PHYSICAL AND BEHAVIORAL DESCRIPTION OF A CAPTIVE SAOLA, *PSEUDORYX NGHETINHENSIS*

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Since the discovery of the saola, Pseudoryx nghetinhensis, in central Viet Nam in 1992, little has been learned about this new bovid's behavior or ecology, and its taxonomic position remains in question; some place it in the subfamily Bovinae, others in Caprinae. In January 1996, a pregnant female was captured in central Laos and placed in a nearby menagerie. This was the first adult saola seen by the outside world and provided an opportunity to gather basic information about the species. The animal survived 18 days, during which time notes were made of her morphology and behavior. Noteworthy among physical traits were size and complexity of her maxillary glands and presence of pored skin nodules corresponding to white markings on the face. The saola exhibited remarkably tame behavior among humans, but intense stereotyped reactions toward domestic dogs. Characteristics such as round pupils and presence of four mammae fell more into the pattern of Bovinae than Caprinae. Other traits such as unique development of the maxillary gland were unlike either subfamily. This was among thirteen saola known to have been captured in Viet Nam and Laos since 1994, all of which soon died except one that was released. Consequently, basic field studies of the animal's requirements should probably precede any further attempts at live capture.

Key words: Pseudoryx nghetinhensis, saola, behavior, bovid, glands, Laos

Little has been learned about the ecology, behavior, or phylogeny of the saola (Pseudoryx nghetinhensis) since its discovery from horns in hunter's houses in Viet Nam in 1992 (Dung et al., 1993). Although known to be a bovid, little further consensus has been reached on its taxonomy. Based on DNA analysis, Dung et al. (1993) placed saola in the subfamily Bovinae and within the Bovinae provisionally with nilgai (Boselaphus tragocamelus) in the tribe Boselaphini on the basis of some shared morphological features. Schaller and Rabinowitz (1995) noted resemblances to the tribe Tragelaphini but also point out that if a different set of features was considered saola more closely resemble the anoas, primitive Bovini. Based on a detailed analysis of the skull and dentition, Thomas (1994) concluded that saola did not belong in Bovinae but was allied more closely to the subfamily Caprinae, represented in southeastern Asia by serows (Capricornis) and gorals (Nemorhaedus).

Despite surveys for saola in Viet Nam (Dung et al., 1993; Kemp et al., 1997; S. Dawson, in litt.) and Laos (Schaller and Rabinowitz, 1995; W. G. Robichaud, in litt.), biologists have not yet observed it in the wild and attempts to photograph it with camera traps have not succeeded (S. Dawson, in litt.). In 1994, two juveniles were captured by villagers near the border of Laos and Viet Nam and sent to Hanoi, Viet Nam, where they were kept in the botanical garden of the Forestry Inventory and Planning Institute. These were the first live saola seen by anyone but local people in its small range, but each survived <5 months in captivity (D. Hulse, World Wildlife Fund for Nature, pers. comm.).

On 8 January 1996, Hmong hill tribesmen in the central Lao province of Bolikhamxay captured a pregnant saola, ca. 15 km northwest of the northern boundary of



Fig. 1.—The adult female saola in the Lak Xao menagerie, Laos in January 1996 (photograph by W. G. Robichaud).

the Nakai-Nam Theun National Biodiversity Conservation Area. Two days later, it was moved by helicopter to a small semiprivate menagerie in the nearby town of Lak Xao ("B. Lak 20" on Lao government topographic maps). This was the first adult saola seen by the outside world and provided an opportunity to gather basic information about this enigmatic species. The animal survived just 18 days in captivity but during this time, observations were made of her physical characteristics and behavior. These observations are the first detailed description of a living saola. Comparisons are drawn to members of those bovid subfamilies and tribes that have been suggested variously as the taxonomic home of saola.

MATERIALS AND METHODS

The saola (Fig. 1) was kept by Bolisat Phattana Khet Phoudoi (BPKP), a parastatal development company in central Laos, at its small menagerie in the town of Lak Xao, Khammouane Province. The animal was housed in a concrete-floored rectangular cage 4.35 m by 4.1 m by ca. 2 m high. The pen had a cave-like shelter of rock and concrete, 1.75 m² by ca. 1.25 m high, and a column of rock and concrete ca. 1-m diameter by 0.75 m high. The enclosure had housed a single southern serow (*Capricornis sumatraensis*) that was moved to an adjoining cage when the saola arrived.

The saola was fed fresh vegetation generally in the morning and afternoon, at which times the concrete floor of the pen was usually swept and sometimes hosed with water. The animal had access to a plastic pan of water for drinking and was given access to salt after ca. 2 weeks. Visitors were allowed to approach the cage and sometimes numbered ≥20/day.

When the saola arrived in the menagerie on 10 January 1996, she suffered from a injured right eye and minor abrasions and she favored her left rear leg—injuries apparently sustained during her capture. The animal was treated with injections of antibiotics by staff of the Carnivore Preservation Trust in Lak Xao and was subsequently examined by W. Karesh, field veterinar-

TABLE 1.—Measurements of a captive female saola (Pseudoryx nghetinhensis) from Laos.

Variable	Measure- ment (cm)
Height at top of shoulder	84
Tallest height along the back	96
Clearance between belly and ground	45.5
Head-body length (along dorsal contour)	150
Tail length	23
Ear length (right)	11.5
Neck girth at narrowest point behind jaw	43.5
Body girth at broadest point (belly)	108a
Horns	
Interior distance between bases	4
Tip spread	25
Basal circumference (right/left)	12.5/13
Length along dorsal contour (right/left)	43/42.5
Length of chord (right/left)	42/41

^{*} Animal pregnant, measured after it died in thin condition.

ian of the Wildlife Conservation Society. Karesh diagnosed mild pneumonia, discontinued injections, and treated the animal with oral and topical antibiotics; the mild pneumonia, eye ailment, and abrasions improved.

I began observations on 11 January and watched the animal from a distance of ca. 7 m. She appeared surprisingly oblivious to my presence at this range but did not otherwise appear unduly stressed or lethargic. Observations totaled 39 h spread over 9 days between 11 and 26 January, including about 5 h of darkness (defined as any period when there was insufficient light for reading) about equally split between evening and pre-dawn. Observations ended with the death of the saola on the evening of 26 January. Cause of death was undetermined, but gradual weight loss was noted, and it is possible the animal received an inadequate diet.

RESULTS

General physical description.—Descriptions of saola appearance, based on a few skins and other remains, were given by Dung et al. (1993, 1995) and Schaller and Rabinowitz (1995). Further details were gathered from observations of the captive female. Various body measurements were taken while the animal was alive—unrestrained and in an apparently relaxed natural posture (Table 1). They match measure-

ments derived from saola remains with the exception of two horn measurements: width between tips and length of female horns. Of the 22 sets of horns measured by Dung et al. (1993, 1995) and Schaller and Rabinowitz (1995), maximum tip spread was 20 cm, a measurement significantly exceeded by horns of the captive animal (Table 1). In fact, tip spread was nearly double the mean of 17 horn sets measured by Dung et al. (1993). Furthermore, her horns were longer than those of all seven females and five of 11 males listed by Dung et al. (1995), who did not state, however, how they assigned sex to the horns that they measured. It may have been from information supplied by local hunters, which is sometimes inaccurate.

The female's horns diverged markedly with a distance of 7.5 cm between basal centers compared to 25 cm between tips. However, Dung et al. (1993, 1994) considered divergence to be characteristic of male horns only with those of females almost parallel. Schaller and Rabinowitz (1995) disagreed, finding no significant difference in horn divergence between sexes. Dung et al. (1995) clarified that the angle of horn divergence at the base was the same for males and females, and therefore divergence at the tips was a function of horn length only. Yet a pair of long horns (identified as female) pictured in Schaller and Rabinowitz (1995) were clearly parallel or slightly convergent, and the authors reported occasional cross-tipped horns. Clearly, there is wide variation in orientation of saola horns within and between sexes.

There also appears to be variation in cross-sectional shape of horns. Dung et al. (1994) stated that saola horns were peculiar in being almost circular in cross-section, but in the captive female, that was true only at the bases; her horns became strongly ovoid toward the tips. More precisely, toward the tips, they flattened in cross-section into isosceles triangles with rounded corners; the long base of the triangle formed the anterior (i.e., upper) face of the horn. Schaller and Rabinowitz (1995) also noted

oval horns but, in contrast, described the apices of the ovals as pointing anterior in cross-section, a 90° shift in orientation from the captive female's horns. Lateral and medial surfaces of the female's horn bases were rough and pitted, a characteristic found in other saola horns (Schaller and Rabinowitz, 1995).

Several sources (Dung et al., 1994, 1995; Schaller and Rabinowitz, 1995) report that saola means "spindlehorn" and the name derives from the similarity in shape of a pointed saola horn to a weaving spindle. This is not quite correct. In the Lao and Lao-related languages in the animal's range on both sides of the Laos-Viet Nam border, saola is the word for a pair of parallel wooden posts that support part of a local apparatus that is similar to a spinning wheel (sao = post(s); la is the apparatus). Indigenous people gave this name to the animal because the tapering posts resemble a pair of saola horns. An approximate translation of the species' common name, then, is "spinning wheel posts." In pronunciation, saola has only two syllables and rhymes with the English words "now, ha."

Pupils of the saola's eyes were round, the irises were dark brown, and eyes were reflective, glowing orange in a flashlight beam. The flesh of the nose was chocolate brown. The tongue of the animal was very long; the saola was able to extend it at least 16 cm to lick her eye and upper portions of her face. The upper surface of the tongue was covered by fine rearward-pointing barbs, and fleshy margins of the inside of the mouth were covered with large (5 mm long by 3 mm basal diameter) cone-shaped spicules.

The saola had four mammae. They were distended, but there was no lactation indicating that she had previously, but not recently, nursed young (W. Karesh, pers. comm.). Based on tooth wear, the saola's age was estimated at 8–9 years, and her weight 5 days before her death was estimated at 85 kg (W. Karesh, pers. comm.).

Pelage.—Hair on the upper parts of the

female was straight, 1.5-2.5 cm long, and shortest on the neck and head. The coat was soft and rather thin considering that at least part of the animal's range encompasses a montane habitat that is very damp and cool for several months of the year (Dung et al., 1993: Schaller and Rabinowitz, 1995: Timmins, in press). Hair on the belly and insides of the forelegs was curly and thicker than elsewhere, giving a woolly quality. Pelage color of the upperparts of the body was medium chocolate brown without any of the reddish tones found in some skins examined by Dung et al. (1993). Brown pelage of the neck, starting abruptly forward of the shoulder, was paler. As a consequence, the neck in side view appeared as a pale patch between darker pelage of the trunk and head. The skin of an inferred female examined by Dung et al. (1994) had white patches on the sides of the neck, but the female that I observed lacked any such markings, although there were diffuse white patches on the throat. A 0.5-cm wide medial black dorsal stripe extended from between the shoulders down the back and faded out in the top of the tail—a feature apparently shared by all saola material thus examined (Dung et al., 1993). The belly was brown but paler than the upper body and similar in shade to the neck.

The tail was tricolored and split evenly into three horizontal bands of, from base to tip, the same medium brown of the upper body, cream, and black. With the tail relaxed, these bands blended into corresponding zones of color on the rump and hind-quarters (Fig. 2). A drawing of a saola in Dung et al. (1994, 1995) depicted the tail held at an angle, but in the living animal, it normally hung flat against the body. A cluster of white whiskers ca. 2 cm long protruded from the end of the chin and presumably had a tactile function.

Saola have several striking markings on various parts of their pelage; position, prominence, and uniqueness of some suggest an intraspecific behavioral function. Those described by (Dung et al., 1993)—

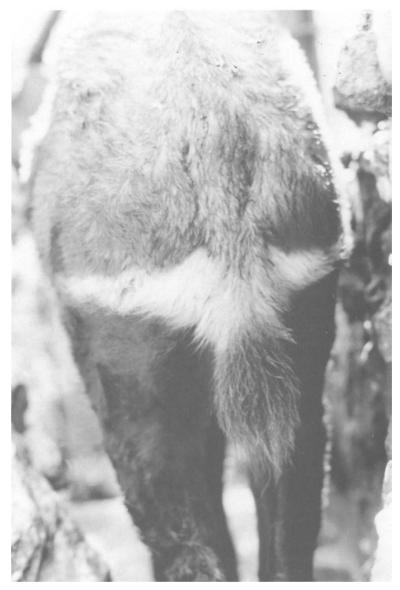


Fig. 2.—Tail of the saola showing tricolored pattern (photograph by W. G. Robichaud).

namely white patches on the face, white bands above the hooves, and a creamy band across the rump—were consistent with markings on the female. The number and distribution of white spots and slashes on the sides of the captive female's face (Fig. 3) matched those in a calendar photograph of one of the juveniles kept in Hanoi but differed markedly from those in the portrait of a saola in Dung, et al. (1994), which pre-

sumably was based on a skin. The captive female also had a sharply defined black chinstrap with single black spot anterior (Fig. 4).

Glands.—Saola possess a pair of well-developed maxillary glands (Dung et al., 1993; Schaller and Rabinowitz, 1995). The external fleshy portions on the captive female's were very large. Each gland comprised a roughly rectangular shallow de-



Fig. 3.—White facial markings of the saola and maxillary gland in closed position (photograph by W. G. Robichaud). According to Hmong hill tribesmen, the twig on the collar is medicinal and repels flies.



Fig. 4.—Throat and chin of the saola showing wide black chinstrap (photograph by W. G. Robichaud).



FIG. 5.—Maxillary gland of the deceased saola with pores visible along the inside edge where the lid joins the gland; the lid was held in about the same position by the saola each time she opened and scent marked with the gland (photograph by W. G. Robichaud).

pression along the upper muzzle, 9 cm long by 3.5 cm wide by 1.5 cm deep. The entire gland was covered by a muscular flap or lid, 0.8 cm thick, which the animal could raise ca. 3 cm like an awning to expose the gland (Figs. 3 and 5). These may be the largest maxillary-preorbital glands of any extant animal species, and such a highly developed lid is probably unique.

The glandular depression beneath the lid was covered by sparse flattened hair and coated by a thick paste-like grayish-green secretion with a very pungent and foul odor, reminiscent of the musk of mustelids. A row of about eight 1-mm diameter pores pierced the upper edge of the depression and about six other pores were scattered just below this. The pores penetrated ca. 5 mm deep to bone and were probably the sites of secretion into the gland. Some smaller pores were found on the underside of the lid.

Concealed in the white markings on the sides of the face were several small dermal nodules, singly or in clusters of two or three. Each white facial spot and slash had an associated nodule or nodule cluster, and the nodules occurred nowhere else on the face. Representative nodules measured 3 by 2 mm high and 2 by 1 mm high. Two that were closely examined were pierced on top by single pores, which implied a secretory function, possibly as scent glands. A few long (2–2.5 cm) white or black whisker-like hairs protruded from most of the nodules. No glands were found on the legs, and it is not known if pedal glands were present.

Tracks.—The saola left tracks in modeling clay that measured 5.0-6.0 cm long by 5.3-6.4 cm wide for the forehooves and 6.0 cm long by 5.7-6.0 cm wide for the hindhooves. Tracks were intermediate in size between those of the two widespread cervids in Laos, Indian muntjac (Muntiacus muntjak) and sambar (Cervus unicolor), with a different shape. Muntjac and sambar tracks are widest near the rear and thus heart-shaped; the saola's tracks were widest across the middle, relatively broader (width about equaled length, unlike cervid tracks),

and the tips were more blunt. However, they were not nearly as rounded at the tips as tracks of wild pig (Sus scrofa). They were closer in size and shape to tracks of serow, but serow tracks differ in having widely splayed tips.

General behavior.—The most striking aspect of the captive saola's behavior was her tameness in the presence of humans. Within a day of arriving at the menagerie (3 days after her capture), she seemed to ignore humans who entered her cage and calmly accepted food from the hand. Within 2-3 days, she could be touched and stroked without apparent reaction. It is unlikely that this immediate tameness was a manifestation of the stress of her captivity or injuries because she fed, drank, groomed, and showed interest in her surroundings (e.g., stretching her neck to sniff a hand), and her feces and urine appeared healthy. Furthermore, she reacted strongly to dogs.

The saola's tameness contrasted with the skittish behavior and fear of humans shown by the neighboring serow and some muntjacs in the menagerie, even though these had been in the zoo >1 year. Information from local people familiar with saola suggest that tame behavior of the captive female may be typical of the species. One said that saola are known locally as the "polite animal" because "they always step slowly and quietly through the forest" and are not obstinate or excitable. Another stated, "The only thing saola are afraid of is dogs." This informant also reported that in August or September 1995 Hmong tribesmen in another area of Bolikhamxay Province captured two saola (adult and juvenile males) that were so tame the Hmong kept them in their village like pets for 2 weeks. The Hmong then tried to walk them ca. 60 km to Lak Xao, but the animals died on the way.

The captive saola appeared to be diurnal, or perhaps diurnal and crepuscular. She lay in a posture of apparent deep rest—neck extended, chin resting on the ground and eyes closed—more often at night than during the

day. This contrasted with the nearby serow, which was often active at night. These observations were biased, however, because during the day the saola was exposed to unfamiliar stimuli such as people, flies, and regular feedings, which may have induced some activity. Dung et al. (1995) reported from anecdotal information that saola in the wild are active both day and night. Local people in the saola's range in Laos have said that it is active mornings, late afternoons, sometimes at night, and not when the sun is overhead. When lying down, the saola without exception kept her forelegs tucked back under her body, while the serow frequently lay with them outstretched to front, in the manner of a dog.

Feeding and drinking.—The captive saola was provided daily three species of leafy plants to eat, provisionally identified as Homalomena (Family: Araceae), Asplenium (Family: Aspleniaceae), and a species of broad-leaved shrub or tree possibly in the family Sterculiaceae (P. Phaengsintham, National University of Laos, pers. comm.). Those plants reportedly form part of the species' diet in the wild. The saola ate all three but showed some preference for the unidentified Steruliaceae. She fed at most times of the day but seldom during periods of darkness.

The saola, unlike the serow, rarely jerked or pulled vegetation when feeding. When feeding on branches of the Steruliaceae, for example, she closed her mouth over a column of leaves along a stem with the axis of her head parallel to the stem and perpendicular to the leaves and chewed slowly with her molars and premolars until she had cut the petioles. Pulling or yanking of vegetation typical of many ungulates was almost never observed. Occasionally she pulled leaves into her mouth by grasping them with her long tongue. On one occasion, she consumed one-and-one-half boluses of her fresh dung (R. J. Timmins, Wildlife Conservation Society, pers. comm.). She was observed to ruminate several times, most often in the morning.

The saola sometimes consumed large quantities of water. She once drank for ca. 4 min, with five pauses to lift her head and lick her nose and muzzle. During these 4 minutes, she took 58–59 draughts of water.

Urination and defecation.—During both defecation and urination, the saola spread her rear legs and squatted with her rump low. Feer (1994) found that, unlike some other ruminants, captive female mountain anoas (Bubalus quarlesi) drop the rump significantly lower during defecation than during urination. The female saola, however, held the hindquarters quite low during both actions. Urination and defecation were performed separately, which is the normal bovid pattern. The saola sometimes squatted with her rump lowered for 0.5–3.0 min before and after passing urine or feces.

The first bout of defecation was observed 4 days after the saola's capture and lasted ca. 3 min during which she dropped about eight boluses. Two representative boluses measured 7.5 cm long by 4.5 cm diameter and 7.5 cm long by 5.5-6.0 cm diameter. These were quite large for a ruminant of the saola's body size (G. Schaller, Wildlife Conservation Society, pers. comm.). Boluses were formed of a concretion of moist but separable ovoid pellets. One of the boluses measured above was formed of 46 such pellets, each measuring ca. 2 by 1 by 0.75 cm. This type of feces was passed consistently by the animal during her captivity, with the exception of some loose diarrhetic stools shortly before her death.

The captive saola's feces, being a concretion of pellets, resembled those of a captive sitatunga (*Tragelaphus spekei*) pictured in Nowak (1991) and were unlike the soft loosely formed droppings of cattle. S. Dawson (in litt.) stated that in the field it was difficult to distinguish between feces of saola and serow but gave no description of either. However, feces of the menagerie's serow differed markedly from those of the saola, even though both animals were fed the same leafy diet. The serow's feces did not form boluses but were discrete compact

pellets 1.5 by 0.75 by 0.5 cm, typical of other Caprinae.

Grooming.—The saola spent much time licking parts of her body with her very long tongue. For example, during seven scattered 1-min timings, she licked her body 7, 68, 0, 22, 42, 34, and 12 times ($\bar{X} = 26$ times/ min). Eves and face were licked most often. then flanks, shoulders and forelegs. She also regularly licked her left rear hoof, which was probably injured. She often followed bouts of eating, drinking and rumination, in particular, with bouts of licking her muzzle. However, by far the principal function of licking was apparently to disperse flies, and it was the most frequent technique she used for this. Licking to disperse flies is uncommon in other ungulates, although it is known in the Giraffidae (W. Karesh and R. Cook, Wildlife Conservation Society, pers. comm.). Licking was common among captive mountain anoas (Feer, 1994), but it was described only in a social context as being the most common nonaggressive nonsexual contact between individuals.

Scent marking.—The captive saola was observed to scent mark with the maxillary gland five times-the first on her third day in the menagerie. On each occasion, she marked protruding points of rock on the short rock and concrete column in her pen. She once lowered her head among freshly cut branches and opened the gland, although she was not seen to bring the gland into contact with any of the stems or leaves. Captive mountain anoas, which lack maxillary or preorbital glands, also were observed inserting their heads among small branches in a stereotypical fashion not associated with feeding, but the function was not clear (Feer, 1994). In a typical instance of scent marking, the saola flared open the flap covering each gland and stroked the underside of one flap three times across a point of rock. Later examination showed that some of the pungent secretion was deposited on the site.

Breeding.—After the saola died she was

found to be carrying a male fetus that was crudely weighed at 800–1,000 g. Length along the body contour from nose to rump was 38 cm. The fetus was virtually hairless, but the body, limbs, external features of eyes, nose, ears, genitalia, facial nodules, and maxillary glands were well formed, and it was easily recognizable as a saola. Circular plaques were present on the cranium where horns would form.

On the basis of the measurements and examination of photographs of the fetus, Karesh and fellow veterinarian R. Cook of the Wildlife Conservation Society concluded that pregnancy was in its second trimester. Although gestation period of saola is not known, gestation periods of two Tragelaphini similar in size to saola, sitatunga and nyala (Tragelaphus angasi), are 247 days and ca. 220 days, respectively (Nowak 1991). If the average of these 2 periods, 234 days or ca. 33 weeks, is taken as a benchmark for saola, the fetus would have been 11-22 weeks old. That places conception between late August and mid-November (mid-rainy to early dry season in Laos) and birth between mid-April and late June (late dry to early or mid-rainy season when it is warm). This is consistent with information gathered by Schaller and Rabinowitz (1995) and therefore suggests a fixed breeding season. These dates would remain about the same if the gestation period of serow, of ca. 7 months (Nowak, 1991) was used instead. A freshly killed giant muntjac (Megamuntiacus vuquangensis) also was found to be pregnant with a small fetus in January in central Laos (Schaller and Vrba, 1996). If the giant muntjac and her fetus had lived, birth would have occurred more and less concurrently with the birth period calculated for saola near the start of the warm rainy season.

Vocalizations.—The saola was heard to bleat on three occasions early in her captivity. Once she gave two bleats separated by a 5-s pause, another time two bleats separated by a 1-s pause, and she once gave a single bleat. Each bleat was a soft mono-

tone of ca. 1-s duration with little of the familiar vibrato quality typical of domestic goats.

Defensive-aggressive reactions.—In her first 2-3 days in the menagerie, the saola responded to a hand touching her back with mild backward thrusts of her horns. On the saola's fourth day in captivity, a small dog about the size of a large house cat approached the cage within ca. 7 m of the saola, which was lying down. The saola's head immediately came up, her ears came forward, and she stared straight at the dog. I approached to within 2 m of the saola, but she paid no attention and followed only the movements of the dog. She displayed more attention to this small dog than she had thus far shown to any human or to the serow in an adjoining pen.

In the evening of the same day, the small dog approached within 3 m of the saola while she was tied in the rear yard of a house near the menagerie. The saola reacted in a seemingly stereotyped fashion. Standing stiffly and facing the dog, she brought all four hooves together, thereby arching her back. She dropped her head and pointed her muzzle down and back a few degrees toward her forelegs, thereby bringing the tips of her horns forward toward the dog. Her ears pointed up and faced backward, their backs pressed against the posterior face of her horns. Her tongue hung from her mouth, and she drooled. At the same time, she flared her maxillary glands and snorted two or three times-each snort consisting of a loud exhale through the nostrils of ca. 2-3 seconds duration. A scent of musk in the air was noted (eversion of the preorbital glands when in the proximity of potential predators has been observed in blackbuck, Antilope cervicapra, and sambar; Pocock, 1910). The saola relaxed those postures when the dog moved away.

Similar behavior in response to the approach of a small dog during the saola's first day in the menagerie was observed by others (M. Etter and N. Ruggeri, Wildlife Conservation Society, pers. comm.). This

behavior was not observed at any other time, nor were there any other instances of approach by dogs. Local villages repeated what others had told Schaller and Rabinowitz (1995), that a saola pursued by domestic hunting dogs invariably makes a stand in a stream with horns lowered and her rump to a boulder or to the streambank. The female was reportedly lassoed and captured when she did this.

DISCUSSION

Examination of DNA, cranial features, and general morphology have led to different conclusions about the phylogeny of saola. More than 5 years after the species' discovery, we are still uncertain if the saola evolved within Bovinae, Caprinae, or another group. Although genetic analysis will be the best means to pursue a solution, it may be worthwhile to consider manifestations of the genetic makeup in the living animal.

Several external physical traits of the captive saola were more akin to Bovinae than Caprinae: round pupils, four mammae, long tongue, and pelage that is short, straight and soft. In addition, several of her behaviors differed from serow and Caprinae in general and were more typical of Bovinae, such as frequent licking and resting with the forelegs tucked under the body and never outstretched. Other characteristics of the captive saola were typical of neither Caprinae nor Bovinae, such as the unprecedented development of her maxillary gland, presence of facial nodules, and the frequent use of licking to disperse flies. In summary, these limited observations of a single living saola suggest an affinity closer to Bovinae than Caprinae with the possibility that it belongs in neither subfamily.

The female saola was captured in January in the middle of the cool dry season in a relatively low (ca. 700 m above mean see level) degraded area. Local informants reported that this was not unusual for the time of year, but that in June and July, which are warm and rainy, saola can be found only in

densely forested mountains near the Viet Nam border. Dung et al. (1994) reported a pattern of seasonal altitudinal movements by saola in Viet Nam. They believed that the movements were related to availability of water; in the dry season, mountain streams dry up and saola move into lower areas with more abundant water. This is unlikely in Laos; when the female was captured in January, saola habitat along the border is quite wet, unlike the rest of the country at this time. The northeast monsoon, which affects little of Laos, spills from Viet Nam through border passes in the Annamites Chain and penetrates several kilometers into Lao territory, bringing months of near-constant cold mist and rain at a time when the rest of Laos is dry and sunny. In light of the saola's thin short coat, perhaps animals on the Lao side move in winter away from the Vietnamese border into other habitat not to find water but to escape cold wet weather. Alternatively, reported concentrations of saola in dense forests in June and July could be a consequence of the onset of the birth season.

The significance of the curious pored nodules on the sides of the saola's face is unknown; I could not find any reference to their presence in other taxa. Their association with long stiff hairs could mean a tactile function, but presence of pores suggests that they are scent glands, which also would be consistent with presence of hairs as wicks. It is noteworthy that the nodules correspond precisely to the position of the white facial markings, resulting in the juxtaposition of a visual signal with what may be an olfactory one. If the nodules are indeed scent glands, it can be expected that either saola deposit scent by rubbing nodules on some object, trees or another saola, for example, or other saola smell nodules directly without an intermediate substrate for the scent. If saola rubbed these nodules on objects, this would provide no explanation for correspondence of nodules to white facial markings, and the captive female was never observed to rub this area on anything during her captivity. Perhaps other saola sniff the nodules and are guided where to sniff by the facial markings.

Perhaps the most striking characteristic of the saola was her tame acceptance of people, which belies a tragic frailty in captivity. In addition to this female and the two young animals kept briefly in Hanoi, at least 10 other saola have been captured in Laos and Viet Nam since 1994 (W. G. Robichaud, in litt.). The only animal to survive its captivity was one reportedly released back into the wild by the Lao villagers who captured it. Of the other animals, some died immediately (probably from capture injuries), some were kept in villages, some were kept under the watch of biologists, one was kept in a fenced area of forest in the species' range, and one was attended by an experienced wildlife veterinarian. However, none survived >5 months. Consequently, basic ecological studies to determine the species' requirements should probably precede any further attempts at live capture. Following the death of the two juvenile saola in Hanoi, Viet Nam's Ministry of Forestry issued a ban on further capture, trade, or holding of saola and ordered that no financial compensation be paid to anyone found in possession of a saola. Such initiatives should be sustained and supported at least until more is learned about basic dietary and other requirements of this rare animal.

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