bite at an object while standing on hindlegs	147	0.01	0	147	0	0	0	0.00	0.03	0.00	0.00	0.00	
Hind legs bite coy	Making general (not Ag) bites at another Coyote while standing on hindlegs	390	0.00	0	390	0	0	0	0.00	0.01	0.00	0.00	0.00	
Stretch	Stretching body while standing	59	0.14	59	136	128	77	62	0.07	0.04	0.18	0.29	0.09	
Alt & stretch	Same as above while alert	94	0.00	0	0	0	0	94	0.00	0.00	0.00	0.00	0.01	
Stretch yawn	Yawning while stretching	177	0.01	214	0	177	303	0	0.01	0.00	0.03	0.01	0.00	
Stretch urinate	Stretching and squat-urinating at same time while standing	367	0.00	0	0	0	367	0	0.00	0.00	0.00	0.01	0.00	
Rub body	Rubbing body against an object (fence, tree) in standing position	81	0.18	126	153	134	97	81	0.03	0.09	0.31	0.20	0.25	
Scratch	Scratching self while standing	45	0.02	379	453	134	67	45	0.03	0.04	0.01	0.02	0.02	
Shake body	Shaking body - to dry or get dust off self	37	0.12	38	37	43	45	39	0.13	0.11	0.11	0.12	0.14	
Shake head	Twist or shake just the head and neck	149	0.04	527	528	429	295	149	0.03	0.07	0.06	0.03	0.02	
Paw object	Pawing at something halfheartedly; not really investigating	142	0.00	0	0	0	142	0	0.00	0.00	0.00	0.02	0.00	
Hold object	Pawing at something in mouth while standing	111	0.02	111	143	122	138	136	0.01	0.01	0.02	0.03	0.01	
Drop object	Releasing an object from mouth while standing	338	0.00	0	0	0	499	338	0.00	0.00	0.00	0.01	0.01	
Defecate	Defecating, in a squatting position	37	0.12	44	43	38	37	65	0.16	0.15	0.10	0.08	0.11	
St br	General term for going to bathroom; then divided into urinate and defecate	35	0.01	35	45	44	52	0	0.01	0.01	0.03	0.02	0.00	
Urinate	Urinating by leaning forward or standing	34	0.12	38	37	40	39	39	0.10	0.07	0.04	0.22	0.17	
FLU	Flex leg urination; flexing forward and partially lifting a hindleg	499	0.02	527	499	512	531	505	0.02	0.04	0.02	0.01	0.01	
RLU	Raised leg urination; lifting a hindleg	303	0.00	0	0	0	303	0	0.00	0.00	0.00	0.02	0.00	
Alt hindlegs	Standing alert while on hindlegs (looking like a standing human)	58	0.03	430	73	64	58	112	0.01	0.03	0.02	0.07	0.01	
Over others	Standing over another Coyote but not really looking at anything; no aggression seen - head alertness not noted	34	0.09	39	34	49	38	185	0.29	0.06	0.01	0.07	0.03	
Over others alt	Same as above while focused on something	317	0.04	317	525	402	0	0	0.20	0.01	0.01	0.00	0.00	
Over alt pt	Same as above while panting	512	0.00	0	518	512	0	0	0.00	0.01	0.01	0.00	0.00	
Over coy hd down	Same as above while head is down (not focused on anything)	534	0.00	534	0	0	0	0	0.01	0.00	0.00	0.00	0.00	
Over coy head down pt	Same as above while panting	464	0.01	0	464	512	0	0	0.00	0.01	0.01	0.00	0.00	
Over coy look ar	Same as above while looking around	498	0.01	498	0	0	0	0	0.03	0.00	0.00	0.00	0.00	
Alt body low wag tail	Standing alert with body low while wagging tail; nervous behaviour of submissive Coyotes	380	0.00	0	380	0	0	0	0.00	0.01	0.00	0.00	0.00	
Vomit	Convulsing/throw up while standing	110	0.03	126	0	0	115	110	0.05	0.00	0.00	0.03	0.05	
Sneeze	Sneezing in a standing position	225	0.00	443	0	225	0	532	0.01	0.00	0.01	0.00	0.01	
White	Whining; not really looking around but eyes open	34	0.23	35	34	34	34	34	0.13	0.11	0.38	0.43	0.11	

TABLE 1. Ethogram on eastern Coyotes (*continued*)

Parent Subcategory	Description	Age		Age		Age		Age		Age		Age		Age			
		All 5	%	All 5	%	Caon	Late	Lupe	Trans	Caon	Late	Lupe	Trans	Caon	Late	Lupe	Trans
A wk limp	Approaching a Coyote while walking with a limp	43	0.00	0	43	0	0	0	0	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Trot	Trotting while looking down; not focused on anything; going the equivalent of jogging pace for humans (includes loping and cantering) where left front and right rear legs touch ground at same time, and vice versa	48	1.84	80	77	48	80	48	0	1.93	2.18	1.61	1.28	2.21			
Trot pt	Trotting and panting while looking down	107	0.14	122	174	119	135	107	0	0.10	0.16	0.18	0.11	0.14			
Trot alt	Trotting and focused on something	88	1.49	135	124	88	135	129	0	1.89	1.33	1.70	0.87	1.69			
Trot alt pant	Same as above while panting	394	0.12	413	469	417	410	394	0	0.07	0.03	0.27	0.05	0.18			
Trot tail high	Trotting with tail high; done by a confident, more dominant Coyote	236	0.00	236	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00			
Trot alt tail high	Same as above while alert	250	0.00	0	250	0	0	0	0	0.00	0.01	0.00	0.00	0.00			
Trot wag tail	Wagging tail while trotting; sign of excitement	257	0.01	0	257	0	0	0	0	0.00	0.03	0.00	0.00	0.00			
Trot alt wag tail	Trotting and alert while wagging tail	375	0.01	469	375	550	0	0	0	0.01	0.01	0.01	0.00	0.00			
Trot pt wag tail	Trotting and panting while wagging tail	453	0.00	0	453	0	0	0	0	0.00	0.01	0.00	0.00	0.00			
Trot whine	Trotting and whining; clearly anxious about something	344	0.01	0	344	374	0	0	0	0.00	0.01	0.02	0.00	0.00			
Trot alt whine	Trotting alertly while whining	379	0.00	0	379	0	0	0	0	0.00	0.00	0.02	0.00	0.00			
Trot alt woof	Trotting alertly while barking at something, usually human	235	0.02	0	536	235	341	338	0	0.00	0.01	0.06	0.01	0.01			
Trot tail low	Trotting with tail low; social implications (subordination)	373	0.00	0	373	0	0	0	0	0.00	0.01	0.00	0.00	0.00			
Trot body low	Trotting with whole body low; social subordination	44	0.01	44	373	462	0	44	0	0.01	0.05	0.01	0.00	0.01			
Trot yawn	Trotting and yawning	365	0.00	452	0	365	0	429	0	0.01	0.00	0.01	0.00	0.01			
Trot with obj	Trotting with object in mouth	126	0.06	145	156	150	126	136	0	0.07	0.04	0.11	0.04	0.03			
Gr trot	Trotting as a group (with ≥ 2 others) from one place to another	109	0.02	236	448	365	109	170	0	0.02	0.01	0.01	0.01	0.03			
Trot follow	Trotting and following other Coyote(s)	59	0.11	59	124	74	97	107	0	0.04	0.08	0.17	0.07	0.19			
Trot follow coy pt	Same as above while panting	469	0.01	469	0	497	0	527	0	0.01	0.00	0.02	0.00	0.02			
Trot follow me	Following JGW at a trot while he moves	59	0.00	0	59	0	0	0	0	0.00	0.01	0.00	0.00	0.00			
A trot	Approach human (JGW) or Coyote at a trot	27	0.59	38	34	39	27	33	0	0.67	0.70	0.49	0.45	0.63			
A trot gr	Approach group at a trot	221	0.00	0	221	0	221	0	0	0.00	0.01	0.00	0.01	0.00			
Run	Moving at a fast pace; body stretched out; not focused on anything; all four legs often in the air	33	0.33	33	45	44	44	45	0	0.39	0.32	0.43	0.22	0.29			
Run alt	Running while alert - focused on something	165	0.03	294	167	235	193	165	0	0.03	0.01	0.07	0.01	0.05			
Run alt pt	Running while alert and panting	423	0.00	0	0	423	0	0	0	0.00	0.00	0.01	0.00	0.00			
Run alt woof	Running and alert while barking at something	341	0.00	0	0	0	341	0	0	0.00	0.00	0.00	0.01	0.00			
Run with obj	Running with object in mouth	194	0.00	0	194	0	0	0	0	0.00	0.01	0.00	0.00	0.00			
Run howl	Running and howling at same time	362	0.00	0	0	0	362	0	0	0.00	0.00	0.00	0.01	0.00			
Run body low	Running with body low; social subordination	344	0.00	0	344	0	0	0	0	0.00	0.01	0.00	0.00	0.00			
Run tail tucked	Running with tail tucked; social subordination	181	0.00	0	413	181	0	0	0	0.00	0.01	0.00	0.00	0.00			
Run follow	Running while following another Coyote(s); no interactions taking place with that Coyote	47	0.01	340	0	105	0	47	0	0.01	0.00	0.02	0.00	0.02			
A run	Approaching something at a run	91	0.01	0	0	167	91	285	0	0.00	0.00	0.01	0.01	0.01			
Flee	Reflex-like response of running away from something	73	0.00	0	0	0	0	73	0	0.00	0.00	0.00	0.00	0.01			

Run tail tucked
Run follow
A run
Flee
Running with tail tucked; social subordination
place with that Coyote
Approaching something at a run
Reflex-like response of running away from something

T	N = 63	Total percentage for T:	11.50	12.99	11.32	11.32	9.02	12.85					
Export/Investigate (E/I)		Exploring/investigating surroundings; moving in a non-direct manner	27	7.10	33	34	27	33	7.69	6.12	6.78	7.76	7.13
Pt		General e/i behaviour while panting	94	0.00	0	0	0	94	0.00	0.00	0.00	0.00	0.01
Stand (st) sn		Standing and sniffing something (ground, tree, branch)	33	8.12	49	37	51	34	8.83	7.86	7.98	7.11	8.85
St sn & alt		Standing and sniffing (usually the air) something while alert	34	0.02	120	0	128	34	0.05	0.00	0.01	0.01	0.01
St sn pt		Standing and sniffing something while panting	151	0.01	0	0	0	486	0.00	0.00	0.01	0.01	0.03
St sn stretch		Standing and sniffing something while stretching	172	0.00	0	0	172	0	0.00	0.00	0.00	0.01	0.00
St sn wag tail		Standing and sniffing while wagging tail; excitement indicated	214	0.01	214	518	0	548	0.01	0.01	0.00	0.01	0.01
St sn urinate		Standing and sniffing while urinating	82	0.00	0	257	0	82	0.00	0.01	0.00	0.01	0.00
St sn whine		Standing and sniffing while whining (anxiety)	397	0.00	0	397	0	0	0.00	0.00	0.01	0.01	0.00
St sn Coyote		Standing and sniffing another Coyote	80	0.15	80	96	132	82	0.14	0.22	0.09	0.19	0.11
St sn (me)		Standing and sniffing JGW	227	0.00	0	227	0	0	0.00	0.01	0.00	0.00	0.00
St sn gr		Standing and sniffing as a group	88	0.01	181	127	88	178	0.01	0.01	0.01	0.03	0.01
St sn & bite		Standing and sniffing something while biting an object	121	0.01	0	121	122	0	0.00	0.01	0.03	0.00	0.01
St sn & chew		Standing and sniffing something while chewing on an object	85	0.02	85	0	0	537	0.07	0.00	0.00	0.02	0.00
St sn & pull at		Standing and sniffing something while pulling on an object	142	0.00	142	0	0	0	0.01	0.00	0.00	0.00	0.00
Hind legs		Investigate something on hind legs	59	0.10	60	64	59	62	0.10	0.06	0.09	0.09	0.16
Sn hind legs		Sniff something on hind legs	52	0.05	52	62	59	53	0.05	0.06	0.01	0.05	0.06
Look around (ar)		Looking around; usually standing but sometimes involves moving around (stepping) slowly from side-to-side	34	2.46	42	53	81	34	3.13	2.13	2.09	2.20	2.77
Look ar pant		Same as above while panting	406	0.53	413	413	407	410	0.31	0.49	0.94	0.39	0.54
Look ar tail up		Looking around with tail up; a sign of dominance	528	0.00	0	0	528	0	0.00	0.00	0.01	0.00	0.00
Look ar wag tail		Same as above while wagging tail	318	0.04	413	453	550	318	0.03	0.05	0.01	0.07	0.04
Look ar wag tail pt		Looking around while wagging tail and panting	413	0.01	0	413	0	519	0.00	0.01	0.00	0.04	0.00
Look ar sneeze		Looking around and sneezing	541	0.00	0	0	541	0	0.00	0.00	0.01	0.00	0.00
Look ar whine		Looking around and whining	518	0.01	0	0	518	0	0.00	0.00	0.01	0.00	0.00
Step sn		Stepping to side with front legs while sniffing; formerly classified as wk sn but documented more often after this study	564	0.00	564	0	0	0	0.01	0.00	0.00	0.00	0.00
Walk (wk) around		Walking around with no apparent direction in mind; usually looking at different things while walking	59	5.23	59	85	60	70	5.07	6.79	6.34	3.68	4.30
Wk ar pant		Same as above while panting	339	0.79	413	413	339	410	0.59	1.23	1.01	0.48	0.67
Wk ar yawn		Same as above while panting	499	0.00	0	499	0	0	0.00	0.01	0.00	0.00	0.00
Wk ar wag tail		Walking around and wagging tail indicating excitement	302	0.08	302	344	379	414	0.07	0.22	0.04	0.02	0.04
Wk ar pt wag tail		Same as above while panting	469	0.01	0	469	0	531	0.00	0.01	0.00	0.02	0.00
Wk ar body low		Walking around with body low; social subordination	399	0.01	0	399	451	0	0.00	0.06	0.01	0.00	0.00
Wk ar limp		Walking around and limping on a leg	43	0.00	0	43	0	0	0.00	0.01	0.00	0.00	0.00
Wk ar whine		Walking around while whining; implying anxiousness	339	0.02	0	413	339	0	0.00	0.01	0.07	0.00	0.00
Wk ar whin tl high		Walking around while whining but tail high; confusion apparent where Coyote whines but has tail up indicating confidence	518	0.00	0	0	518	0	0.00	0.00	0.01	0.00	0.00
Wk ar & woof		Walk around and make warning calls	368	0.00	0	431	368	0	0.00	0.01	0.01	0.00	0.00
Wk and look ar		Exaggerated movements of looking everywhere while walking around.	94	0.05	120	131	141	526	0.01	0.04	0.01	0.02	0.17

	31.07	32.30	36.0	26.71	30.18
Dig & chew	0	0	125	0	0
Cache	0	0	0	0	0
Cache & whine	49	0	39	341	0
Push obj	0	0	39	0	0
Pull obj	367	0	0	0	367
Whine	47	0	68	62	47
	39	0	53	43	39

E&I	N = 72	Total percentage for E/I:				
		31.07	32.30	36.0	26.71	30.18
Hunting (HU)		32.23				
Hunting behavior; actively trying to catch or kill an object; it was difficult to distinguish between a Coyote's behavior/intentions/body language when hunting mice or stalking conspecifics so they are merged together	49	0.02	59	73	122	237
Pawing/batting (with paw) at something like a mouse	241	0.01	261	0	277	0
Trying to stab something with quick paw movements	260	0.01	0	0	260	367
Biting air while typically trying to catch birds in flight	106	0.00	0	0	277	106
Jumping at prey, mostly birds in flight	228	0.00	0	0	270	0
Jumping up and landing on prey (e.g., mousing)	176	0.01	261	0	198	0
Ambush-crouch						
sit1						
Intently watching Coyote or prey while hiding in sit1	469	0.00	469	0	0	0
near ground; body tense; ears pricked forward, eyes locked on target						
Amb-cr sit2						
Same as above but in sit2 position	391	0.00	0	0	391	532
Ambush-crouch St						
Same as above but in a standing position	40	0.10	40	48	51	102
Ambush-stalk						
Creeching up on a Coyote or prey; body still very tense; ears pricked forward	39	0.24	39	43	51	58
Ambush-rush						
Running towards prey/Coyote; context not always clear when after a Coyote (e.g., initiating play, practicing hunting, disciplining other)	39	0.04	39	40	125	178
Full speed chase to catch prey	106	0.10	226	167	213	106
N = 12						
			0.48	0.36	0.55	0.38
			0.53			0.20
Feeding (FE)						
Feeding; ingesting something	27	1.16	33	34	34	27
Alert	129	0.00	0	0	0	0
Standing alert while feeding; usually while standing	77	0.00	0	0	77	0
Sit1	35	0.14	35	39	40	42
Grass	54	0.00	54	0	0	97
Eating grass - standing	33	0.59	33	50	48	60
Eating dog food (dry chow); usually while standing	33	0.03	33	194	0	34
Eating meat (supplied by zookeepers); usually while standing	33	0.01	33	42	0	51
Eating a rat or guinea pig or something they killed; this is most often in sit1	39	0.13	52	53	48	39
Eating a bone - usually the fat on the bone	177	0.01	177	0	0	0
Ice	40	0.46	64	40	59	67
Chewing and eating ice	37	0.16	47	37	43	39
Drink	39	0.04	39	47	86	39
Drinking water; usually while standing	78	0.00	0	0	78	0
Misc						
Ingesting something (undetermined)						
T walk						
Eating (usually dry dog food) while walking						
T run						
Eating (usually dry dog food) while running						
N = 14						
		2.72				
			2.53	2.44	3.24	2.75
						2.65
Infantile (IN)						
Infantile; neonatal (close body) contact and/or licking/ grooming (non-face areas) ≥ 1 other Coyotes	27	0.50	38	37	40	27
Re position on each other clearly for close contact; not really looking at anything; typically was done during rain						
Same as above while sleeping	37	0.28	50	48	59	37
Same as above but in sit1	59	0.01	0	59	0	0
Sit1	119	0.01	0	131	119	0
			0.63	0.56	0.34	0.75
						0.22
						0.38
						0.00
						0.00
						0.01
						0.00
						0.01
						0.02

E&I	N = 72	Total percentage for E/I:				
		31.07	32.30	36.0	26.71	30.18
Hunting (HU)		32.23				
Hunting behavior; actively trying to catch or kill an object; it was difficult to distinguish between a Coyote's behavior/intentions/body language when hunting mice or stalking conspecifics so they are merged together	49	0.02	59	73	122	237
Pawing/batting (with paw) at something like a mouse	241	0.01	261	0	277	0
Trying to stab something with quick paw movements	260	0.01	0	0	260	367
Biting air while typically trying to catch birds in flight	106	0.00	0	0	277	106
Jumping at prey, mostly birds in flight	228	0.00	0	0	270	0
Jumping up and landing on prey (e.g., mousing)	176	0.01	261	0	198	0
Ambush-crouch						
sit1						
Intently watching Coyote or prey while hiding in sit1	469	0.00	469	0	0	0
near ground; body tense; ears pricked forward, eyes locked on target						
Amb-cr sit2						
Same as above but in sit2 position	391	0.00	0	0	391	532
Ambush-crouch St						
Same as above but in a standing position	40	0.10	40	48	51	102
Ambush-stalk						
Creeching up on a Coyote or prey; body still very tense; ears pricked forward	39	0.24	39	43	51	58
Ambush-rush						
Running towards prey/Coyote; context not always clear when after a Coyote (e.g., initiating play, practicing hunting, disciplining other)	39	0.04	39	40	125	178
Full speed chase to catch prey	106	0.10	226	167	213	106
N = 12						
			0.48	0.36	0.55	0.38
			0.53			0.20
Feeding (FE)						
Feeding; ingesting something	27	1.16	33	34	34	27
Alert	129	0.00	0	0	0	0
Standing alert while feeding; usually while standing	77	0.00	0	0	77	0
Sit1	35	0.14	35	39	40	42
Grass	54	0.00	54	0	0	97
Eating grass - standing	33	0.59	33	50	48	60
Eating dog food (dry chow); usually while standing	33	0.03	33	194	0	34
Eating meat (supplied by zookeepers); usually while standing	33	0.01	33	42	0	51
Eating a rat or guinea pig or something they killed; this is most often in sit1	39	0.13	52	53	48	39
Eating a bone - usually the fat on the bone	177	0.01	177	0	0	0
Ice	40	0.46	64	40	59	67
Chewing and eating ice	37	0.16	47	37	43	39
Drink	39	0.04	39	47	86	39
Drinking water; usually while standing	78	0.00	0	0	78	0
Misc						
Ingesting something (undetermined)						
T walk						
Eating (usually dry dog food) while walking						
T run						
Eating (usually dry dog food) while running						
N = 14						
		2.72				
			2.53	2.44	3.24	2.75
						2.65
Infantile (IN)						
Infantile; neonatal (close body) contact and/or licking/ grooming (non-face areas) ≥ 1 other Coyotes	27	0.50	38	37	40	27
Re position on each other clearly for close contact; not really looking at anything; typically was done during rain						
Same as above while sleeping	37	0.28	50	48	59	37
Same as above but in sit1	59	0.01	0	59	0	0
Sit1	119	0.01	0	131	119	0
			0.63	0.56	0.34	0.75
						0.22
						0.38
						0.00
						0.00
						0.01
						0.00
						0.01
						0.02

1.33 1.19 2.08 1.31 1.26 0.81

	27	0.84	33	39	38	27	35	0.78	0.58	1.47	0.90	0.49
Play Self (PS)	Self play incorporating many concepts of play; movements are exaggerated and random, wide-eyes, jaws open, lips retracted (play face), appears pleasurable											
Gm	General movements such as walking around, moving head and eyes;											
erratic, clearly having fun	49	0.00	0	0	49	0	0	0.00	0.00	0.01	0.00	0.00
Chasing own tail	55	0.01	498	55	80	0	148	0.01	0.03	0.01	0.00	0.01
Shaking head exaggeratedly for no apparent other reason	79	0.11	91	92	88	79	160	0.16	0.07	0.13	0.19	0.01
In H2O	60	0.08	60	64	86	93	486	0.03	0.15	0.05	0.16	0.02
Paw	49	0.06	49	109	51	80	110	0.07	0.04	0.10	0.10	0.01
Paw/hit self	70	0.00	0	0	0	70	0	0.00	0.00	0.00	0.01	0.00
Tug	54	0.04	54	62	74	62	60	0.03	0.07	0.04	0.04	0.03
Bite air	395	0.00	0	395	0	0	0	0.00	0.01	0.00	0.00	0.00
Bite self	71	0.00	0	0	71	0	0	0.00	0.00	0.01	0.00	0.00
Bite object	59	0.02	59	59	67	77	0	0.07	0.01	0.01	0.02	0.00
Tear obj	91	0.01	91	156	302	158	202	0.01	0.01	0.01	0.01	0.01
Push obj	221	0.00	0	221	0	391	382	0.00	0.01	0.00	0.01	0.01
Toss obj	71	0.19	120	92	96	111	71	0.20	0.27	0.22	0.15	0.13
Head toss	39	0.00	0	39	171	0	0	0.00	0.01	0.01	0.00	0.00
Pounce obj												
practicing hunting												
Erratically running around in circles	51	0.03	98	73	51	158	97	0.03	0.05	0.06	0.01	0.02
Roll	49	0.02	60	92	49	93	82	0.03	0.01	0.04	0.02	0.01
Rolling around while exaggerating movements	74	0.03	0	121	74	80	0	0.00	0.01	0.08	0.05	0.00
Jumping up and down	85	0.01	96	0	85	299	0	0.01	0.00	0.01	0.01	0.00
A/w	53	0.01	192	0	53	93	225	0.01	0.00	0.04	0.01	0.01
N = 20		1.50						1.43	1.33	2.32	1.68	0.75

	27	0.08	33	40	38	27	35	0.12	0.06	0.06	0.08	0.07
Play Initiation (PI)	Play initiation; actively soliciting play with others; previously not engaged in play before doing PI with a Coyote											
Gm	27	0.08	33	40	38	27	35	0.12	0.06	0.06	0.08	0.07
Wag tail	52	0.01	52	0	154	27	0	0.01	0.00	0.01	0.03	0.00
Bow	148	0.00	0	161	0	221	148	0.00	0.01	0.00	0.01	0.01
Bark	39	0.05	39	47	93	39	39	0.07	0.05	0.03	0.07	0.04
Sup	78	0.00	0	0	78	0	0	0.00	0.00	0.02	0.00	0.00
Approach	363	0.00	0	0	0	0	363	0.00	0.00	0.00	0.00	0.01
A/W	47	0.01	0	47	0	73	79	0.00	0.01	0.00	0.01	0.01
A/w gr	44	0.07	52	47	51	62	44	0.06	0.06	0.10	0.07	0.08
SuA-ca	128	0.00	128	0	0	0	0	0.01	0.00	0.00	0.00	0.00
Bump other	45	0.00	0	0	0	0	45	0.00	0.00	0.00	0.00	0.01
Paw	85	0.01	0	85	0	106	107	0.00	0.02	0.00	0.01	0.01
Face paw	62	0.03	85	62	113	82	97	0.02	0.03	0.03	0.06	0.03
Flaunt with obj	27	0.01	0	0	0	27	0	0.00	0.00	0.00	0.03	0.00
Bite	126	0.00	0	0	141	126	0	0.00	0.00	0.01	0.01	0.00
Bite at/intentions	51	0.04	59	131	51	67	99	0.05	0.04	0.06	0.01	0.03
Jump	51	0.06	137	153	51	80	68	0.03	0.01	0.08	0.10	0.08
LL	73	0.01	73	124	167	0	0	0.01	0.01	0.01	0.00	0.00
	48	0.01	0	48	59	0	0	0.00	0.01	0.02	0.00	0.00

TABLE 1. Ethogram on eastern Coyotes (continued)

Parent Subcategory	Description	Age		%									
		All 5	All 5	Cane	Caon	Late	Lupe	Trans					
		59	0.02	64	77	59	0	0	0.04	0.02	0.04	0.00	0.00
Pounce	Jumping in front of another Coyote	39	0.03	60	79	85	148	39	0.03	0.01	0.01	0.03	0.06
Run around	Running quickly around trying to get others to join the chase	150	0.00	177	0	150	0	0	0.01	0.00	0.01	0.00	0.00
Run w object	Same as above but with something in its mouth	199	0.00	0	0	0	199	0	0.00	0.00	0.00	0.01	0.00
Bite and run	Nipping another playfully then running around	47	0.00	0	47	0	0	81	0.00	0.01	0.00	0.00	0.01
Ch	Chasing a Coyote to try and start a game of chase	75	0.00	0	75	0	102	0	0.00	0.01	0.00	0.01	0.00
Circling	Circling another with play face apparent												
N = 24	Total percentage for PI:		0.46						0.46	0.35	0.48	0.54	0.47
Play (P)	Social play; see text for the characteristics of play; exaggerated and unpredictable movements; pleasurable activities; play face apparent	33	1.73	33	34	38	34	33	2.26	1.85	1.14	1.47	1.91
Group (gr)	General group (≥2 Coyotes) play where a lot is happening but one thing doesn't predominate like wrestling or playing	42	0.36	47	42	51	60	47	0.33	0.32	0.47	0.35	0.34
Periphery	Mocking the movements (running, wrestling) of the 2 Coyotes playing; done at the edge (1-2 m away) of the Coyotes	47	0.01	0	0	47	0	0	0.00	0.00	0.07	0.00	0.00
Periphery gr	Same as above but ≥3 of the Coyotes are playing	52	0.01	0	0	52	0	0	0.00	0.00	0.07	0.00	0.00
Gm	General movements such as walking around others, moving head and eyes; erratic movements; basically, play was occurring but it was hard to classify in any other category	33	0.07	33	98	185	52	33	0.07	0.05	0.03	0.12	0.07
Gm gr	Same as above in a group	102	0.19	162	167	162	102	103	0.20	0.14	0.13	0.32	0.18
Eee	Making a squealing sound during play	65	0.00	65	0	0	0	0	0.01	0.00	0.00	0.00	0.00
Growl	Play growling without serious threats	81	0.00	0	0	81	0	0	0.00	0.00	0.01	0.00	0.00
Paw other	Pawing another Coyote during play	33	0.01	45	0	85	0	33	0.02	0.00	0.01	0.00	0.01
Face paw	Pawing another Coyote in the face during play	49	0.01	49	0	0	52	0	0.01	0.00	0.00	0.03	0.00
Head shake other	Grabbing neck with mouth and head shaking another during play	155	0.00	0	0	0	155	0	0.00	0.00	0.00	0.01	0.00
Bow	Lowering foreleg and elevating hind leg while wagging tail in the middle of play	43	0.01	0	0	0	43	43	0.00	0.00	0.00	0.02	0.01
L.L.	Leap-leap; two successive leaps during play	27	0.01	0	34	0	27	48	0.00	0.02	0.00	0.03	0.01
Walk around	Play face apparent while Coyotes are walking; play is occurring before and after these short walks; for example, this usually occurs in between wrestling bouts	125	0.01	0	0	125	0	0	0.00	0.00	0.03	0.00	0.00
Wk as gr	Same as above but while in a group	126	0.00	0	0	0	126	0	0.00	0.00	0.00	0.01	0.00
Trot around	Same as above but while trotting	80	0.03	80	284	0	174	330	0.03	0.01	0.00	0.08	0.02
Trot with coy	Trotting with Coyote with play-like body gestures	142	0.00	142	0	0	0	0	0.01	0.00	0.00	0.00	0.00
Trot gr	Same as above but while in a group (≥2 others)	163	0.02	257	0	323	163	297	0.07	0.00	0.01	0.03	0.02
Run around	Same as above but while running	39	0.08	60	73	49	44	39	0.14	0.02	0.06	0.04	0.14
Follow/trot	Same as above but while following another Coyote; again, clearly play is occurring during these activities	54	0.05	71	92	60	54	68	0.04	0.06	0.04	0.03	0.11
A/W	During play, another Coyote approaches and withdraws from another Coyote	44	0.07	44	86	53	97	48	0.06	0.07	0.10	0.05	0.04
A/W gr	Same as above but in a group (≥2 others)	98	0.04	98	141	141	120	99	0.03	0.04	0.03	0.05	0.08
Ch	One Coyote full speed chases another Coyote around	39	0.86	39	39	51	39	39	0.95	0.62	0.61	0.79	1.34
Periph	Same as above but in a group (≥2 others)	55	0.52	55	55	55	55	55	0.52	0.52	0.52	0.52	0.52

Follow/rot
A/W

A/W gr	98	0.04	98	141	141	120	99	0.03	0.04	0.03	0.05	0.08
Ch gr	39	0.86	39	39	51	39	39	0.95	0.62	0.61	0.79	1.34
Ch gr	55	0.53	80	80	81	58	55	0.63	0.33	0.36	0.54	0.77
Periphery ch gr	167	0.00	0	0	167	0	0	0.00	0.00	0.01	0.00	0.00
Circle	45	0.05	45	153	144	148	47	0.02	0.06	0.04	0.02	0.08
Circle gr	115	0.12	154	170	162	115	129	0.10	0.08	0.12	0.13	0.18
Hide-n-seek	52	0.04	52	59	72	52	52	0.03	0.05	0.03	0.03	0.06
Tug o war	48	0.22	54	48	51	51	48	0.23	0.27	0.11	0.36	0.14
Tug o war gr	111	0.07	111	124	125	111	0	0.17	0.01	0.03	0.11	0.00
Wrestle (Wr)	27	1.36	38	39	34	27	39	1.61	0.79	0.94	1.36	2.11
Wr gr	45	0.42	45	48	85	79	55	0.54	0.25	0.20	0.46	0.65
Wr wk	543	0.00	0	0	0	543	0	0.00	0.00	0.00	0.01	0.00
Wr trot	60	0.00	0	0	60	405	0	0.00	0.00	0.01	0.01	0.00
Wr Sup	44	0.19	44	71	51	73	44	0.27	0.06	0.15	0.12	0.35
Wr SuP gr	55	0.06	80	71	105	99	55	0.03	0.07	0.10	0.05	0.04
Pinning	37	0.20	40	40	78	37	65	0.21	0.19	0.19	0.20	0.22
Pinning gr	51	0.07	98	124	100	51	94	0.08	0.05	0.03	0.04	0.13
Wr & whine	80	0.00	0	0	80	0	0	0.00	0.00	0.01	0.00	0.00
Wr & growl	71	0.01	71	71	74	80	0	0.01	0.01	0.02	0.01	0.00
Wr ch	48	0.02	128	0	105	51	48	0.01	0.00	0.03	0.01	0.04
Wr ch gr	234	0.01	0	284	0	0	234	0.00	0.01	0.00	0.00	0.03
Body/hip slam	39	0.00	0	179	39	0	0	0.00	0.01	0.01	0.00	0.00
Bite	44	0.11	44	45	44	44	45	0.05	0.13	0.12	0.14	0.10
Bite gr	115	0.03	0	153	0	115	136	0.00	0.03	0.00	0.03	0.08
Jaw wrestle	42	1.30	45	42	57	45	59	1.64	0.97	0.88	1.55	1.44
Jaw wr gr	94	0.14	132	100	110	115	94	0.16	0.09	0.13	0.13	0.18
Jaw wr SuP	106	0.11	106	131	119	142	118	0.11	0.13	0.09	0.14	0.10
Jaw wr SuP gr	119	0.01	214	131	119	257	0	0.01	0.01	0.03	0.01	0.00
Jaw wr & wk	443	0.00	443	0	0	0	0	0.01	0.00	0.00	0.00	0.00
Sexual	42	0.03	132	43	42	42	81	0.04	0.01	0.07	0.01	0.01
N = 51		8.67						10.16	6.81	6.50	8.88	10.95

Agnostic (Ag)	33	0.09	44	34	34	34	33	0.03	0.15	0.08	0.11	0.10
Group	37	0.01	0	50	132	37	0	0.00	0.01	0.01	0.01	0.00
SuP	33	0.44	33	34	34	39	33	0.27	0.78	0.78	0.01	0.39
Sup whine	34	0.01	0	239	34	0	0	0.00	0.01	0.06	0.00	0.00
SuP gr	105	0.03	0	373	105	0	0	0.00	0.07	0.07	0.00	0.00

Same as above but in a group (≥ 2 others)
 One Coyote full speed chases another Coyote around
 Same as above but in a group (≥ 2 others)
 Same as above but in a full speed chase; this Coyote has no contact with the group during play bout
 Two Coyotes circle each other; other play actions occur before and/or after these encounters
 Same as above but with ≥ 2 other Coyotes
 One Coyote hiding and another finding it; chasing usually occurs after this
 At least 2 Coyotes pulling simultaneously on an object (branch)
 Same as above but with ≥ 2 other Coyotes
 Two Coyotes wrestling each other; fighting not observed
 Same as above but with ≥ 2 other Coyotes
 Walking while wrestling
 Trotting while wrestling
 During play one Coyote submits to another and will wrestle from a SuP position; role reversal often occurs where a more dominant Coyote submits
 Same as above but with ≥ 2 other Coyotes
 Opposite of SuP where 1 Coyote pins another; role reversal is common here where the less dominant Coyote is the pinner
 Same as above but with ≥ 2 other Coyotes
 Whining while wrestling in a friendly manner
 Whining while growling, but in a friendly manner
 While chasing/moving, 2 Coyotes are wrestling with each other
 Same as above but with ≥ 2 other Coyotes
 Running into another Coyote forcefully but in good spirits
 Playful bite encounters
 Same as above but with ≥ 2 other Coyotes
 Two Coyotes wrestling with their heads and biting neck and face
 Same as above but with ≥ 2 other Coyotes
 Same as Wr SuP but one Coyote Jaw Wr from SuP position
 Same as above but with ≥ 2 other Coyotes
 Walking while jaw wrestling
 Playful mounting (includes same-sex dyads) of another
 Total percentage for P:

Agonistic or aggressive acts associated with conflict
 General aggression amongst group
 Passive submission during dominance displays; not the same as in play; paws often raised at another while lying on back to keep head away from neck
 Whining while in SuP position
 One Coyote giving SuP to ≥ 2 others during agonistic situations

TABLE 1. Ethogram on eastern Coyotes (continued)

Parent Subcategory	Description	Age		Age		%								
		All 5	All 5	Cane	Late	Lupe	Trans	Cane	Caon	Late	Lupe	Trans		
Whine	Coyote on alert and directing whine towards another; intimidated; ears back	331	0.00	0	0	331	0	0	0	0.00	0.00	0.01	0.00	0.00
Dominance (D)	Opposite of SuP where one Coyote stands over (usually tail is high) another Coyote; growling is common; fur sometimes piloerected	27	0.40	38	34	0	27	33	33	0.39	0.60	0.00	0.31	0.71
Shrill/screech	Similar to whine but more intense; i.e., very scared	62	0.00	0	0	74	0	62	0	0.00	0.00	0.01	0.00	0.01
Bark at others	Aggressively barking at others when close by	85	0.00	0	0	85	0	0	0	0.00	0.00	0.01	0.00	0.00
Growl	Growling at another—a low pitched rumble; agonistic pucker (vertical retraction of lips) evident; body position not noted	33	0.69	38	34	40	34	33	33	0.14	1.69	1.00	0.28	0.39
Growl SuP	Growling while getting pinned; this is not common because SuP is usually a very submissive act	176	0.00	0	0	331	0	176	0	0.00	0.00	0.01	0.00	0.01
Growl & wh	Growling and whining; clearly submissive and nervous	448	0.00	0	448	0	583	0	0	0.00	0.01	0.00	0.01	0.00
Growl (st)	Growling in a standing position	39	0.02	0	39	40	0	0	0	0.00	0.04	0.06	0.00	0.00
Growl push	Pushing another while growling	391	0.00	0	0	0	391	0	0	0.00	0.00	0.00	0.01	0.00
Growl sit1	Same as growl but in sit1	67	0.03	79	153	67	142	85	0	0.01	0.06	0.05	0.03	0.02
Growl gr sit1	Same as above but in a group	514	0.00	0	0	0	514	544	0	0.00	0.00	0.00	0.01	0.01
Growl sit2	Same as growl but in sit2	97	0.01	0	0	331	97	0	0	0.00	0.00	0.03	0.02	0.00
Growl wk	Same as above but in a group	486	0.00	0	0	0	486	0	0	0.00	0.00	0.00	0.01	0.00
Growl gr sit2	Same as above but in a group	171	0.03	507	362	171	0	483	0	0.01	0.11	0.01	0.00	0.03
Growl wk	Growling while walking	363	0.02	0	518	484	0	363	0	0.00	0.04	0.03	0.00	0.01
Growl trot	Growling at another Coyote while trotting by it	394	0.00	0	0	394	0	0	0	0.00	0.00	0.01	0.00	0.00
Growl follow	Growling at another Coyote while following it	407	0.00	0	0	407	0	0	0	0.00	0.00	0.01	0.00	0.00
Growl ch	Chasing another Coyote while growling	522	0.00	0	0	522	0	0	0	0.00	0.00	0.02	0.00	0.00
Growl lunge	Growling and lunging at a Coyote	547	0.00	0	547	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Def growl	Growling but body in a defensive position (head down, ears to side) position	81	0.01	0	551	134	0	81	0	0.00	0.01	0.01	0.00	0.01
Def st	Standing in a defensive position (head down, ears to side, little movement); SuP like but not on back	479	0.00	0	479	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Def st whine	Same as above with whining	513	0.00	0	513	0	0	0	0	0.00	0.02	0.00	0.00	0.00
Def st growl	Same as above with growling	362	0.00	0	362	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Def sit1	Same as def st but in sit1	339	0.00	0	0	339	0	0	0	0.00	0.00	0.01	0.00	0.00
Def sit1 alt	Protecting its rear end from others (commonly against a fence); faces others; and usually has agonistic pucker, done by lower ranking Coyotes	78	0.01	0	105	78	0	0	0	0.00	0.02	0.03	0.00	0.00
Def sit2	Same as def sit1 alt but in sit2 position	331	0.00	0	513	331	0	0	0	0.00	0.01	0.01	0.00	0.00
Def sit2 alt	Same as above but alert	331	0.01	0	499	331	0	0	0	0.00	0.02	0.01	0.00	0.00
Def sit2 wh	Same as above but whining	185	0.00	0	518	185	0	0	0	0.00	0.01	0.01	0.00	0.00
Def st alt	Same as def st but alert	141	0.00	0	0	141	0	0	0	0.00	0.01	0.00	0.00	0.00
Def wk	Walking with Coyote in immediate vicinity	525	0.00	0	525	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Def wk body low	Walking with body low with Coyote in immediate vicinity	513	0.00	0	513	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Circle def	Walking in a circle to avoid another Coyote	513	0.00	0	513	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Circle def whine	Same as above while whining	513	0.00	0	513	0	0	0	0	0.00	0.01	0.00	0.00	0.00
Def lunge	Jumping at a Coyote to protect its body from being bitten	513	0.01	0	513	0	0	0	0	0.00	0.04	0.00	0.00	0.00
Paw other	Pawing another to try and get it to stop an Ag encounter; done by a													

more submissive Coyote; a jaulen sound is often emitted

59 0.00 0 250 0 59 0 0.00 0.01 0.00 0.01 0.00

183	0.00	0	0	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00
141	0.00	0	141	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00
525	0.00	0	525	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00
513	0.00	0	513	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00
513	0.00	0	513	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00
513	0.01	0	513	0	0	0	0	0	0.00	0.04	0.00	0.00	0.00

Push	59	0.00	0	250	0	59	0	0.00	0.01	0.00	0.01	0.00	0.01
Bare teeth	563	0.00	0	0	0	563	0	0.00	0.00	0.00	0.00	0.00	0.01
Bite others	263	0.01	0	380	263	0	382	0.00	0.01	0.01	0.01	0.00	0.01
St def bite	38	0.10	38	66	67	43	43	0.12	0.13	0.10	0.07	0.08	0.00
Flee trot	513	0.00	0	513	0	0	0	0.00	0.01	0.00	0.00	0.00	0.00
Flee run	569	0.00	577	569	0	0	0	0.01	0.01	0.00	0.00	0.00	0.00
Flee run whine	479	0.00	0	479	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00
Ch	462	0.00	0	462	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00
Tackle/Wr	59	0.02	0	303	132	59	508	0.00	0.01	0.03	0.02	0.02	0.00
Wr gr	38	0.01	38	314	85	183	540	0.01	0.01	0.01	0.01	0.01	0.01
Gr mob	339	0.01	0	339	531	505	0.00	0.00	0.00	0.03	0.01	0.01	0.01
mobbed by others	395	0.01	395	448	0	414	458	0.02	0.01	0.00	0.01	0.00	0.01
Fight	413	0.00	0	413	0	0	0	0.00	0.02	0.00	0.00	0.00	0.00
N = 52	33	0.11	33	34	42	34	33	0.11	0.12	0.03	0.18	0.09	0.00

Total percentage for agonistic:													
Miscellaneous (MISC)	96	0.10	114	105	96	133	394	0.12	0.13	0.10	0.10	0.10	0.07
Sit down	42	0.06	106	119	42	102	140	0.04	0.04	0.06	0.12	0.04	0.04
Stand up	499	0.00	0	0	0	499	0	0.00	0.00	0.00	0.01	0.00	0.00
St up w obj	48	0.01	71	48	0	0	0	0.03	0.01	0.00	0.00	0.00	0.00
Bite intention	102	0.02	102	0	298	0	0	0.03	0.00	0.05	0.00	0.00	0.00
Roll	39	0.05	39	47	49	58	52	0.13	0.07	0.02	0.01	0.04	0.00
Jump	33	0.01	35	40	43	0	33	0.03	0.02	0.01	0.00	0.01	0.00
Climb	59	0.00	59	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00
Crawl	33	0.02	278	0	34	37	33	0.01	0.00	0.07	0.02	0.01	0.00
Inguinal	33	0.02	278	0	34	37	33	0.01	0.00	0.07	0.02	0.01	0.00

N = 9	0.28	0.40	0.27	0.31	0.26	0.16
-------	------	------	------	------	------	------

more submissive Coyote; a jaulen sound is often emitted from getting beat up by pushing the aggressor (3rd Coyote) away Agonistic pucker where threat face is made but no growling; ears usually up in a confident Coyote and down if Coyote is nervous/submissive Biting at others with Ag face (threat face) Biting at another while standing defensively Fleeing an aggressive Coyote at a trot Fleeing an aggressive Coyote at a run Same as above while whining Chasing another Coyote while growling; clearly going after it Aggressive tackling of another Coyote; growling common Same as above but in a group (≥ 2 others) Where ≥ 2 Coyotes encircle and chase a Coyote; not as much body contact as a wrestle; lots of nipping and biting at the mobbee; often injurious Where a Coyote is mobbed by ≥ 2 others Where 2 Coyotes go all out at each other; loud growling; biting usually to neck and/or hind-end

Miscellaneous categories that do not fit anywhere else Going from a standing to sitting Going from a sitting position to standing. Same as above but with object in mouth Biting at another; not sure if play or agonistic Rolling on the ground Jumping to something like on a rock or box; occurred in different contexts than other jumps (e.g., during self play or play initiation) Climbing on objects (e.g., fence) Belly on the ground; arms used to drag self around; hind legs propel self Raising one hind leg to expose abdominal area when facing opposite direction of conspecific; difficult to classify; didn't seem to be greeting or agonistic towards one another

active in JGW's presence than other times of the day (Stone Zoo Keepers, personal communication).

Traveling T was defined as a Coyote moving with purpose from one place to another (i.e., from point A to point B). A Coyote, when traveling, would move in a straight line and would waste little energy investigating other objects until it reached its destination. This differed from explore/investigate E/I activities, where animals were characterized by actively sniffing objects or other Coyotes, digging, and moving around in a non-direct way in order to explore their surroundings. E/I behaviour is typically not described in the literature for canids (but see Scott and Fuller 1965) yet was an important activity that our Coyotes engaged in, by far the most frequently of any parent category (Table 1; 32% of activity). The difference between explore/investigate and traveling activities would be interesting to compare between wild and captive canids. The captive Coyotes that we studied were very active but did more exploring than traveling because of the relatively small area that they lived in. Conversely, Coyotes in the wild routinely have to traverse their home ranges (Camenzind 1978; Gese et al. 1996; Way 2000) and potentially might do more traveling than exploring.

Hunting (HU) behaviour was classified when a Coyote was actively trying to catch/kill another object. Many small mammals and birds entered their enclosure, giving the Coyotes the opportunity to hunt (although we occasionally gave them live chicken chicks, we never scored the Coyotes when they were killing them). Additionally, when a Coyote was attempting to ambush a conspecific, we also classified this as hunting because its intentions were very similar to hunting prey: i.e., body very alert and focused, in a crouched position, and rushing at its intended target. Furthermore, different results occurred after an ambush; e.g., no social interactions occurred (i.e., both individuals walked away from one another), a play initiation was given once the ambusher got within close range of the Coyote, play immediately started, or fighting or agonistic behaviour ensued. Parks (1979) classified "ambushing" as a separate category in her thesis but perhaps the larger size of the exhibit in which we studied our Coyotes allowed us to detect the similarity to hunting.

Feeding was simply associated with ingesting something. Although we documented our Coyotes feeding (FE) we attempted to avoid conducting behaviours around any type of feeding time (e.g., we did not do a behavioural bout when dog chow was just placed out or when meat, rats or mice were just given to them) to avoid biasing the data.

Infantile (IN) behaviours were associated with neonatal contact as described by Parks (1979), but we also included licking/grooming one another. Because the Coyotes were in contact with other Coyotes, we believed that this was an important division for a parent category even though other behavioural complexes, such as resting, sit1 and sit 2, are included in this category. These behaviours were intermittently seen



FIGURE 1. JGW (first author) conducting a focal animal sampling bout on the Coyote to the right of him.



FIGURES 2 and 3. Coyotes sleeping in rest position.



FIGURE 4. Coyote in Sit1 Alert position.



FIGURE 5. Close-up of Coyote in Figure 4.



FIGURE 9. Coyote in Stand Alert position.



FIGURE 6. Coyotes in Sit1 Alert Pant position.



FIGURE 10. Coyote Standing and Howling alone (lone howl).

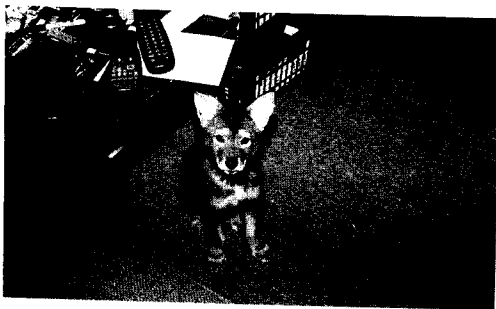


FIGURE 7. Coyote pup in sit2 Alert position in JGW's house.



FIGURE 11. Coyotes Standing and Group Howling.



FIGURE 8. Coyote on left in Sit1 Alert Pant position; Coyote on right in Sit2 Alert position.



FIGURE 12. Coyote on the right and in the back are Traveling and Trot Following the Coyote in the front.



FIGURE 13. Coyote in E/I (Explore/Investigate) Walk Sniff mode.



FIGURE 14. Coyote pack E/I Stand Sniffing.



FIGURE 15. Coyote in foreground in Hunt Ambush Crouch (Sit1) position. Coyote in background in Ambush-rush Conspecific position. This behavior can quickly turn into an Approach (Travel trot towards) when the Coyote is not in a crouched hunting mode and is moving towards another Coyote.



FIGURE 16. Coyote in Hunting mode, chasing and catching a bird.



FIGURE 17. Coyote Feeding on a rat.

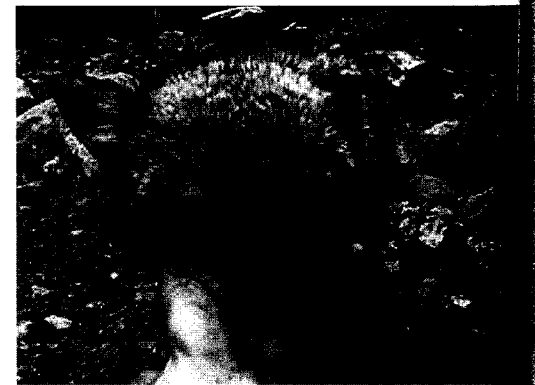


FIGURE 18. Coyote Greeting Person (JGW).



FIGURE 19. Coyote in a true Greeting with JGW.



FIGURE 23. Two Coyotes Play Jaw Wrestling.



FIGURE 20. Coyote Self Playing in water.



FIGURE 24. Coyote trying to Play Initiate with JGW by Lying on back and Pawing.



FIGURE 21. Coyotes in Play Chase mode.



FIGURE 25. Agonistic display. Coyote on top is in an Agonistic Dominance Display while the Coyote pinned to the ground is in Agonistic SuP (passive submission).



FIGURE 22. Coyotes Play Group Wrestling.

throughout the 18 months of observation when Coyotes would occasionally sleep on one another (especially on rainy days) or one Coyote would lick another but was not greeting it. A licking Coyote appeared to be grooming the recipient, which made it hard to place into any other category (i.e., it was doing more than simply greeting another Coyote).

Greetings (GR) were classified when non-agonistic and/or non-play interactions occurred between ≥ 2 Coyotes. Zimen (1982) classified many of these behaviours as neutral social contacts but we separated Zimen's descriptions of sniffing other Coyotes and left them in the explore/investigate category because the motivation was not always clear (e.g., was sniffing another Coyote a social contact or just a Coyote curious to smell another one?). Simply put, when both Coyotes licked and/or had muzzle contact with each other and/or wagged their tails in excitement to see one another, then we classified this as a greeting.

We used Bekoff's (1972a,b) definition of "play" to define our category, where play was the behaviour that was performed during social interactions in which there was a decrease in social distance between the interactants, and no evidence of social investigation or of agonistic or passive-submissive behaviours on the part of the members playing, although these actions may occur as derived acts during play (e.g., passive submission during a play bout). Bekoff (1974) also classified play as: (1) incorporating various contexts into unpredictable temporal sequences; (2) preceded by a metacommunicative signal (which we have a separate category for: i.e., play initiation); (3) certain actions are repeated and performed in an exaggerated manner; and (4) the activity appears pleasurable to the participants: a play face (wide open jaws and eyes) is apparent.

We also included the numerous role reversals in this category where more dominant Coyotes allowed lower ranked Coyotes to pin them to the ground; this was never documented during agonistic displays. Bekoff (1974) includes a description of this occurring amongst western Coyotes but does not delineate it as part of classifying play. Additionally, we separated play initiation from play because the attempter was not always successful in initiating play during an attempt; i.e., they appeared to be two separate categories. We observed many play initiation-like (e.g., approach/withdraw and general movements) behaviours occurring during play, but because they happened during play we kept them in this category; i.e., play was already initiated. Self play (PS) was similar to play but when a Coyote was by itself. Altogether, play-like sequences accounted for ca. 10% of all observations (Table 1).

Agonistic (AG) behaviours were classified as aggressive acts associated with conflict where there were clear acts of dominance and submission or where growling or fighting was observed (Fox 1969; Scott and Fuller 1965; Zimen 1982). About 2% of all activities were aggressive, especially towards the end of the study when Coyotes were separated. Finally, a miscellaneous (MISC) category was one where we could not classify the behaviour pattern into any of the other parent systems; these were very infrequent (Table 1).

Despite the large number of behavioural patterns described herein, there are some important omissions in our ethogram. First, because the Coyotes were all siblings and were young adults (18 months) when the

study ended, we did not notice any sexual/reproductive behaviours (although it was witnessed during their second winter: J. Way, unpublished data). Future ethograms should add this behaviour as a separate (parent) category much as Scott and Fuller (1965), Zimen (1982), and Goodmann and Klinghammer (1990) did with their respective ethograms. Second, because the Coyotes were taken from the wild at 25 days of age, we missed many basic neonatal behaviours, such as crawling and nursing (Scott and Fuller 1965; Scott 1967; Parks 1979). Third, because the Coyotes were all siblings and of the same age, we could not document any adult-pup interactions such as epimeletic behaviours, i.e., the giving of care (Scott and Fuller 1965). However, many times we did document et-epimeletic behaviours where the Coyotes were soliciting or calling for care where they would whine, wag their tails for a greeting (with JGW and/or another Coyote), and lick one another. Fourth, the full range of hunting behaviours (e.g., killing/biting prey) was not documented mainly because of the rarity of observing a kill – especially during the 15 sec intervals when we recorded data. Finally, there were some different behavioural actions that we could have added but simply did not because of the sheer volume of our ethogram. For example, under infantile behaviour we have sit1 and sit2 although we do not note if their eyes are open or closed. Because both examples were rarely observed, this was a minor detail in the overall scheme of Table 1, but it does illustrate the arbitrarily defined nature of any ethogram (Schleidt et al. 1984), no matter how simple (i.e., the parent categories) or complex (i.e., the behavioural actions) it is. Also, we thought that sit1 and sit2 were logical separations due to the noticeably different body positions; however, we theoretically could have had many more sitting positions based on a combination of head, body, and leg positions.

Although we attempted to be consistent with our behavioural classifications, there was no doubt that drift occurred in our categorizations (MacDonald et al. 2001). For example, many of the behaviours occurred well before first noted on Table 1. Although usually very similar to other categories (for example E/I w/sn and E/I st sn versus E/I step sn; Table 1) a new category randomly created during the study certainly introduces a bias to the final tally of percentages in Table 1. However, the goal of this study was to produce an end product (i.e., the ethogram) even at the expense of being consistent throughout – i.e., there was no available model of a typical ethogram on wild canids. Also, a number of simple, but newly recorded behaviours occurred after the study concluded. For example, E/I step sniff became much more frequent no doubt because of the new category described not because a Coyote just started doing that action pattern. Also, stand step alert and stand alert move head were described soon after this ethogram was finalized (J. Way, unpublished data). Although these were commonly recorded after the Coyotes were separated they

were not described herein. That being said, we believe that the ethogram is largely complete and that these slight nuances are offset by our rationale of producing the ethogram when all five Coyotes were housed together (i.e., before they were permanently separated) and the fact that the main categories would stay virtually identical even with these changes.

The categories that we created are intended for ease of use in the field where a researcher can simply note the major behavioural system observed and the behavioural pattern associated with it. One advantage of this ethogram is that it is in discrete units (i.e., the behavioural patterns). However, data could always be lumped together (i.e., into general behavioural systems or ≥ 2 behavioural patterns could potentially be combined into one action) if the data/list are unmanageably large (e.g., when studying wild Coyotes). The disadvantage of merging behaviours into more broad groupings is that parent categories or lumped behavioural patterns can never be split back into more distinct behavioural patterns if not done at the outset; as Bekoff (1972b) indicated, this would cause data to be irreversibly lost.

The previous studies that have described canid behaviours were quite variable (Scott and Fuller 1965; Silver and Silver 1969; Bekoff 1972a; Parks 1979; Zimen 1982) so we basically combined data/categories from all of these studies and made modifications or additions as needed in order to try to create an accurate yet practical guide for researchers studying canids in the field. Future research should try to generate similar ethograms for other species and should continue to modify and/or expand our list if new behavioural actions are found with Coyotes. Analyzing ethograms of closely related species may be one technique to effectively discriminate between them (e.g., Western Coyotes, Eastern Coyotes and Wolves – Silver and Silver 1969; Bekoff 1978).

Acknowledgments

This study would not have been possible without the support from the staff at Zoo New England, including the keepers, management, veterinarians and their technicians, and security. In-kind benefits from the Way family were invaluable. Peter Auger and the Biology Department and Urban Ecology Institute at Boston College provided support. Katie-Jo Glover and Kelly Holland assisted with data entry. The Town of Falmouth's Animal Control and Department of Natural Resources were instrumental in helping JGW obtain the wild-born pups.

Literature Cited

- Bekoff, M.** 1972a. An ethological study of the development of social interactions in canids: a dyadic analysis. Ph.D. thesis, Washington University, St. Louis, Missouri.
- Bekoff, M.** 1972b. The development of social interaction, play, and metacommunication in mammals: an ethological perspective. *Quarterly Review of Biology* 47: 412-434.

- Bekoff, M.** 1974. Social play and play-soliciting by infant canids. *American Zoologist* 14: 323-340.
- Bekoff, M.** 1978. Behavioral development in coyotes and eastern coyotes. Pages 97-126 in *Coyotes: biology, behavior and management*. Edited by M. Bekoff, Reprint 2001, The Blackburn Press, Caldwell, New Jersey.
- Bekoff, M.** 1989. Behavioral development of terrestrial carnivores. Pages 267-294 in *Carnivore behavior, ecology, and evolution*. Edited by J. L. Gittleman, Volume 1, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Bekoff, M., and R. Jamieson.** 1975. Physical development in coyotes (*Canis latrans*) with a comparison to other canids. *Journal of Mammalogy* 56: 685-692.
- Bekoff, M., and M. C. Wells.** 1981. Behavioural budgeting by wild coyotes: the influence of food resources and social organization. *Animal Behaviour* 29: 794-801.
- Camenzind, F. J.** 1978. Behavioral ecology of coyotes on the national elk refuge, Jackson, Wyoming. Pages 267-294 in *Coyotes: biology, behavior and management*. Edited by M. Bekoff, Reprint 2001, The Blackburn Press, Caldwell, New Jersey.
- Ewer, R. F.** 1973. *The carnivores*. Cornell University Press, Ithaca, New York.
- Fox, M. W.** 1969. The anatomy of aggression and its ritualization in canidae: a developmental and comparative study. *Behaviour* 35: 242-258.
- Fox, M. W.** 1970. A comparative study of the development of facial expressions in canids; wolf, coyote and foxes. *Behaviour* 36: 49-73.
- Frank, H.** 1987. *Man and wolf: advances, issues and problems in captive wolf research*. Dr. W. Junk, Boston, Massachusetts.
- Gese, E. M., R. L. Ruff, and R. L. Crabtree.** 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. *Canadian Journal of Zoology* 74: 769-783.
- Goodall, J.** 1986. *The chimpanzees of Gombe: patterns of behavior*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Goodmann, P. A., and E. Klinghammer.** 1990. *Wolf ethogram*. Revised edition. Ethology Series Number 3. North American Wildlife Park Foundation (Wolf Park), Battle Ground, Indiana.
- Jennings, H. S.** 1906. *Behavior of the lower organisms*. Columbia University Press, New York, New York.
- Lehner, P. N.** 1978. Coyote communication. Pages 127-162 in *Coyotes: biology, behavior and management*. Edited by M. Bekoff, Reprint 2001, The Blackburn Press, Caldwell, New Jersey.
- Lorenz, K.** 1971. *Studies in animal and human behaviour*. Volume 2. Harvard University Press, Cambridge, Massachusetts.
- Macdonald, D. W., P. D. Stewart, P. Stopka, and N. Yamaguchi.** 2000. Measuring the dynamics of mammalian societies: an ecologist's guide to ethological methods. Pages 332-388 in *Research techniques in animal ecology: controversies and consequences*. Edited by L. Boitani and T. K. Fuller. Columbia University Press, New York, New York.
- Makkink, G. F.** 1936. An attempt at an ethogram of the European avocet (*Recurvirostra avosetta* L.) with ethological and psychological remarks. *Ardea* 25: 1-60.
- Martin, P., and P. Bateson.** 1986. *Measuring behaviour*. Cambridge University Press, New York, New York.

- Mech, L. D.** 1970. The wolf: the ecology and behavior of an endangered species. Reprint 1995, University of Minnesota Press, Minneapolis, Minnesota.
- Parks, M. B.** 1979. Physical and behavioral development of captive eastern coyote pups. M.S. thesis, University of Maine, Orono.
- Ryon, J.** 1986. Den digging and pup care in captive coyotes (*Canis latrans*). *Canadian Journal of Zoology* 64: 1582-1585.
- Schleidt, W. M., G. Yakalis, M. Donnelly, and J. McGarry.** 1984. A proposal for a standard ethogram, exemplified by an ethogram of the bluebreasted quail (*Coturnix chinensis*). *Zeitschrift für Tierpsychologie* 64: 193-220.
- Scott, J. P.** 1967. The evolution of social behavior in dogs and wolves. *American Zoologist* 7: 373-381.
- Scott, J. P., and J. L. Fuller.** 1965. Genetics and the social behavior of the dog. The University of Chicago Press, Chicago, Illinois.
- Silver, H., and W. T. Silver.** 1969. Growth and behavior of the coyote-like canid of northern New England with observations of canid hybrids. *Wildlife Monographs* 17: 1-41.
- Snow, C. J.** 1967. Some observations on the behavioral and morphological development of coyote pups. *American Zoologist* 7: 353-355.
- Tinbergen, N.** 1959. Comparative studies of the behavior of gulls (Laridae): a progress report. *Behaviour* 15: 1-70.
- Way, J. G.** 2000. Ecology of Cape Cod coyotes (*Canis latrans* var.). M.S. thesis, University of Connecticut, Storrs.
- Way, J. G.** 2001. The eastern coyote: documenting the habits of one of Cape Cod's newest residents. *Conservation Perspectives*, the online journal of the New England Chapter of the Society for Conservation Biology. URL: <http://www.nescb.org/epublications/spring2001/coyotes.html>.
- Wozencraft, W. C.** 1989. Appendix: classification of the recent Carnivora. Pages 569-593 in *Carnivore behavior, ecology, and evolution*. Edited by J. L. Gittleman. Volume 1. Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Zimen, E.** 1982. A wolf pack sociogram. Pages 282-322 in *Wolves of the world: perspectives of behavior, ecology, and conservation*. Edited by F. H. Harrington and P. C. Paquet. Noyes Publications, Park Ridge, New Jersey.

Received 7 March 2005

Accepted 30 January 2007

Editor's Note

A description of these Coyotes "in layman's language" is now available.

Way, J. G. 2007. Suburban howls: tracking the eastern Coyote in Urban Massachusetts. Dog Ear Publishing, Indianapolis, Indiana. <http://www.easterncoyotereseach.com>

Firs
Pop

NGAI
JASON

¹Anglia

²Canadi

³Avian

⁴Parc na

⁵Étude

⁶Cégep

Richard

o

I

Baseline

Saint-H

Screech-

occupied

Northern

lets retrie

of 1.77 g

Meadow

da macr

The spec

ited amo

the owl's

the speci

are discus

Key Word

le

m

The E

extensive

and Hen

received

der, whe

Quebec,

and gene

part of a

Owl to p

pple ord

d. 2004,

he specie

ation of

resides in

f Quebec

Method

apping t

We obd

proie (

r for the