



A whistle in the woods: an ethogram and activity budget for the dhole in central India

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The dhole (*Cuon alpinus*) is an endangered social canid that inhabits the forests of southern and southeastern Asia. A scarcity of field studies and inconsistent findings have led to a poor understanding of their ecology and conservation status. We compiled an ethogram of dhole behavior based on analysis of 395.35 min of video recordings. We recorded 3,394 behavioral events in 1,654 video clips lasting 10 s each. We classified behavioral events into 6 categories: Locomotion, Resting, Social Behavior, Feeding, Scent Marking, and Miscellaneous. Behavioral events associated with Locomotion were most frequent (40.95%), as was the proportion of time spent on such behaviors (41.89%). Dholes spent the least time exhibiting Miscellaneous and Scent Marking behaviors (1.45% and 2.64%, respectively), as well as the lowest frequency (0.74% and 4.01%, respectively). Although scent marking was relatively rare, we observed unique scent-marking behaviors in this study, including “hind bounce” and “hind scrub.” The time spent on different categories of behaviors differed significantly among males, females, and subadults. We also used camera traps and opportunistic observations to investigate the activity patterns of dholes in dry deciduous forest of Tadoba-Andhari Tiger Reserve in central India, where they are sympatric with other large predators including tigers (*Panthera tigris*) and leopards (*P. pardus*). Our findings suggested that dholes were primarily crepuscular. Fundamental knowledge about behavioral ecology is crucial for the conservation of any species, and our findings provide a new foundation for future behavioral research on this endangered social canid.

Key words: activity, behavior, dhole, dry deciduous forest, ethogram

The dhole or Asiatic wild dog (*Cuon alpinus*) is an elusive, pack-hunting, social carnivore that is classified as endangered (Kamler et al. 2015); it ranges throughout most of southern and southeastern Asia (Johnsingh 1980; Acharya 2007). Throughout most of its range, dholes coexist with other large predators, such as the tiger (*Panthera tigris*) and leopard (*P. pardus*—Johnsingh 1980; Acharya 2007; Majumder 2011). Previous studies by Johnsingh (1980), Fox (1984), Venkataraman et al. (1995), Acharya (2007), and Hayward et al. (2014) have investigated various aspects of dhole ecology. Several studies have described the social and reproductive behavior of dholes (Johnsingh 1992; Venkataraman 1998; Venkataraman and Johnsingh 2004), but there have been no long-term studies of their behavioral ecology. The largest extant population of dholes occurs in India (Kamler et al. 2015); yet, < 5 zoos have dholes in captivity. The decreasing trend among wild dhole populations, coupled with their scarcity in zoos, could create significant conservation issues for the dhole in India. Fundamental studies of dhole

behavior in the wild will help inform current and future conservation efforts for this endangered species.

In recent years, the focus of behavioral science has shifted from making direct observations in the field to conducting statistical analyses and interpreting resulting models (Boitani and Fuller 2000). However, such observations provide a fundamental understanding of the behavioral repertoire of target species and remain an important component of behavioral ecology, especially for little-known species like the dhole. These observations are used to compile “ethograms” that provide a comprehensive inventory of individual behaviors and behavioral interactions (Bekoff 1978; McDonnell and Haviland 1995). Ethograms may consist of a simple listing of behaviors by name, or may include detailed descriptive text, line drawings of behavioral elements or sequences, or pictorial representations of interactive sequences (McDonnell and Poulin 2002). Except for the wolf (*Canis lupus*), coyote (*C. latrans*), red fox (*Vulpes vulpes*), and singing bush dog (*Canis hallstromi*),

detailed ethograms have not been developed for most canids (Ewer 1973; Wozencraft 1989; Way et al. 2006). Designing ethograms is crucial to the study of animal behavior because it delineates the scope of analysis and often guides the course of future research (Bekoff 1979; MacNulty et al. 2007). Without such ethograms, animal behaviors are open to interpretation and studies of behavioral ecology may become ambiguous. The activity patterns of each species evolved to optimize the timing of behaviors needed for survival and reproduction (Schmidt et al. 2009).

Like many tropical forest species, the dhole is shy, elusive, and extremely difficult to study in the wild. Consequently, we used opportunistic video clips and camera trapping to study the behavioral repertoire and activity patterns of dholes, respectively. In this study, we develop the first ethogram for the dhole, estimate their activity budget in the wild, and discuss the potential importance of observed behaviors for their conservation.

MATERIALS AND METHODS

Study area.—The Tadoba-Andhari Tiger Reserve (TATR; 20°04'53" to 20°25'5"N and 79°13'13" to 79°33'34"E) is a 1,700-km² protected area located in the Chandrapur district of the state of Maharashtra, India. The reserve contains an important source population of tigers and supports remnant populations of dholes in the central Indian region. This biodiverse region contains 41 species of mammals, > 195 birds, 111 butterflies, and 30 reptiles (Nagendra et al. 2006; Tiple 2012). Our study was conducted in a 625.40-km² core area within the TATR (Fig. 1), which is classified as southern tropical dry deciduous forest (Champion and Seth 1968). Large carnivores in our study area included tigers, leopards, dholes, and sloth bears (*Melursus ursinus*). Smaller carnivores included jungle cats (*Felis chaus*), palm civets (*Paradoxurus hermaphroditus*), small Indian civets (*Viverricula indica*), ruddy mongooses (*Herpestes smithii*), common mongooses (*H. edwardsi*), and ratels (*Mellivora capensis*). Chitals (*Axis axis*), sambars (*Cervus unicolor*), nilgais (*Bosephalus tragocamelus*), gaurs (*Bos gaurus*), wild pigs (*Sus scrofa*), chausingas (*Tetracerus quadricornis*), barking deer (*Muntiacus muntjak*), common langurs (*Semnopithecus entellus*), black-naped hares (*Lepus nigricollis*), and Indian porcupines (*Hystrix indica*) formed the potential prey base for carnivores in TATR. The buffer zone contains villages, tourist facilities, and croplands (Nagendra et al. 2006); there are 79 villages in the buffer zone but only 3 in the core area (Dhanwatey 2013).

Field methods.—Behavioral data on dholes were collected opportunistically using a Canon Powershot SX 50 digital camera; accordingly, distances from the observer to study animals varied. We also included several video clips in our analyses that were collected during our study by forest guards and tourists that were taken on digital cameras, camcorders, or mobile phones. The TATR has been open to tourism for > 10 years, and we found no evidence that dholes behaved differently in the presence of vehicles or humans (Supplementary Data SD1). We located dholes by receiving reports from forest guards that

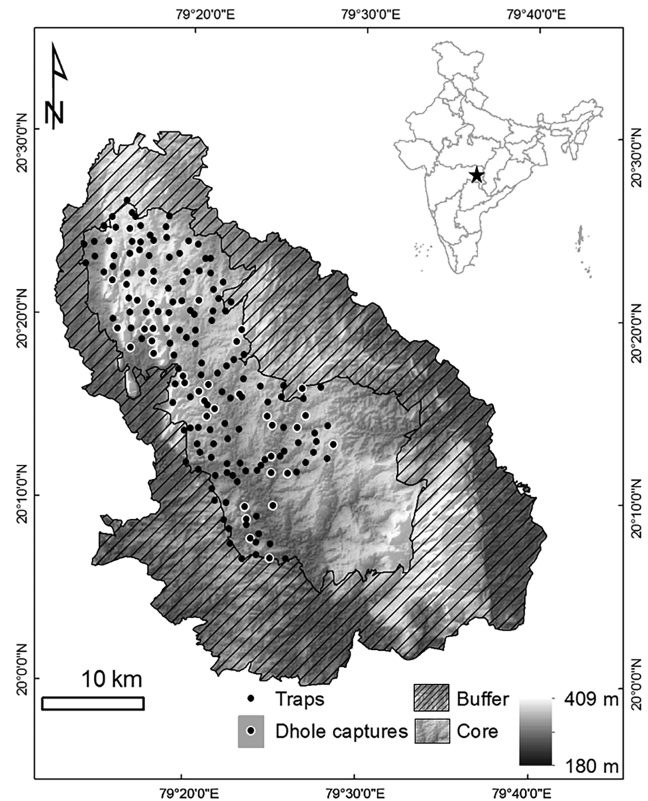


Fig. 1.—Map showing study area of Tadoba-Andhari Tiger Reserve, Maharashtra, India. The star symbol on the map of India marks the location of the Tadoba-Andhari Tiger Reserve in central India. Camera traps deployed are shown as black dots and those with dhole (*Cuon alpinus*) captures are shown as black dots with a white border.

live in the Reserve and by searching early in the morning for fresh scats or tracks.

To estimate the dhole's activity budget, we used photographs obtained by camera traps from January to April of 2014 and 2015 (Habib et al. 2014). We monitored 62 camera stations for 21 days each that were deployed in a square grid with 1.4-km spacing; camera traps were active continuously during each trapping session. Each camera station included 2 passive white-flash cameras (Cuddeback Attack Model 1149 and Moultrie Game Spy D55). To maximize photo-captures, we placed camera traps along roads, trails, or streambeds.

Analyses.—We used the software package CowLog 2.0 (Hänninen and Pastell 2009) to construct an ethogram for the dhole and to estimate its activity budget. CowLog 2.0 tracks the time code from video files and transfers the amount of time spent on each behavior to a data file; resulting data are then analyzed manually. We defined 6 behavioral classes for our analyses: Locomotion, Resting, Social Behavior, Feeding, Scent Marking, and Miscellaneous (Koler-Matznick et al. 2005). We coded specific behaviors (events) within each category, as appropriate. Multiple events occurring at the same time were coded and tracked separately, and videos were played at various speeds for ease of interpretation. We conducted additional data analyses using Microsoft Excel 2013.

Each individual in a pack whose behavior was recorded on a video clip was analyzed separately (Altmann 1974). For example, a video of 4 individuals was studied 4 times, each time focused on a different individual in the video clip. To avoid observer bias, all video clips were analyzed by a single member of the research team. Because the behavioral literature on dholes was so sparse, we used published ethograms for other canids (Koler-Matznick et al. 2005; MacNulty et al. 2007) to guide the development of our ethogram for the dhole.

To develop an activity budget for the dhole, we calculated the frequency of behaviors in each category and recorded the duration (in seconds) of each behavioral event. We analyzed videos in 10-s clips and considered behavioral events occurring in consecutive clips to represent single events. We estimated activity budgets by calculating the proportion of time that dominant males, dominant females, and subadults spent performing various behaviors; we did not study the behavior of pups. In each pack, only the dominant female is allowed to breed (Venkataraman 1998). Because our study coincided with the breeding season, dominant females were identified by the presence of teats or interactions with pups. Dominant males were identified by the presence of white hair on the neck and chest (Venkataraman 1998) and regular interactions with the dominant female. Subadults were smaller than adults and had little or no white hair. We standardized the data by calculating the percentage of time spent on each behavioral category by each group. We used chi-square tests to identify significant differences in the activity budgets of dominant males, dominant females, and subadults.

To identify temporal patterns in the dhole's activity budget, we used the statistical software R (ver. 3.0.1—R Development Core Team 2013, <http://www.R-project.org>). Following Ridout and Linkie (2009), we used the package “overlap” to calculate the kernel density activity pattern nonparametrically. Data are regarded as a random sample from the underlying distribution that describes the probability of a photograph being taken during each time interval. The probability density function of this distribution represents the activity pattern, which assumes that the animal is equally likely to be photographed at all times when it is active (Ridout and Linkie 2009).

RESULTS

We obtained 395.35 min (6.58 h) of video data collected at various times of the day and identified 3,394 behavioral events

contained in 1,654 10-s video clips (Table 1). Of the 139 videos we used for our analyses, 8 were contributed by forest guards and 2 by tourists. Most behavioral events were in the categories Locomotion (41%) and Resting (37%). Feeding, Social Behavior, Scent Marking, and Miscellaneous were of decreasing importance. The detailed ethogram is presented in Table 2. The activity budget showed that dholes spent 44.89% of their time in Locomotion (Fig. 2), suggesting that dholes spend a high proportion of their available time searching for food or patrolling their territories, and then Resting (40.01%). We also found that the percent occurrence (10.67%) of Feeding behaviors exceeded the proportion of time spent Feeding (4.76%; Table 1). We observed 2 previously undescribed behaviors that appeared to be associated with Scent Marking, which we termed “hind bounce,” and the less common ‘hind scrub’ (Figs. 3d and 3e; Supplementary Data SD2). Although not depicted here, ‘observation stand’ involved standing erect on the hind legs with the forelegs in mid-air. We observed this behavior when dholes were moving fast and then paused momentarily to assess their surroundings. Chi-square tests revealed significant differences in activity budgets among dominant males, dominant females, and subadults in all 6 behavioral categories (Locomotion: $\chi^2_2 = 89.764$, $P < 0.001$; Resting: $\chi^2_2 = 69.272$, $P < 0.001$; Social Behavior: $\chi^2_2 = 30.808$, $P < 0.001$; Feeding: $\chi^2_2 = 16.29$, $P < 0.001$; Scent Marking: $\chi^2_2 = 335.61$, $P < 0.001$; Miscellaneous: $\chi^2_2 = 480.87$, $P < 0.001$).

Dholes were also observed vocalizing when they engaged in other activities; consequently, we did not include vocalizations as a parent category for the ethogram. Nonetheless, we compiled a vocal repertoire for the dhole (Table 3), which included the characteristic whistle for which it is known as the “whistling hunter.”

We obtained 71 digital images of dholes from 7,584 camera-trap nights in 2014 and 37 images from 3,420 camera-trap nights in 2015. We also included time-stamped video clips that provided an additional 69 detections in 2015. During the 2 years of our study, dholes exhibited a bimodal activity pattern that peaked each day at approximately 0600 and 1800 h, suggesting a crepuscular pattern of activity. Figure 4 represents a comparison of the activity patterns between 2 consecutive years which showed an overlap of 78% ($\Delta = 0.78$).

DISCUSSION

Both the number of events and the time spent on each behavior were similar except for Feeding, which could be an artifact

Table 1.—Behavioral categories and the total time and events recorded for each category of dhole (*Cuon alpinus*) behavioral events in Tadoba-Andhari Tiger Reserve, central India.

Behavioral category	Total time (min)	Percent time spent on behaviors			Total number of events	Percent frequency of behaviors
		Adult males	Adult females	Subadults		
Locomotion	177.28	39.42	48.78	47.27	1,390	40.95
Resting	158.05	45.66	37.21	41.43	1,261	37.15
Social Behavior	24.62	6.02	8.37	7.35	220	6.48
Feeding	18.83	3.46	0.91	2.44	362	10.67
Scent Marking	10.44	5.32	1.21	1.33	136	4.01
Miscellaneous	5.73	0.10	3.51	0.18	25	0.74
Total	394.95	100	100	100	3,394	100

Table 2.—An ethogram of dhole (*Cuon alpinus*) behavior observed in Tadoba-Andhari Tiger Reserve, central India, 2014–2015.

Behavior	Definition
Locomotion	
Walk	Ambulatory gait; the slowest upright gait, in which 3 feet are supporting the body at all times, each paw lifting from the ground 1 at a time in a regular sequence.
Trot	A rhythmic 2-beat gait in which the diagonally opposite feet strike the ground together.
Tail chase	The individual notices and tries to grab its own tail in its mouth by circling around.
Circle	To move around an object or another individual in a tight circle.
Gallop	A 4-beat gait, often with an extra period of suspension during which all 4 feet are off the ground. The hind feet strike almost in unison.
Hunt-Approach	Travelling toward potential prey.
Hunt-Watch	Assessing a group of prey to (probably) decide upon a strategy to take down the quarry.
Hunt-Chase	To run after a prey (may be a group of animals or a single prey).
Hunt-Surround and eviscerate	Typical dhole behavior with the prey encircled followed by the pack members taking bites at the prey without necessarily killing it completely.
Resting	
Resting	Lying down with eyes open or closed.
Sphinx Rest	Lying on the belly with forelegs extended to the front, hind legs bent and resting close to the body on each respective side, or with the body twisted and both hind legs to one side. Head may or may not be lowered to rest on the forelegs or the ground.
Sit	Resting on the hocks and ischia.
Stand	Assuming an upright position with the weight of the body on all 4 legs.
Observation Stand	Standing upright on the hind legs with front legs folded to observe an object of interest above eye level or to avoid obstruction like tall grass and view the object of interest.
Social Behavior	
Amicable dhole	Lick, paw, or groom (allo-groom); often with a tail wag.
Snarl	Expose canines usually with ears down and raised hackles.
Submissive	Evade, cower, roll over with ears lowered.
Sniff dog	Nose to any area of a conspecific.
Solicit play	Bow, short charges with bouncing gait, swift and short charges with head lowered.
Body slam	Throwing self at another conspecific in a nonaggressive manner with tail wagging and open mouth. Accompanied often by bites.
Mount	The actor clasps the receiver with its forelegs around the flanks, or sometimes the back. Includes pelvic thrusting, and frequently is accompanied by hackle licking and hackle biting. Non-estrus clasping during play or to show dominance.
Feeding	
Eat	Act of ingestion of food items once prey was completely killed and dholes are at rest.
Drink	Lapping up water with the tongue.
Scent Marking	
Autogroom	An act of maintenance that an individual directs at its skin, coat, or claws and will usually involve licking, scratching, or shaking.
Sniffing	Investigating either an object or the air for olfactory cues.
Scent mark-Squat	To urinate on an object or place after investigating it (SQU).
Scent mark-Raised leg	To urinate on an object or place with 1 hind leg raised (RLU).
Scent mark-Handstand	To urinate on an object or place previously marked by another individual(s) by balancing on the 2 forelegs.
Scent mark-Hind bounce	Sitting on hocks with anus touching the ground accompanied by sudden springing at the same place.
Scent mark-Hind scrubbing	Scrubbing the buttocks across the ground to express anal glands.
Body rub	Rubbing body against an object, ground, or conspecific.
Trail	To follow a ground scent, sniffing the ground, bushes, and other vegetation, usually at a WALK or slow TROT.

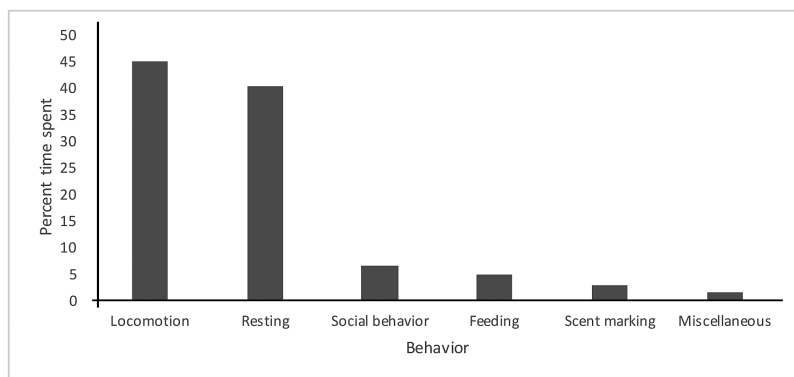


Fig. 2.—Percent time spent by dholes (*Cuon alpinus*) in each behavioral category (Locomotion, Resting, Social Behavior, Feeding, Scent Marking, and Miscellaneous) in Tadoba-Andhari Tiger Reserve, central India.

of small sample size. However, our observations suggest that dholes consume their prey quickly. Dholes were extremely alert while eating and drinking, which probably reflects competition with other predators in our study area. Based on the outcomes of observed hunts ($n = 7$), we believe that hunting may be a rather spontaneous event. The dominant male led the hunt on all but 1 occasion and was often observed chasing prey toward other pack members, as reported by [Johnsingh \(1980\)](#). Except for this behavior, however, the roles that other pack members

took during a hunt seemed to arise spontaneously. In all cases, prey were eviscerated before being killed.

Physical contact seemed to be important for maintaining the pack bond. The dominant male and female were highly social, frequently body slamming or rolling over each other. Subadults were more amicable toward each other than with adults. The behavioral events grouped under the Miscellaneous category also involved considerable physical contact ([Fig. 3a](#)). Mating was observed on 1 occasion, during which the dominant male mounted the female several times ([Fig. 3b](#)). The dholes did not exhibit a copulation knot, which is characteristic of the canid copulation process wherein the dogs assume a back-to-back position. A brief copulatory knot was reported in African wild dogs ([Kleiman and Eisenberg 1973](#)). In contrast to [Fox's \(1984\)](#) contention, dholes also did not lie next to each other after mating. On 1 occasion, the female mounted the male and, on another, the male mounted the female from the front ([Fig. 3c](#)).

Dholes were commonly observed to rest at trail junctions or along forest paths for short periods. Whether dhole packs maintain their territories by scent marking is not clear from our observations, but we did observe significant territorial overlap among neighboring dhole packs. As observed in African wild dogs ([Johnson 1973](#)), dominant males tend to scent mark more frequently than other groups. Dominant males and females exhibited a scent-marking ritual whereby they took turns marking the same spot, and then the male ended the ritual by raising his leg and urinating ([Figs. 3g and 3h](#)). On several occasions, however, we observed the female compulsively scent marking over the male. This behavior has also been reported in wolves ([Rothman and Mech 1979](#)), golden jackals (*Canis aureus*—[Golani and Mendelsohn 1971](#); [Moehlman 1983](#)), crab-eating foxes (*Cerdocyon thous*—[Brady 1979](#)), and bat-eared foxes (*Otocyon megalotis*—[Lamprecht 1979](#)). This cross-marking ritual is believed to synchronize reproductive states and inform conspecifics of the pair's bond ([Rothman and Mech 1979](#)). On 2 occasions, dholes cross-marked on tiger scent posts by rubbing their body on the ground next to the post or by squatting and urinating. Cross-marking intensively on the scent posts of other species has also been observed in some species of mongoose ([Ewer 1973](#)).

[Johnsingh \(1980\)](#) described 2 studies of African wild dogs (*Lycaon pictus*—[Van Lawick-Goodall and Van Lawick-Goodall 1971](#); [Keller 1973](#)) in which they were observed balancing on their forelegs while urinating and scent marking over the marks of a pack member. We observed such hand-stand urination behavior in dholes on 4 occasions involving both males and females ([Figs. 3g and 3h](#); [Supplementary Data SD2](#)). This behavior has also been observed in bush dogs (but

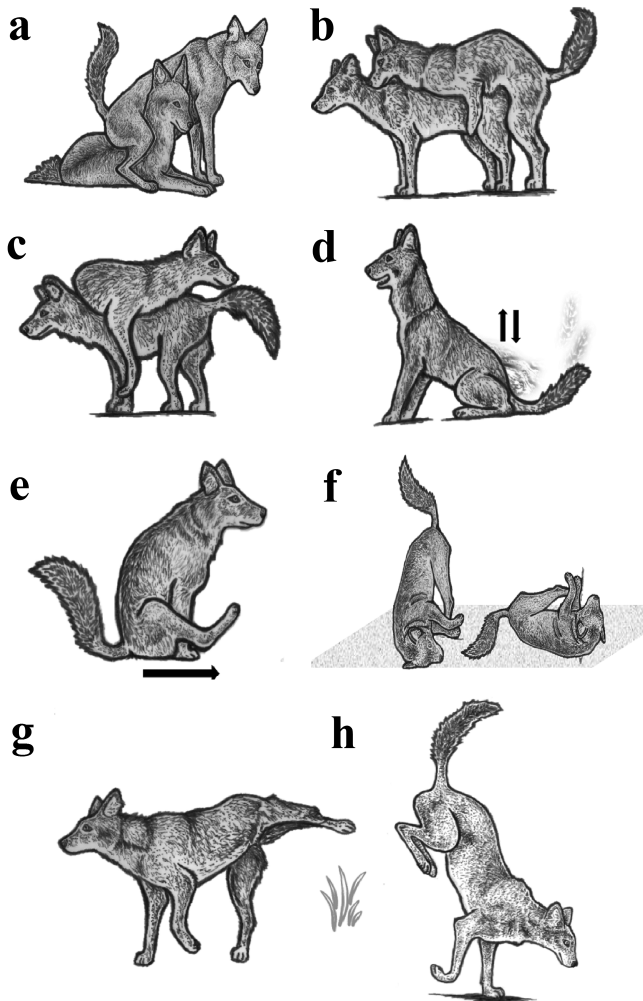


Fig. 3.—Illustrations depicting the scent-marking behaviors of dholes (*Cuon alpinus*): a) Miscellaneous, b) Typical Mount, c) Front Mount, d) Hind bounce (scent-marking behavior), e) Hind scrub (scent-marking behavior), f) Body Rub (scent-marking behavior), g) Raised-Leg Urination (scent-marking behavior), h) Hand-stand Urination (scent-marking behavior).

Table 3.—A vocal repertoire of dholes (*Cuon alpinus*) in Tadoba-Andhari Tiger Reserve, central India.

Event	Definition
Whistle	Emit a clear, high-pitched sound by forcing air through the nose
Yelp	A short, sharp, high-pitch cry, especially of pain or alarm, mainly by young individuals
Screech	High-frequency cry by subadults or adults during amicable interactions between 2 individuals as a result of being momentarily startled
Bark	A typical dog bark (heard only when alarmed)
Chuckle	A low-pitched, 5-note sound accompanied by screeching when threatened, alert, scared

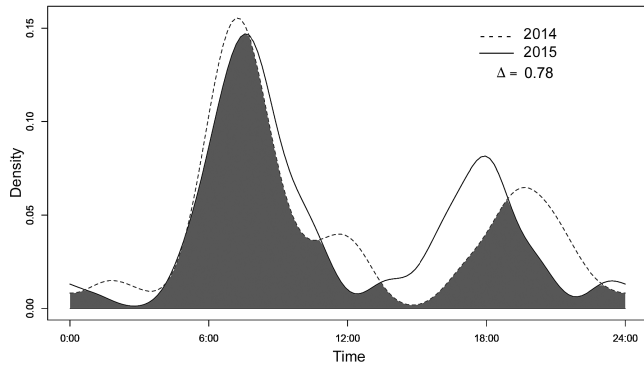


Fig. 4.—Graph showing dhole (*Cuon alpinus*) activity patterns in Tadoba-Andhari Tiger Reserve, Maharashtra, India for 2014 and 2015. Between these years, there was an overlap of about 78%.

only among females—Porton 1983; Müller-Schwarze 1999), genets (*Genetta genetta*—Wemmer 1977), and dwarf mongooses (*Helogale parvula*—Rasa 1973). Among giant pandas (*Ailuropoda melanoleuca*), only the males were observed to scent mark this way (Kleiman et al. 1979). The function of this behavior is still unknown, but it may enable animals to mark higher on scent posts, enabling it to last longer (Ewer 1973), or provide a visual cue for identifying an individual's sex (Porton 1983).

The characteristic erratic bouncing of a dog over grass or ground was observed on several occasions, which we called the “hind bounce” (Fig. 3d). This behavior probably helps to deposit secretions of the anal glands onto the substrate. Another behavior that we called the “hind scrub” (Fig. 3e), which is very similar to “scooting” whereby a domestic dog expresses its anal glands when in discomfort. Among dholes, however, the hind scrub seems to be important for scent marking because we usually observed it in association with other scent-marking events and it was done by apparently healthy individuals (usually the dominant male). Body rubbing was a common method of scent marking. Dominant males rubbed their bodies against the dominant female, possibly signifying mate guarding (Ewer 1973), and both sexes were also observed rubbing their bodies on the ground (Fig. 3f).

Some aggression between pack members was observed when the kill was small (e.g., chital or sambar fawns) and had to be shared. Mild aggression at a kill site with diminishing food has been reported previously in wolves, foxes, and even dholes (Macdonald 1977; Packard et al. 1980; Venkataraman 1996). For larger kills, dominant males stood guard until the other pack members had finished feeding before taking their turns to feed. Pack members took turns feeding, but in no discernable pattern. Pups fed first at the kill and were also fed organ meat by subordinates. Similar observations were reported by Venkataraman (1996).

Dholes are considered to be primarily diurnal in habit (Johnsingh 1980; Acharya 2007; Kawanishi and Sunquist 2008; Majumder 2011); however, we observed a crepuscular activity pattern similar to that reported by Nurvianto et al. (2015) in Java, Indonesia. The dhole's vocal repertoire was similar to that reported by Johnsingh (1982), with the exception of “Chuckle”

(Table 3). Additional research focused on vocalizations will be needed to compile a comprehensive vocal repertoire for the dhole.

In India, dholes have been extirpated from 60% of their historical range (Karanth et al. 2009, 2010), and only a few zoos have dholes. The dhole's status in India has been assessed recently (Bashir et al. 2014; Srivathsa et al. 2014), but there have been no recent studies of their behavioral ecology or the evolution of social behavior in dholes. Fundamental behavioral studies of endangered species can help conservationists assess the risk of growing anthropogenic pressures, plan captive breeding programs or reintroductions, and monitor extant populations (Reed and Dobson 1993; Caro and Sherman 2011). The loss of behaviors that are critical for survival and reproduction can, in turn, threaten a species' survival. In the Bavarian Alps, human disturbance caused the black grouse to abandon its lekking sites (Zeitler 2000), potentially threatening their reproductive success. Frid and Dill (2002) provide additional examples of how human disturbances can alter key animal behaviors. A thorough understanding of the dhole's behavioral repertoire can help to identify and conserve characteristic behaviors that are essential for their population persistence. Empirical studies based on the ecology, demographics, and genetics of dholes would be crucial for future conservation efforts.

SUPPLEMENTARY DATA

Supplementary Data SD1.—A video showing dholes not being affected by the presence of tourists and other humans in Tadoba-Andhari Tiger Reserve, central India.

Supplementary Data SD2.—A video compilation of scent-marking behaviors (hind bounce, hind scrub, and hand-stand urination).

ACKNOWLEDGMENTS

We thank the Maharashtra Forest Department for providing permission to undertake this study, and the National Tiger Conservation Authority, Maharashtra Forest Department, and the Wildlife Institute of India (WII) for financial assistance. We also thank the Director, Dean, and Research Coordinator (WII), Chief Wildlife Warden Maharashtra, Field Director Tadoba, Deputy Director (Core and Buffer) Tadoba, TATR Long-term tiger monitoring team, and our field staff for logistical support and permits. We are grateful to L. Hennelly for her wonderful illustrations of dholes. Lastly, we thank the reviewers and editors for their invaluable comments and suggestions which helped improve our manuscript.

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Submitted 30 December 2015. Accepted 8 August 2016.

Associate Editor was Keith Aubry.