

An updated description of the New Guinea singing dog (*Canis hallstromi*, Troughton 1957)

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Abstract

In 1957, Troughton described the wild dog of New Guinea, naming it *Canis hallstromi*. Here the description given by Troughton is expanded by the addition of morphological, molecular and behavioural information collected from both captive and wild New Guinea singing dogs subsequent to the original description. The data support Troughton's identification of this canid as a unique taxon, although further studies are needed to clarify the exact level of taxonomic differentiation of this rare and possibly highly endangered canid.

Key words: *Canis*, *Canis hallstromi*, New Guinea, dingo, dog

INTRODUCTION

Canis hallstromi, popularly called the New Guinea singing dog (NGSD), was described by Troughton (1957) from two specimens at the Taronga Zoo, Sydney, Australia. Opinions concerning taxonomic designation and phylogenetic relationships of this canid have varied (Schultz, 1969; Troughton, 1971; Voth, 1988; Brisbin *et al.*, 1994; Corbett, 1995; Flannery, 1995). The NGSD has often been dismissed, without investigation, as a feral domestic dog, based on its morphological similarity to *Canis familiaris* L. The information presented here was collected from captive North American NGSDs, and from local New Guinea informants, subsequent to the original description.

MATERIAL AND METHODS

Body measurements were obtained from 10 male and 9 female adult captive dogs, and weights from 8 male and 7 female adult captive dogs. Behavioural observations consisted of *c.* 2000 h of direct observation of 81 dogs: 21 over 1 year of age and 60 puppies (age range: birth to 19 years). Observations were made all year in outdoor enclosures (7 m², 0.33 ha) and indoors.

A Sony TC-D5M portable audio recorder and GW Instruments SoundScope system were used to analyse NGSD vocalizations. Vocal anatomy data were obtained

from *in vivo* throat radiographs and sonograms of 8 dogs, and by post-mortem dissection of the throat of 1 12-year-old male and 1 13-year-old female, who had died from natural causes.

Digital callipers and linear spreading callipers were used to measure (0.01 mm, to nearest 0.1 mm) 5 male and 7 female skulls of captive adults and 1 unsexed wild skull. Measurements taken: nos 1, 2, 18, 29, 30, 31, 32, 33, 34, 36, 40 (Driesch, 1976: 4243); no. 19 (Lawrence & Bossert, 1967: 231); the angle of the orbits (Ilgin, 1941). Museum specimens examined included all those currently available in U.S.A. collections: University of Nebraska State Museum, UNSM ZM-20933 (female); University of California at Berkeley Museum of Vertebrate Zoology, MVZ 158038 (female) and MVZ 175994 (male); Berenice Bishop Museum, Honolulu, Hawaii, BBM X157422 (female) and BBM X157421 (male); collection of Janice Koler-Matznick, JKM 1 (male) and JKM 2 (female). M. Crowther (pers. comm.), provided measurements for Australian Museum Papuan strain specimens: M8502 (male, holotype), M7989 (male), M9135 (female), M9185 (female), M8917 (female, allotype).

The additional skull examined, collected in 1996 by J. McIntyre at Mount Mekil, Sanduan Province, Papua New Guinea, and presently held by Koler-Matznick, was identified by a local informant as a wild dog killed by a hunter (J. McIntyre, pers. comm.).

All captive specimens studied were pedigreed zoo stock. The holotype and allotype, and their descendants are designated as 'Papuan strain'. In 1976, W. Nelke collected 5 live NGSDs while on expedition to the

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Eipomek river valley, Irian Jaya, for the Museum of Ethnography, State Museums, Berlin (Schultz, 1978; Voth, 1988). These were deposited with the Kiel Domestic Animal Institute, Kiel, Germany (Voth, 1988). Their offspring are the 'Irian Jaya strain'.

Live dogs studied were crosses of Papuan × Irian Jaya strains. About one-third of the live specimens studied also had, within their first 2 ancestral pedigree generations, a male born in captivity in 1981 at the Baiyer River Sanctuary, Papua New Guinea. He was born to a Papuan strain male × wild caught female (L. Lim, pers. comm.). The BBM and MVZ skulls were of pure Papuan descent. The Koler-Matznick skulls were Papuan × Irian Jaya. The University of Nebraska specimen was Baiyer River male × Irian Jaya dam.

Additional data from 2 Papuan strain skulls, Australian National University, TPZ 03 (female) and TPZ 04 (female), measured by K. Gollan (1982), were included (see Table 2).

Besides the above, the only other known NGSD skeletal specimens with secure identification are at the Domestic Animal Institute, Kiel, Germany. Fourteen specimens from this collection were measured by Schultz (1969) and compared to zoo stock *Canis dingo*. DeVis (1911), Longman (1928), and Wood-Jones (1929) briefly describe 2 skulls of assumed wild dogs collected on Mt Scratchley, 'Northern Division', Papua New Guinea in 1889 (Queensland Museum no. 3751: skeleton, skin) and 1918 (Queensland Museum no. 3223: skin; no. 4083: skeleton). However, although the shape of the illustrated skull (Wood-Jones, 1929: 330, fig. 1; 332, fig. 2) is similar to known NGSDs, the general physical description of the single complete specimen, QM no. 3751, does not match the NGSD as described here and in Troughton (1957). As they were apparently obtained from the indigenous people, their provenance is uncertain and they were not included in this study.

SYNONYMY

Canis hallstromi Troughton, 1957

Canis hallstromi Troughton, 1957: 93, 1971: 93; Schultz, 1969: 47; Koler-Matznick, Brisbin & McNytre, 2000: 239.

Canis familiaris hallstromi: Manwell & Baker, 1983: 215, 1984: 234; Sheldon, 1992: 5.

Canis lupus f. *familiaris*: Voth, 1988: 1.

Canis lupus dingo: Brisbin *et al.*, 1994: 30; Bino, 1996: 43.

Canis familiaris; Flannery, 1995: 56.

Type material

Holotype

Male, collected live, 1956, Lavani Valley, Huri-Duna, Southern Highlands District, Papua New Guinea. Housed

at the Taronga Zoo, Sydney, Australia. Died 1964 Australian Museum No. M8502 Skull, skin.

Allotype

Female, collected and handled as holotype. Died 1967 Australian Museum No. M8917 Skull, skeleton, skin.

Diagnosis

The NGSD is relatively short-legged and large-headed compared to other *Canis* species. The NGSD can be distinguished from the smallest extant subspecies of *Canis lupus*, such as *C. lupus arabs*, and from the smallest *Canis dingo* (the central desert variety) by its proportionally shorter height at the withers. The NGSD has smaller shoulder height/head-body length ratios than any of the compared natural canids (Table 1). The NGSD also has a larger ratio of head length to shoulder height than the Papuan village dogs and comparable wild species, with the exception of *C. lupus pallipes* and *C. l. arabs* (see note (c) in Table 3). The NGSD skull can be distinguished from that of *Canis aureus* and small *C. dingo* by its greater relative zygomatic width. Papuan village dogs have relatively shorter fur without undercoat and no brush on the underside of the tail. Outside of New Guinea, the closest purebred domestic dog to the NGSD in morphology and size, is the Japanese Shiba Inu, which has a relatively shorter back, smaller muzzle (creating an artificially high zygomatic width/condylobasal length ratio), shorter fur, relatively smaller ears and feet, and a tail which curls much more tightly over the back. Table 1 provides some comparative measures.

Description

Physical description

General appearance. Figure 1 is a typical captive NGSD. Resembles *C. dingo*, but smaller, with proportionately shorter legs and broader head (Schultz, 1969). Table 2 lists body measurements and weights. Rear dewclaws not present. All specimens examined had 10 mammae.

Coat. Coat has four hair types on the dorsum: innermost, fine underfur; medium-length hair (0.5–1.0 cm); coarser guard hairs (2.5–3.0 cm on the hackles); an outer layer of scattered, protruding over-hairs. Hairs on central back, shoulders to rump, very stiff.

Coat colour. Neonatal coat dark chocolate showing gold flecks and reddish tinges, changing to light brown by 6 weeks. Adult coat starts emerging at 4 months.

Wild population. All reports of adult wild specimens and museum specimens: brown, black with tan, or black, all with white points (DeVis, 1911; Longman, 1928; Tate, 1944; Van Deusen, 1972; Hope, 1976; Flannery, 1995; local informant reports collected by J. McNytre 1996, R. Singadan 1998, and M. Wilangue 2001). Captive

Table 1. Comparison of New Guinea singing dog *Canis hallstromi* body measurements collected in this study to other canids. Sexes combined. Measurements: mm, rounded to nearest whole number; ZW/CBL, zygomatic width/condylobasal length; SH, shoulder height; SH/H-BL, shoulder height/head-body length; HL/SH, head length/shoulder height; NA, data not available

	ZW/CBL	SH	SH/H-BL	HL/SH
NGSD	0.64–0.74 ^a	318–457	0.45–0.47	0.52–0.54
Thai dog ^b	0.58 ^c	447–530	0.60–0.63	0.38–0.39
Desert <i>Canis dingo</i> ²	0.57 ^d –0.65	546–605	0.64–0.66	0.37–0.38
<i>Canis aureus</i>	0.53–0.59 ^e	350–500 ^f	0.57–0.63 ^g	0.31–0.37 ^h
<i>Canis lupus pallipes/arabs</i>	0.56–0.62 ⁱ (0.56 ^j)	400–700 ^k	0.71–0.72 ^g	0.55–0.62 ^l
Papuan dog ^m	0.61–0.62	378–450	NA	0.33–0.34 ⁿ
Shiba Inu	0.64 ^o	355–368 ^p	NA	0.40–0.42 ^o

^a Skull data on captive NGSDs from Schultz (1969).

^b Data from Corbett (1995).

^c One Thai dog zygomatic width estimated from Higham, Kjingam & Manly (1980: 160, fig. 6).

^d Ratio 0.57 from Clutton-Brock, Corbet & Hills (1976). Remainder from data on captive dingoes in Schultz (1969). Note: varieties not given.

^e Data from Harrison (1973).

^f Combined data from Ginsberg & Macdonald (1990), and Corbet & Hill (1992).

^g Data from Gurung & Singh (1996).

^h Data from Harrison & Bates (1991).

ⁱ Data from Harrison & Bates (1991). Subspecies combined.

^j Data on *C. l. arabs* from Harrison (1973).

^k Data from Corbet & Hill (1992).

^l This ratio seems anomalous as *C. lupus* is noted for being long-legged: confirmation with additional data needed.

^m Data from Boessneck & Meyer-Lempennau (1969).

ⁿ Head length data not found. Total skull length used as an approximation of HL is probably slightly smaller owing to lack of the extension of the nose pad beyond the prosthion.

^o Data from Shigehara *et al.* (1998).

^p Data from DePrisco & Johnson (1990).



Fig. 1. A typical young adult male New Guinea singing dog *Canis hallstromi* in the North American captive population.

population: brown; black with tan on muzzle, legs, vent; sable (brown with heavy overlay of dark-tipped guard hairs). Only the brown variety was available for detailed

Table 2. Captive New Guinea singing dog *Canis hallstromi* body measurements (mm) (10 males, nine females) and weights (kg) (eight males, seven females)

Measurement	Range	Mean
Head-body length (male)	780.0–910.0	848.7
Head-body length (female)	710.0–889.0	802.1
Tail length (male)	220.0–280.0	251.6
Tail length (female)	230.0–250.0	234.8
Head length (male)	190.0–235.0	216.4
Head length (female)	172.0–220.0	199.1
Shoulder height (male)	350.0–457.0	435.7
Shoulder height (female)	317.5–421.8	396.4
Ear length (male)	70.0–110.0	94.7
Ear length (female)	65.0–105.0	89.9
Hind foot (male)	140.0–168.3	156.1
Hind foot (female)	130.0–160.0	148.4
Weight (male)	9.3–14.4	12.2
Weight (female)	8.6–12.5	10.9

description: pale brown, ginger, or russet counter-shaded with lighter shades on belly, inner surfaces of legs, and ventral brush of tail. Sides of neck and zonal strip behind scapula golden. Black or very dark brown guard hairs usually lightly scattered throughout the dorsal coat, concentrated on backs of ears and dorsal surface of tail above white tip. Muzzle and loci where superciliary, interramal, and genal vibrissae emerge all black in young specimens. All colours usually have white on underside of chin, paws, chest, and tail tip. About one-third also have white on muzzle, face, and neck. Piebald spotting never observed. By 7 years, the black muzzle turns grey.

Table 3. Measurements of 5 male/7 female adult New Guinea singing dog *Canis hallstromi* skulls from the Australian and North American captive population and of a reportedly wild skull collected in Papua New Guinea. D[n], as given by Driesch (1976); LB[n], as given by Lawrence & Bossert (1967) Absent

Measurement (mm)	Male range (mean)	SD	Fe range (mean)	SD	Papuan
Greatest length (D1) ^a	166.0–188.0 (173.4)	8.66	147.2–167.5 (157.8)	7.75	168.5
Condylar-basal length (D2) ^b	152.8–174.0 (163.7)	7.53	140.5–156.0 (149.9)	7.11	Absent
Zygomatic width (D30) ^a	93.2–106.9 (101.5)	8.66	89.2–99.9 (94.2)	3.38	102.8
Width at p ⁴ (D34) ^a	54.3–61.6 (57.9)	3.07	51.0–57.3 (53.9)	2.05	56.0
Palate width at p ¹ (LB19)	20.5–24.8 (23.1)	1.76	20.9–23.0 (22.0)	0.87	22.0
Width at c ¹ (D36)	28.7–36.7 (33.8)	3.47	29.5–35.9 (31.4)	2.35	30.0
Frontal width (D32) ^a	40.5–48.5 (44.4)	3.81	38.1–44.3 (40.4)	2.43	44.5
P ⁴ length (D18) ^a	15.2–17.0 (15.8)	0.75	13.3–16.0 (14.8)	0.69	17.3
Enterorbital width (D33) ^a	28.1–33.8 (30.8)	2.19	26.0–30.2 (28.2)	1.63	31.6
Postorbital width (D31) ^a	26.4–31.7 (29.2)	2.05	22.0–31.3 (29.8)	3.14	31.0
Greatest width of braincase (D29) ^a	49.70–54.4 (52.1)	1.70	47.8–52.0 (49.6)	1.75	54.5
Occipital triangle height (D40)	42.8–50.0 (45.5)	2.99	38.2–43.7 (42.1)	1.81	Absent
Angle orbits (Iljin, 1941) ^c	45–48 (46.5)		45–49 (47.3)		47

^a Data includes measurements from Gollan (1982): total of five males and nine females.

^b Data includes five males and six females.

^c Data includes three males and four females.

Eye. Openings almond-shaped, angled upwards from the inner to outer corners. Eye rims dark. Irises dark amber to dark brown. Sclera often shows in inner corner. Tapetum highly reflective, bright green.

Ear. Pinnae cupped (tulip petal shape): inner surface furred. When at alert held slightly forward of perpendicular. Can rotate independently, and be lowered forward of alert position and down slightly on the sides of the head.

Tail. Cream brush on underside (longest hairs 5.5–6.0 cm). When the dog is relaxed, insecure, or in searching phase of hunting, tail usually carried drooping down. When the dog is displaying confidence, or alert in the presence of possible prey, tail carried above the level of the back displaying the pale brush in a curve varying from a fish-hook shape to half circle.

Throat anatomy. Radiographic, ultrasound and visual examination of the vocal tract of eight mature dogs (three males/five females) revealed the presence of a rudimentary two-lobed uvula at the free border of the soft palate. This structure was verified on post-mortem examination of one 12-year-old male and one 13-year-old female. Uvulas have not been reported for any other canid.

Skull. Dentition as in other *Canis* spp.: i 3/3, c 1/1, pm 4/4, m 2/3 All specimens examined had complete, uncrowded dentition. Specimen JKM 1 had one diminutive supernumerary m₃ Skull differs from *C. dingo* in being proportionately wider (Schultz, 1969; Gollan, 1982). The following *C. familiaris*-like traits (c.f. Nowak, 1979) are present: relatively small bullae; palate relatively broad and often extending beyond M2; frontals inflated; cranium relatively broad. Zygomata very flared (wide). Occipital condyles nearly perpendicular rather than slanted obliquely backward as in *C. dingo*/*C. familiaris* (foramen magnum opens more ventrally); supraoccipital extension extends beyond the condyles (Schultz, 1969; this study). Bulla shape sexually dimorphic in specimens

examined (this study): female rounded, unribbed; male flatter, ribbed. Table 3 presents skull measurements.

Allozymes

Simonsen's (1976) electrophoretic study of 18 canid blood enzymes, the only enzyme study located that included the NGSD, found no differences between *Canis lupus*, *C. familiaris* and *C. dingo*. However, the NGSD enzyme 6-phosphogluconate dehydrogenase matched *Canis latrans* and the NGSD glucose-6-phosphate dehydrogenase matched *C. latrans* and *Vulpes vulpes*. Simonsen (1976:15) concludes: 'The Hallstrom-dog [NGSD] and coyote have electrophoretic identical enzymes, except PGI.' The PGI (phosphoglucose isomerase) of *C. latrans* matched *Canis aureus* and *V. vulpes*, while the NGSD has the type shared by the other species sampled.

mtDNA

Captive NGSDs sampled ($n=9$) show three maternal lines, none shared with *C. lupus* or *C. latrans* (Vilà *et al.*, 1997; P. Savolainen, pers. comm.). One NGSD type, d18, is shared with *C. dingo* and some Asian-origin *C. familiaris* (cf. Vilà *et al.*, 1997). The two unique NGSD types each differ from d18 by one substitution (P. Savolainen, pers. comm.).

Reproduction

Captive NGSDs have one annual breeding season, starting in August (Koler-Matznick, Brisbin & McInyre, 2000). Local informants report wild pups sighted starting in December, suggesting that wild NGSDs have a similar cycle (M. Wilangue, pers. comm.). Records of 25 captive females from 1988 to 2000 show that if they do not

conceive during their first annual oestrous, *c.* 65% have repeat oestrous cycles 8–16 weeks later (Koler-Matznick, Brisbin & McIntyre, 2000). Second oestruses are physiologically complete: seven pregnancies resulted from matings during repeat cycles. Gestation averages 63 days. Puppies from 20 litters yielded a sex ratio of 45 males/38 females, which did not differ significantly from 1:1 ($\chi^2 = 0.59$; d.f. = 1, $P > 0.05$).

Development

Median birth weight (18 pups/five litters) 260 g. Neonates gain an average of 50 g daily up to 4 weeks. Eyes and ears open at 12–14 days. Deciduous p^3 is erupted by 12 days and p_3 by about 15 days. This is significantly different from *C. familiaris* deciduous carnassials, which erupt between 4 and 10 weeks (Harvey, 1993; Wiggs & Lobprise, 1997) and *Vulpes vulpes* at 29 days (Linhart, 1968). Descriptions of deciduous cheek tooth eruption timing for other canids could not be found. Incisors and canines erupt by 21 days. Pups *c.* one-third adult weight at 8 weeks. Physical maturation completed by about 4 years. Detailed growth curves given by Schultz (1969).

Behaviour

Flannery's (1998) brief narrative about wild NGSDs approaching what they assumed was a deserted camp, in the Star Mountains of Papua New Guinea near the Irian Jaya border, is the only available report of direct observations. He calls the wild NGSDs 'extraordinarily shy' and 'almost preternaturally canny animals' and states (1998: 174): 'Like dingoes, they howl in chorus. The haunting call is usually heard at day's start and end. For me, it is always evocative of the mountains of New Guinea.'

In general, NGSDs show all the behaviours described for other *Canis* species (e.g. Scott & Fuller, 1965; Kleiman, 1967; Schenkel, 1967; Fox, 1969, 1971a,b; Bekoff, 1974; Cohen & Fox, 1976; Fagen, 1981; Bradshaw & Nott, 1995; Serpell & Jagoe, 1995; Goodman, Klinghammer & Willard, 2002). However, their behaviour often has a lower threshold compared to *C. familiaris* (e.g. scent rolling), an earlier developmental onset than *C. familiaris* or *C. lupus* (e.g. hackle biting at 2 weeks compared to *C. familiaris/C. lupus* at 6 weeks), or a quantitative difference (e.g. reduced expression of intraspecific affiliative behaviours compared to *C. familiaris/C. lupus*; Voth, 1988). One common *Canis* behaviour was absent from the NGSD repertoire. We never observed NGSDs performing the universal stereotyped canid play bow (Bekoff, 1977). See Koler-Matznick, Brisbin & Feinstein (2001) for a complete description of NGSD behaviours and the contexts in which they occur.

Unique behaviours

Seven NGSD behaviours observed during this study seem to be unique within the genus *Canis*. Due to space limitations only three are described below.

(1) *Head toss*. This behaviour, shown by every individual observed, is an attention or food solicitation, or sign of frustration, expressed to varying degrees depending on arousal level. In complete expression, the head is swept to one side, nose rotated through a 90° arc to midline, then rapidly returned to the starting position. The entire sequence takes 1–2 s. The mildest expression is a slight flick of the head to the side and back. During this behaviour, the characteristic contrasting black and white chin markings are displayed.

(2) *Copulation scream*. At the copulatory tie, the female emits a repetitive sequence of loud, high-pitched yelp-screams for *c.* 3 min. This scream has a strong arousal effect on most NGSDs and domestic dogs within auditory range.

(3) *Copulation contractions*. About 3 min into the tie, females begin a series of rhythmic abdominal contractions. During each contraction, the skin of the flanks and lumbar area is drawn forward. These contractions are accompanied by groans and occur regularly, several seconds apart (they may pause intermittently), continuing for the length of the tie.

In addition to these three behaviours, NGSDs have an unusual form of auto-erotic stimulation, a strong tendency to target the genitals for both playful and aggressive bites, a cheek-rub that may be a marking behaviour (a similar behaviour is seen in *Vulpes* sp., D. Macdonald, pers. comm.), and a tooth-gnashing threat.

Social behaviour

From captive behaviour, we infer that wild NGSDs do not form permanent packs (Voth, 1988; Koler-Matznick, Brisbin & McIntyre, 2000). During oestrous, if a potential mate is present, same-sex specimens often fight to the point of severe injury (Koler-Matznick, Brisbin & McIntyre, 2000; Koler-Matznick, Brisbin & Feinstein, 2001) or death (Voth, 1988). Adults also display a high degree of aggression toward unfamiliar canids, an indication that they may be strongly territorial. All wild sightings and signs reported to date are of single specimens or pairs (e.g. Hope, 1976; Bino, 1996; local informant reports collected by J. McIntyre, M. Wilangue, and R. Singadan). Captive males kept with their mates and offspring often provide parental care, including regurgitation. However, during the first breeding season following their birth, especially if there is a potential mate present, offspring are often aggressively attacked by the same-sex parent.

Distinctive vocalizations

Howl

The dramatic frequency modulation of the NGSD howl is not generally characteristic of other canids (Cohen & Fox, 1976; Schassburger, 1987; Brisbin *et al.*, 1994). The typical starting frequency of a howl is 600–800 Hz, then

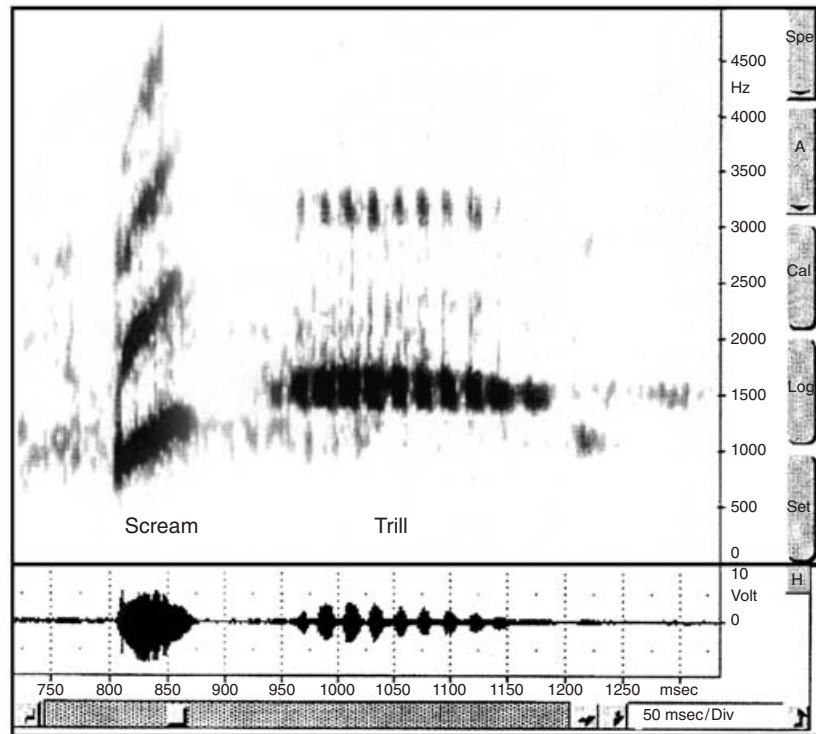


Fig. 2. Sonogram of a captive New Guinea singing dog *Canis hallstromi* scream followed by a trill.

varies from 300 to 1700 Hz. Individual howl duration is 0.5–5 s (mean 3 s). Frequency invariably rises from the outset. The remainder of the event is occasionally rather steady, but typically exhibits abrupt frequency changes up or down. Modulation may occur rapidly, every 300–500 ms, or as gradually as every second. Five to eight well-defined harmonics can normally be discerned in spectrographic analyses of NGSD howls. Ortolani (1990) reports that NGSD and *C. dingo* howls are identifiably distinct from each other and both differ significantly from those of *C. lupus* and *C. latrans*.

Chorus howl

A session of polyphonic simultaneous howling by two or more NGSDs. A single individual initiates, and respondent(s) quickly join in. The respondent howls are typically well-synchronized; all members of the chorus cease howling almost simultaneously. The duration of bouts is 0.5–10 min (mean slightly < 1 min). Spontaneous choruses are most frequent in evening/morning hours (Flannery, 1998; Koler-Matznick, Brisbin & Feinstein, 2001; local informants).

Trill

Emitted during high arousal, this vocalization has a distinctly ‘bird-like’ auditory character. It is a high-frequency, pulsed signal whose spectral appearance suggests a continuous source that is periodically interrupted.

This effect may be produced by rapid vibration of the (rudimentary) uvula. The event can last as long as 800 ms and is characterized by an evenly timed series of 10 to several dozen short (5–20 ms) bursts at an average fundamental frequency of 1500 Hz. This trill has not been described for any other canid, although Volodin, Volodina & Isaeva (2001) have recorded a similar but lower frequency vocalization in a captive Indian dhole (*Cuon alpinus*) at the Moscow Zoo. Figure 2 illustrates the NGSD trill and an initial scream, which occasionally accompanies the trill.

Ecology and distribution

The following includes all the information currently available concerning the wild population.

Range

The range of NGSDs is reported from *c.* 2500–4700 m throughout the mountains of New Guinea (Tate, 1944; Van Deusen, 1972; R. Bulmer, 1976; Hope, 1976; Brisbin *et al.*, 1994; Flannery, 1995). The only other *Canis* species that regularly ranges to such high altitudes is the Ethiopian wolf *Canis simensis* (Gottelli & Sillero-Zubiri, 1992). The main vegetation zones are (lowest to highest elevations): mixed forest; beech and mossy forest; sub-alpine coniferous forest; alpine grassland (Van Deusen, 1972). It can be argued on archaeological, ethnographic, and circumstantial evidence that NGSDs

originally occupied all ecological zones of New Guinea, but were later restricted to the upper mountains by the occupation of the mid-montane zone by human agriculturalists from 9000 years ago (S. Bulmer, 2001).

Niche

All local informant reports, Van Deusen (1972) and Bino (1996) indicate that NGSDs are generalist, opportunistic predator/scavengers, feeding upon small- to medium-sized marsupials, rodents, birds and fruits. They are reported to consume prey in neglected hunter traps, appropriate kills of the New Guinea Harpy eagle *Harpyopsis novaeguinae*, and possibly attack dwarf cassowaries *Casuarius benetti* (Bino, 1996). To date there are no reports of NGSD predation endangering any prey species.

Interactions with humans

Local informants (reports collected by R. Singadan, pers. comm.; M. Wilangue, pers. comm.; T. Brookings, pers. comm.), Meggitt (1958) and R. Bulmer (1976) report that wild NGSDs are shy, avoid humans, and never live in or near human settlements, unless captured as pups and raised by humans. The Kalam people, Papuan Highlands, were reported by R. Bulmer (1976) to capture young pups and raise them as hunting aides, but did not breed them. The Eipo tribe of the Irian Jaya Highlands kept and bred tamed NGSDs as social partners and playmates for children (Schultz, 1978; Voth, 1988). Although most Highland tribes never eat their village dogs (S. Bulmer, 2001), a few eat wild NGSDs that are caught in traps or killed opportunistically (Bino, 1996). Dog finds in archaeological sites in New Guinea are rare, consisting mainly of teeth (used as ornaments), trophy skulls, and one burial (S. Bulmer, 2001). The earliest dog is in a Lowlands site, dated to 5500 BP. The few finds from the Highlands may be as early, on stratigraphic grounds, but have not yet been directly dated (S. Bulmer, 2001). It can be argued that the dog was present earlier, and its absence from hunting middens only means it was not eaten.

DISCUSSION

The NGSD is of uncertain origin. The founders were probably of Indonesian or South-East Asian origin, the nearest sources of placental mammals, but from exactly where and when is a matter of speculation. Until more molecular data become available, some of the phylogenetic relationships of NGSDs to other *Canis* species remain uncertain. Most authors have designated the NGSD as either a species or a subspecies of *C. familiaris* (Troughton, 1957, 1971; Schultz, 1969; Manwell & Baker, 1983; Sheldon, 1992; Koler-Matznick, Brisbin & McIntyre, 2000), indicating they consider the NGSD a diagnosable taxon. Some authors simply call the NGSD, *Canis familiaris*. (Voth, 1988; Flannery, 1995). Due to the general assumption that the grey wolf is the sole

progenitor of the domestic dog and the convention that domestic animals should not be given names separate from their known ancestor, some recent authors designate the domestic dog *Canis lupus familiaris* (Wilson & Reeder, 1993). If it is considered a feral domestic dog, this would preclude subspecific status for the NGSD, unless it is believed to be its own separate subspecies (e.g. *C. lupus hallstromi*), as suggested in Brisbin *et al.* (1994). However, there are arguments that the wolf and dog are separate species with descent from a common ancestor (Manwell & Baker, 1984; Koler-Matznick, 2002), and arguments have been made for using a separate binomial for domesticated animals that have significantly diverged from their ancestor and, like wolves and dogs, now have effective reproductive isolating mechanisms in undisturbed natural environments (Corbet & Hill, 1992; Gentry, Clutton-Brock & Groves, 1996; Gardner, 1997; Mungall, 1997; Brisbin, 1998). We believe that *C. familiaris* is at least such a diverged population. Therefore, if the NGSD is considered merely a diverged population of feral domestic dogs, the name *C. familiaris hallstromi* could be justified.

Some authors have recently used the trinomial *C. lupus dingo* for the Australian dingo and the NGSD (Brisbin *et al.*, 1994; Corbett, 1995), thus recognizing them as separate taxa from domestic dogs, related to the grey wolf. The Australian dingo, also an anciently allopatric dog population of uncertain origin separable from common *C. familiaris* by several morphological, behavioural and genetic characters (Corbett, 1995; Wilton, Steward & Zafiris, 1999; Wilton, 2001; P. Savolainen, pers. comm.), is undoubtedly the NGSD's closest relative. Because it is not known just how the NGSD and dingo are related (sibling taxa from a common ancestor, or one ancestral to the other), we do not support using the same binomial for them.

The common opinion that NGSDs are feral *C. familiaris* is based upon their general dog-like morphology (DeVis, 1911; Schultz, 1969; Voth, 1988; Corbett, 1995; Flannery, 1995) and the assumption that they reached New Guinea only with human assistance, and therefore must have been domesticated at that time. However, prehistorically, non-domesticated canids were also transported by sea (Collins, 1991) and by 22 000–19 000 BP, wild animals were being transported between islands near New Guinea (Flannery & White, 1991; S. Bulmer, 2001). Thus, such human-assisted transportation is not itself proof of domestication. It is possible that the NGSD entered New Guinea as a tamed wild animal, which humans introduced for their own purposes, i.e. to establish a wild dog population as a source of pups to be trained as hunting aides.

There is no archaeological or ethnographic evidence of NGSD domestication and they do not show the characteristic morphological features of domestication. If the ancestor of the NGSD was indeed a domesticated dog, they have now diverged significantly. We also do not support the use of *C. lupus*, as they obviously are not wolves and on biogeographic grounds alone, have not been sympatric with any wolf population for at least several thousands of years.

Although *C. familiaris*, *C. dingo* and *C. hallstromi* share many symplesiomorphies, there are morphological and molecular characters separating the NGSD from *C. dingo* (Schultz, 1969; Simonsen, 1976; Gollan, 1982; P. Savolainen, pers. comm.). Furthermore, there are morphological, molecular, genetic and behavioural traits separating the NGSD from modern *C. familiaris* (Wood-Jones, 1929; Troughton, 1957, 1971; Simonsen, 1976; Brisbin *et al.*, 1994; Koler-Matznick, Brisbin & McIntyre, 2000; P. Savolainen, pers. comm.). For instance, NGSDs have two blood enzyme differences from *C. familiaris*, *C. dingo* and *C. lupus* (Simonsen, 1976), indicating that they may have differentiated in some physiological parameters from those species. Alternatively, the enzyme types of *C. lupus*, *C. dingo* and *C. familiaris* may be apomorphic and those of NGSD plesiomorphic, because the latter match *C. latrans* and *V. vulpes*, both species older than *C. lupus* (Nowak, 1979).

The possibility of hybridization of NGSD with *C. familiaris* should not be considered diagnostic evidence that they are conspecific. In the genus *Canis*, all species have the plesiomorphic ability to produce fertile hybrids and several have hybridized in the wild (Lehman *et al.*, 1991; Gottelli *et al.*, 1994; Sillero-Zubiri & Macdonald, 1997).

The NGSD is not genetically or ecologically exchangeable with any other canid population. Therefore, although the taxonomic identity of the NGSD cannot be unequivocally determined from currently available data, the information reviewed here at minimum indicates the NGSD is an evolutionarily significant unit (cf. Crandall *et al.*, 2000), perhaps a sibling taxon of *C. dingo*. Because these two apparently related populations have diagnostic characters separating them from each other and from the other *Canis* species (Schultz, 1969; Gollan, 1982; this study), their specific binomials with the most priority and usage, *Canis hallstromi* and *Canis dingo*, should be used to identify them appropriately as discernable taxonomic entities within the genus.

As there is little information available about wild NGSDs, this account is of necessity based mainly upon captive specimens. This is not unusual for forest carnivores. *Speotheos venaticus* and *Atelocynus microtis*, for example, have been described mainly from captive specimens (Ginsberg & Macdonald, 1990; Sheldon, 1992; Nowak, 1999). It is unlikely that the unique NGSD characteristics described herein were developed in captivity (post-captivity mutations, founder effect, genetic drift, directed selection). There were two main sets of founders collected 20 years and hundreds of miles apart and a single founder from a third area. Breeding has been non-selective, and the traits identified as typical have 100% expression in the captive population. Moreover, most of these traits, particularly behavioural, are of the kind that are evolutionarily adaptive for a largely monogamous forest-dwelling carnivore living in scattered and isolated family groups.

As stated by Mayr & Ashlock (1991: 50): 'The biological importance of the geographic isolate is that every isolate, regardless of its taxonomic rank, is an incipient

species; it is an important unit of evolution.' Whatever their origin and time of arrival in New Guinea, the information presented here supports the hypothesis that the NGSD is a long-term isolate population of the genus *Canis*, deserving some form of distinct taxonomic recognition, protection, and study.

Like the dingo, the NGSD has been ignored by most biologists and ethnologists as merely a feral domestic dog and therefore 'unworthy' of study (for an exception see Brisbin, 1998). On the other hand, archaeozoologists, who have argued for their conservation, consider both these dogs to be living relics from the earliest dogs, and that they are, at the very least, part of the living heritage of the native peoples of Australia and New Guinea (Clutton-Brock, 2000). The NGSD is clearly a candidate for conservation concern. The captive NGSD breeding population consists of *c.* 50 highly inbred specimens, and recent local informant reports and Brisbin *et al.* (1994) indicate wild NGSDs are absent from several areas of their former range. Unfortunately, the NGSD is caught in a double-bind situation: there is a reluctance to recognize the NGSD as deserving of protection until reliable field data become available, and little interest in undertaking the considerable difficulty of field studies in the mountains of New Guinea until the NGSD is recognized as a unique and endangered taxon. While the NGSD languishes in this conundrum, both the wild and captive populations are in increasing jeopardy. The conservative approach is to protect the evolutionary potential of the NGSD until and unless there is conclusive contrary evidence that the NGSD is not a distinctive form.

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