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Author: Leslie, David M

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Rusa unicolor (Artiodactyla: Cervidae)

DAVID M. LESLIE, JR.

United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078-3051, USA; cleslie@usgs.gov

Abstract: *Rusa unicolor* (Kerr, 1792), or sambar, is the largest Oriental deer. Seven subspecies occur in varied habitats and elevations from India and Sri Lanka throughout southeastern Asia. Body mass and antler length decrease from west to east. *R. unicolor* is considered ancestral relative to the form of its male-only antlers and social behavior. Populations are vulnerable because of overexploitation for subsistence and markets in meat and antlers. *R. unicolor* was elevated by the International Union for Conservation of Nature and Natural Resources from no status in 2006 to "Vulnerable" in 2008 because of >50% decline in many populations over the past 3 generations. It is well represented in zoos and private collections and is introduced in Australia, New Zealand, South Africa, and the United States.

Key words: cervid, deer, exotic species, India, sambar, Southeast Asia, ungulate ecology, vulnerable species

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Rusa Hamilton-Smith, 1827

Cervus: Kerr, 1792:300. Part.

Rusa Hamilton-Smith, 1827a:104. Described as a subgenus of *Cervus* Linnaeus, 1758, to contain *C. hippelaphus*, *C. unicolor*, *C. aristotelis*, *C. equinus*, *C. peronii*, "Rusa of Malacca" (no binomial provided), and *C. mariannus*; type species *Cervus unicolor* Hamilton-Smith, 1827b, by subsequent designation (Kretzoi and Kretzoi 2000a:365, 2000b:574).

Stylocerus Hamilton-Smith, 1827b:319. Part.

Rusas Brookes, 1828:62. Incorrect subsequent spelling of *Rusa* Hamilton-Smith, 1827a.

Hippelaphus: Bonaparte, 1837:unnumbered page associated with fascicolo xv and xvi. Part; type species *Cervus hippelaphus* de Blainville, 1822, by absolute tautonomy (Palmer 1904:325); described as a subgenus of *Cervus* Linnaeus, 1758; preoccupied by *Hippelaphus* Goldfuss, 1820 and *Hippelaphus* Reichenbach, 1835.

Rusa: Hodgson, 1841a:219. First use as a genus.

Russa Gray, 1843:179. Incorrect subsequent spelling of *Rusa* Hamilton-Smith, 1827a.

Russa Müller and Schlegel, 1845:210. Incorrect subsequent spelling of *Rusa* Hamilton-Smith, 1827a.

Axis: Gray, 1843:180. Part, not *Axis* Hamilton-Smith, 1827b.

Hippelaphi Sundevall, 1846:177. Part; incorrect subsequent spelling of *Hippelaphus* Bonaparte, 1837; used as a subgenus of *Cervus* Linnaeus, 1758, to contain *C.*

Fig. 1.—Mature male *Rusa unicolor* in Ranthambhore National Park, Rajasthan, northern India; note the neck "ruff" and simple configuration of the antlers and the acutely angled left brow tine (right brow tine broken off). Photograph by Chris Brunskill (www.ardea.com) used with permission.

japonicus, *C. duvaucelli*, *C. aristotelis*, *C. equinus*, *C. hippelaphus*, *C. moluccenis*, *C. peroni*, *C. kuhlii*, *C. philippinus*, *C. mariannus*, *C. lepidus*, *C. axis*, *C. pseudaxis*, and *C. nudipalpebra*.

Cervulus: Gray, 1861:138. Part, not *Cervulus* de Blainville, 1816.

Rucervus: Gray, 1872:76. Part, not *Rucervus* Hodgson, 1838.

Melanaxis Heude, 1888a:8. Type species *Cervus alfredi* Sclater, 1870, by original designation.

Sambur Heude, 1888a:8. Type species *Cervus aristotelis* G. Cuvier, 1823, by original designation.

Roussa Heude, 1888a:8. Type species *Cervus equinus* Cuvier, 1823, by original designation.

Ussa Heude, 1888a:8; 1888b:22. Type species *Ussa barandanus* Heude, 1888a, by original designation.

Hippelaphus: Heude, 1896:49. First use as a genus.

Sambar Lydekker, 1915:91. Incorrect subsequent spelling of *Sambur* Heude, 1888a.

Context and Content. Order Artiodactyla, suborder Ruminantia, family Cervidae, subfamily Cervinae, tribe Cervini. Currently, 4 species of the Old World *Rusa* are recognized: *unicolor* (sambar), *marianna* (Philippine deer), *timorensis* (rusa), and *alfredi* (Prince Alfred's deer—Grubb 2005). The following key was developed from characteristics provided by Groves and Grubb (1987), Grubb and Groves (1983), Lydekker (1915), and Meijaard and Groves (2004), and information at www.ultimateungulate.com (accessed 6 May 2009):

1. Small, short-legged deer; soft, fine, and spotted pelage on young and adults; shoulder height 64–71 cm; body length generally ≤ 128 cm; antler length of mature males about 24 cm; restricted to Panay and Negros islands, Philippines … *R. alfredi*
   Larger forms with coarse pelage and no spots on adults; shoulder height > 70 cm and body length generally > 130 cm; antler length of mature males often > 60 cm 2
2. Male antlers generally thin and lacking rugosity; dorsal hairs of both sexes annulated; gregarious, occurring in herds; restricted to Java and islands of Indonesia, introduced to most of the latter by humans ..... *R. timorensis*
   Male antlers thicker and rugose; dorsal hairs of both sexes not annulated; not gregarious, typically occurring in mother–offspring social units with males solitary; ranging extensively from India through southeastern Asia or the Philippines 3
3. Small deer; shoulder height about 70 cm; greatest length of skull 200–270 mm; mature males with antlers generally 30–45 cm in length; restricted to the Philippines ..... *R. marianna*
   Large deer, particularly western forms; shoulder height 130–142 cm; greatest length of skull 300–400 mm; mature males with antlers 70–120 cm in length (as small as 40–50 cm in Taiwan); wide ranging from India, Sri Lanka, and Nepal across southern China through southeastern Asia to the Pacific Coast ..... *R. unicolor*

Rusa unicolor (Kerr, 1792)
Sambar

C[*ervus*]. *Axis unicolor* Kerr, 1792:300. Type localities "dry hilly forests of Ceylon [= Sri Lanka], Borneo, Celebes [= 1 of 4 Greater Sundas Islands, Indonesia], and Java;" based on the "Middle-sized Axis" of Pennant (1781:106); restricted to "Ceylon" by Hamilton-Smith (1827b:310).

C[*ervus*]. *Axis major* Kerr, 1792:300. Type localities "marshes of Borneo and Ceylon;" based on the "Great Axis" of Pennant (1781:106); restricted to "Ceylon" by Groves (2003:351).

Cervus unicolor: Bechstein, 1799:112. Name combination.

Cervus albicornis Bechstein, 1799:112. Type locality not given; based on the "Great Axis" of Pennant (1781).

C[*ervus*]. *Niger* de Blainville, 1816:76. Type locality "l'Inde [= India]."

C[*ervus*]. *maximus* de Blainville, 1822:264. Type localities "Ceylan ou Bornéo?"

C[*ervus*]. *hippelaphus* de Blainville, 1822:265. Type localities "Archipel indien [= Indian Archipelago];" modified to "Bengal [= area of West Begal, India, and Bangladesh], Java, Sumatra, and other great islands of the Indian Archipelago" by Hamilton-Smith (1827a:108) and "Java? Bengal chiefly the Jungleberry district" by Hamilton-Smith (1827b:309); preoccupied by *Cervus elaphus hippelaphus* Erxleben, 1777:304 (= *Cervus elaphus* Linnaeus, 1758).

cervus equinus G. Cuvier, 1823:45. Type locality "Sumatra."

cervus Aristotelis G. Cuvier, 1823:503. Type localities "Napaul [= Nepal], et vers l'*Indus* [= India];" restricted to "Bengal in the Prauss Jungles" by Hamilton-Smith (1827b:310).

cervus Leschenauldii G. Cuvier, 1823:506. Type locality "côte de Coromandel [= southeastern coast of India]."

C[*ervus* (*Rusa*)]. *Hippelaphus*: Hamilton-Smith, 1827b:309. Name combination.

C[*ervus* (*Rusa*)]. *Unicolor*: Hamilton-Smith, 1827b:310. Name combination.

C[*ervus* (*Rusa*)]. *Aristotelis*: Hamilton-Smith, 1827b:310. Name combination.

C[*ervus* (*Rusa*)]. *Equinus*: Hamilton-Smith, 1827b:311. Name combination.

Rusas hippelalphus?: Brookes, 1828:62. Name combination.

C[*ervus*]. *Malaccensis* J. B. Fischer, 1829:451. Type locality "peninsula Malacca [= peninsular Malaysia]" (see "Nomenclatural Notes").

Cervus Jarâi Hodgson, 1831:321, pl. XXI. Type localities "sub-Himâlayan ranges, and Saul forest."

[*Rusa*] *Jaraya* Hodgson, 1841a:219. Name combination and incorrect subsequent spelling of *Cervus jarai* Hodgson, 1831.

[*Rusa*] *Nipalensis* Hodgson, 1841a:219. Type locality "Nepal."

C[*ervus*]. *heterocerus* Hodgson, 1841b:unnumbered plate opposite page 722. Type locality "Nepal."

[*Rusa*] *Nepalensis*: Hodgson, 1841c:914. Corrected spelling of *Rusa nipalensis* Hodgson, 1841a.

[*Rusa*] *Heterocervus* Hodgson, 1841c:914. Name combination and incorrect subsequent spelling of *Cervus heterocerus* Hodgson, 1841b.

Russa Hippelaphus: Gray, 1843:179. Name combination.

Rusa Aristotelis: Gray, 1843:179. Name combination.

Rusa Equina: Gray, 1843:179. Name combination.

Axis pennantii Gray, 1843:180. Type locality "India;" said to be Pennant's (1781:106) "Great Axis" of "*Borneo* or *Ceylon.*"

Cervus russa Müller and Schlegel, 1845:212, 217. Type locality "Java, is van daar naar Borneo."

C[*ervus*]. *bengalensis* Schinz, 1845:390. Type locality "Bengala? [= Bengal]," northwestern India.

[*Cervus* (*Hippelaphi*)] *Aristotelis*: Sundevall, 1846:178. Name combination.

C[*ervus* (*Hippelaphi*)]. *equinus*: Sundevall, 1846:178. Name combination.

C[*ervus* (*Hippelaphi*)]. *hippelaphus*: Sundevall, 1846:178. Name combination.

C[*ervus*]. *Leschenaulti* Sundevall, 1846:183. Incorrect subsequent spelling of *Cervus leschenauldii* G. Cuvier, 1823.

Cervulus cambojensis Gray, 1861:138. Type locality "Camboja [= Cambodia]."

Cervus [*Rusa*] *swinhoii* Sclater, 1862:151,152, pl. XVII. Type locality "Formosa [= Taiwan]."

Rusa tarai Hodgson, 1863:ix. Incorrect subsequent spelling of *Cervus jarai* Hodgson, 1831.

Rucervus cambojensis: Gray, 1872:76. Name combination.

C[*ervus*]. *heterocercus* Jerdon, 1874:256. Incorrect subsequent spelling of *Cervus heterocerus* Hodgson, 1841b.

C[*ervus*]. *saumur* Jerdon, 1874:256. Type locality not given; presented as synonym for *Cervus aristotelis* G. Cuvier, 1823, but attributed to Ogilby (1839:lxxii), who only used the local vernacular name "Saumer" in association with *C. hippelaphus*.

C[*ervus*]. *laschenaultii* Jerdon, 1874:256. Incorrect subsequent spelling of *Cervus leschenauldii* G. Cuvier, 1823.

Rusa Aristotelis, *nigra*: Fitzinger, 1875:284. Name combination and correction of gender concordance of *Cervus niger* de Blainville, 1816.

Rusa Aristotelis, *leschenaultia* Fitzinger, 1875:286. Name combination and incorrect subsequent spelling of *Cervus leschenauldii* G. Cuvier, 1823.

Rusa Aristotelis, *unicolor*: Fitzinger, 1875:287. Name combination.

Rusa Aristotelis, *heteroceros* Fitzinger, 1875:289. Name combination and incorrect subsequent spelling of *Cervus heterocerus* Hodgson, 1941b.

Rusa equina, *malaccensis*: Fitzinger, 1875:294. Name combination.

Rusa equina, *Pennantii*: Fitzinger, 1875:296. Name combination.

S[*ambur*]. *curvicornis* Heude, 1888c:41, 42. Type locality "Cochinchine [= 17th century name for southern one-third of Vietnam];" restricted to "Tay-ninh" Province, Vietnam, by Braun et al. (2001:631).

S[*ambur*]. *longicornis* Heude, 1888c:41, 42. Type locality "Cochinchine;" restricted to "Saigon," Vietnam by Braun et al. (2001:632).

S[*ambur*]. *outreyanus* Heude, 1888c:41, 42. Type locality "Cochinchine."

S[*ambur*]. *planidens* Heude, 1888c:41, 43. Type locality "Cochinchine."

S[*ambur*]. *colombertinus* Heude, 1888c:41, 43. Type locality "Cochinchine;" restricted to "Baria [= Bà Ria-Vung Tau]" Province, Vietnam, by Braun et al. (2001:632).

S[*ambur*]. *combalbertinus* Heude, 1888c:41, 43. Type locality "Cochinchine;" restricted to "Baria [= Bà Ria-Vung Tau]" Province, Vietnam, by Braun et al. (2001:632).

S[*ambur*]. *heteroceros* Heude, 1888c:41. Name combination and subsequent incorrect spelling of *Cervus heterocerus* Hodgson 1841b.

S[*ambur*]. *lemeanus* Heude, 1888c:41, 44. Type locality "Cochinchine."

S[*ambur*]. *errardianus* Heude, 1888c:42, 45. Type locality "Cochinchine."

S[*ambur*]. *joubertianus* Heude, 1888c:42, 45. Type locality "Cambodia" based on lectotype selection by Braun et al. (2001:632).

S[*ambur*]. *latidens* Heude, 1888c:42, 45. Type locality "Cochinchine."

S[*ambur*]. *planiceps* Heude, 1888c:45. Type locality "Cochinchine;" restricted to "Baria [= Bà Ria-Vung Tau]" Province, Vietnam, by Braun et al. (2001:632).

S[*ambur*]. *officialis* Heude, 1888c:42, 46. Type locality "Cochinchine;" restricted to "Baria [= Bà Ria-Vung Tau]" Province, Vietnam, based on paratype selection by Braun et al. (2001:632).

S[*ambur*]. *simonianus* Heude, 1888c:42, 46. Type locality "Cochinchine;" restricted to "Baria [= Bà Ria-Vung Tau]" Province, Vietnam, by Braun et al. (2001:632).

S[*ambur*]. *brachyrhinus* Heude, 1888c:42, 46. Type locality "Cochinchine."

S[*ambur*]. *lignarius* Heude, 1888c:44. Type locality "Cochinchine."

S[*ambur*]. *verutus* Heude, 1888c:46. Type locality "Cochinchine."

Cervus brookei Hose, 1893b:206. Type locality "Mount Dulit, E. Sarawak," Malaysia.

Hippelaphus hamiltonianus Heude, 1896:49. Type locality "Sandakan [= Sahab, East Malaysia], nord de Bornéo [= North Borneo]."

Rusa dejeani de Pousargues, 1896:12. Type locality "Setchuan [= Sichuan]," southwestern China.

Cervus dejeani: Ward, 1896:22. Name combination.

Russa equina: Jentink and Büttikofer, 1897:63. Name combination.

Cervus (*Rusa*) *Swinhoei* Nitsche, 1898:32. Incorrect subsequent spelling of *Cervus swinhoii* Sclater, 1862.

Cervus unicolor typicus Lydekker, 1898:146. Usage equivalent to *Cervus unicolor unicolor* and not intended as a new name.

Cervus unicolor swinhoii: Lydekker, 1898:154. Name combination.

Cervus unicolor dejeani: Lydekker, 1898:156. Name combination.

Cervus spatulatus O. Thomas in Sclater, 1901:536. Type locality "central Borneo" (see "Nomenclatural Notes").

Rusa unicolor equinus J. A. Allen, 1906:464, 467. Name combination and incorrect gender concordance.

Rusa brookei: Lyon, 1906:584. Name combination.

Rusa unicolor: Pocock, 1910:946. First use of current name combination.

Cervus unicolor equinus: Lydekker, 1915:78. Name combination.

Cervus unicolor brookei: Lydekker, 1915:80. Name combination.

Cervus unicolor swinhoei Lydekker, 1915:81. Incorrect subsequent spelling of *Cervus swinhoii* Sclater, 1862.

Cervus unicolor oceana Chasen and Kloss, 1928:818. Type locality "Siberut Island, West Sumatra."

Rusa unicolor dejeani: G. M. Allen, 1930:15. Name combination.

Rusa equina brookei: van Bemmel, 1949:210. Name combination.

[C*ervus* (*Rusa*) *unicolor*] *equinus*: Haltenorth, 1963:19, 58. Name combination.

Cervus (*Russa*) *unicolor*: Drozdz, 1973. Name combination.

Rusa unicolor niger: van Bemmel, 1974:297. Name combination.

Rusa equina brooki van Bemmel, 1974:297. Name combination and incorrect subsequent spelling of *Cervus brookei* Hose, 1893a.

Rusa equina swinhoei van Bemmel, 1974:297. Name combination and incorrect subsequent spelling of *Cervus swinhoii* Sclater, 1862.

Cervus unicolor dejeni Wang and Du, 1982:25. Incorrect subsequent spelling of *Rusa dejeani* de Pousargues, 1896.

C[*ervus*]. *unicolor deieni* Wang and Du, 1982:29, fig. 2. Incorrect subsequent spelling of *Rusa dejeani* de Pousargues, 1896.

Cervus unicolor hainana Xu, 1983:395. Type locality "Hainan Dao [= Island]," China.

[*Cervus* (*Rusa*) *unicolor*] *brookei*: Groves and Grubb, 1987:42. Name combination.

[*Cervus* (*Rusa*) *unicolor*] *swinhoei*: Groves and Grubb, 1987:42. Name combination and incorrect subsequent spelling of *Cervus swinhoii* Sclater, 1862.

[*Cervus* (*Rusa*) *unicolor*] *cambojensis*: Groves and Grubb, 1987:42. Name combination.

[*Cervus* (*Rusa*) *unicolor*] *niger*: Groves and Grubb, 1987:42. Name combination.

Cervus unicolor nigar Varman and Sukumar, 1993:273. Incorrect subsequent spelling of *Cervus niger* de Blainville, 1816.

Cervus unicornis Barman, Sarma, Das, and Patgiri, 1999:781. Incorrect subsequent spelling of *Cervus unicolor* Kerr, 1792.

C[*ervus*]. *u*[*nicolor*]. *malaccensis*: Benirschke, 2002:unnumbered page. Name combination.

[*Rusa*] *albicornis*: Grubb, 2005:670. Name combination (see "Nomenclatural Notes").

[*Rusa*] *bengalensis*: Grubb, 2005:670. Name combination.

[*Rusa*] *heterocerus*: Grubb, 2005:670. Name combination.

[*Rusa*] *hippelaphus*: Grubb, 2005:670. Name combination.

[*Rusa*] *jarai*: Grubb, 2005:670. Name combination.

[*Rusa*] *leschenauldii*: Grubb, 2005:670. Name combination.

[*Rusa*] *leschenaulti*: Grubb, 2005:670. Name combination.

[*Rusa*] *major*: Grubb, 2005:670. Name combination.

[*Rusa*] *maxima*: Grubb, 2005:670. Name combination.

[*Rusa*] *nepalensis*: Grubb, 2005:670. Name combination.

[*Rusa*] *nigra*: Grubb, 2005:670. Name combination.

[*Rusa*] *pennantii*: Grubb, 2005:670. Name combination.

[*Rusa*] *tarai*: Grubb, 2005:670. Name combination.

[*Rusa*] *typica*: Grubb, 2005:670. Name combination.

[*Rusa unicolor*] *brookei*: Grubb, 2005:671. Name combination.

[*Rusa*] *hamiltoniana*: Grubb, 2005:671. Name combination.

[*Rusa unicolor*] *cambojensis*: Grubb, 2005:671. Name combination.

[*Rusa*] *brachyrhina*: Grubb, 2005:671. Name combination.

[*Rusa*] *colombertina*: Grubb, 2005:671. Name combination.

[*Rusa*] *combalbertina*: Grubb, 2005:671. Name combination.

[*Rusa*] *curvicornis*: Grubb, 2005:671. Name combination.

[*Rusa*] *errardiana*: Grubb, 2005:671. Name combination.

[*Rusa*] *joubertiana*: Grubb, 2005:671. Name combination.

[*Rusa*] *latidens*: Grubb, 2005:671. Name combination.

[*Rusa*] *lemeana*: Grubb, 2005:671. Name combination.

[*Rusa*] *lignaria*: Grubb, 2005:671. Name combination.
[*Rusa*] *longicornis*: Grubb, 2005:671. Name combination.
[*Rusa*] *officialis*: Grubb, 2005:671. Name combination.
[*Rusa*] *outreyana*: Grubb, 2005:671. Name combination.
[*Rusa*] *planiceps*: Grubb, 2005:671. Name combination.
[*Rusa*] *planidens*: Grubb, 2005:671. Name combination.
[*Rusa*] *simonina*: Grubb, 2005:671. Name combination.
[*Rusa*] *veruta*: Grubb, 2005:671. Name combination.
[*Rusa unicolor*] *dejeani*: Grubb, 2005:671. Name combination.
[*Rusa unicolor*] *equina*: Grubb, 2005:671. Name combination.
[*Rusa*] *malaccensis*: Grubb, 2005:671. Name combination.
[*Rusa*] *oceana*: Grubb, 2005:671. Name combination.
[*Rusa unicolor*] *hainana*: Grubb, 2005:671. Name combination.
[*Rusa unicolor*] *swinhoii*: Grubb, 2005:671. Name combination.
R[*usa*]. *u*[*nicolor*]. *equine* Timmins, Steinmetz, Sagar Baral, et al., 2008:3. Incorrect subsequent spelling of *Cervus equinus* Cuvier, 1823.

CONTEXT AND CONTENT. Context as for genus. Seven subspecies of *Rusa unicolor* are currently recognized (Groves and Grubb 1987; Grubb 2005; and information from *Mammal Species of the World*, www.bucknell.edu, accessed 13 January 2009):

R. u. brookei (Hose, 1893a:206). See above.
R. u. cambojensis (Gray, 1861:138). See above.
R. u. dejeani de Pousargues, 1896:12. See above.
R. u. equina (G. Cuvier, 1823:45). See above.
R. u. hainana (Xu, 1983:395). See above.
R. u. swinhoii (Sclater, 1862:152). See above.
R. u. unicolor (Kerr, 1792:300). See above.

NOMENCLATURAL NOTES. Lydekker's (1898:145) contentions that "few groups of deer are more difficult to understand than the various kinds of sambar" and "very different views have been entertained as to whether the various modifications of the sambar type indicate distinct species, or merely races" are still valid today as morphologists (e.g., Meijaard and Groves 2004) and molecular systematists (e.g., Hernández Fernández and Vrba 2005; Randi et al. 2001) debate the monophyly of *Rusa*. The nomenclatural history of *R. unicolor* is complicated because of its wide distribution from India through southern China and southeastern Asia; its varied mass, color, and antler characteristics; similarity to and sympatry with other Asian cervids; and the rapid pace of collection, description, and publication by notable zoologists such as B. H. Hodgson (1831, 1841a, 1841b, 1841c, 1863) in Nepal and India and P. M. Heude (1888a, 1888b, 1888c, 1888d, 1896) in southeastern Asia in the 1800s. The masterful tome of Braun et al. (2001) on the extensive eastern Asian faunal collections of French Jesuit missionary, Father Pierre Marie Heude, served to clarify types and type localities of his many rusine deer. Lydekker (1915) recognized 13 subspecies of *unicolor* and included Philippine *nigricans*, *nigellus*, *mariannus*, and *philippinus*, and their various synonyms and name combinations, in his synonymies. Based on more recent taxonomic assessments of the rusine deer (Grubb and Groves 1983; Haltenorth 1963), Grubb (2005) did not include them as synonyms of *R. unicolor*. Rusine deer from the Philippines are currently considered by most to be *R. marianna* (Grubb 2005), albeit Francis (2009) still considered them to be *R. unicolor*. Additional phylogenetic analyses are still needed to clarify the phylogeny of rusine deer (Grubb and Groves 1983; Hernández Fernández and Vrba 2005).

Van Bemmel (1949:211) gave "S. Müller & H. Schlegel, 1839–1844" as the authorities and dates for *Russa*, but I credited Gray (1843) with this incorrect spelling of *Rusa* Hamilton-Smith, 1827a. Confusion exists because of the different dates that the various volumes and parts of *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche Overzeesche Bezittingen*, edited by C. J. Temminck, were complied and published (Husson and Holthuis 1955). Mammals were presented in a *Zoologie* volume with 12 numbered parts issued in 1839–1845, and *Russa* was mentioned on page 206 in Number 12, published 26 June 1845 (later than Gray 1843), based on Husson and Holthuis' (1955) evaluation of original wrappers in the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

In Hindi, sambur and the alternate spellings sambar and sambhar are gender neutral. Article 30.2 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999:36) outlines protocols for gender determination of generic names formed from words that are not Latin or Greek. Further, Article 30.2.3 states that "if no gender was specified, the name takes the gender indicated by its combination with one or more adjectival species-group names of the originally included nominal species." Because Latinized species names that Heude (1888c) associated with *Sambur* were masculine, or neuter, and I could find no specific statement by Heude regarding its gender (Article 30.2.2), his use of *Sambur* must be assumed to be masculine. Lydekker (1915) did not present both spellings, so his use of *Sambar* was considered a subsequent misspelling (A. L. Gardner, pers. comm.). Grubb (2005:671) intentionally changed the masculine gender of 11 of Heude's (1888c:42–46) species names to feminine, which was warranted to concord with his combination of Heude's (1888c) species names with *Rusa*, which he assumed to be feminine and rooted in Latin.

Unlike Lydekker (1915:78) and Grubb (2005:671), I credited the synonym *malaccensis* to J. B. Fischer (1829) rather than F. Cuvier (1823). I could not find any reference to *malaccensis* after review of the ruminants in the classic *Histoire Naturelle des Mammifères* of É. Geoffroy Saint-Hilaire and F. Cuvier. This ''publication'' contains a very complicated collection of series (4), tomes (7), livraisons (= deliveries; 72), and plates (431), which were issued, numbered, renumbered, and dated from 1819 through 1842. Frédéric Cuvier authored some of the unnumbered pages of descriptive text associated with the plates that were apparently sold as separate livraisons; some plate-associated texts were simply dated with no author. From 1824 to 1842, livraisons were grouped and dated into 7 tomes, and finally, in 1842, all plates were numbered 1–431. Lydekker (1915:78) gave the abbreviated credit for *malaccensis* as ''F. Cuvier, Hist. Nat. Mamm. vol. i, pl. x, 1824.'' Similarly, J. B. Fischer (1829:451) provided ''Fr. Cuv. et Geoffr. Mamm. fasc. 10.'' In Tome Premier dated 1824, the ''Biche de la Presqu'ile de Malac[c]a [= French for Malayan Peninsula]'' was presented in Livraison X and individually dated September 1819. Nowhere on the plate or in the associated descriptive text (which is not attributed to Cuvier alone), or in various tables of contents and indexes, was the epithet *malaccensis* presented. In fact, in the 1842 retrospective ''Table Générale et Méthodique,'' this plate was numbered 358, attributed to Tome Deuxième, and aligned parenthetically with *Cervus hippelaphus*.

Unlike Grubb (2005), Corbet and Hill (1992:256) included ''*Cervus spatulatus* Thomas, 1901'' as a synonym for *Rusa unicolor*. While Thomas (1901:284) ''exhibited and made remarks on a peculiar Stag's frontlet and horns which [were] obtained from Mr. Charles Hose in Borneo,'' he did not use the specific epithet *Cervus spatulatus*, at least in that published record. Oldfield Thomas was a prolific writer and published 1,090 papers from 1879 to 1929, many of them descriptions of new mammalian species from specimens sent to the British Museum (Hill 1990). Thomas withdrew proofs of only 2 of his many papers during that time period, and one of them included a never-published, but presumably more complete, description of *Cervus spatulatus* ''with three illustrations intended for the Proceedings of the Zoological Society of London'' (Hill 1990:31, 49). In the same year, condensed and paraphrased minutes of the Zoological Society of London, dated 18 June 1901 and authored by Secretary Philip L. Sclater were published in *Zoologischer Anzeiger* along with minutes from other European societies. In those secondarily published minutes, Sclater (1901:536) used the name *Cervus spatulatus*, provided a more detailed description of its ''antlers'' than appeared in Thomas (1901)—perhaps paraphrasing the withdrawn proofs, and gave the type locality as ''Central Borneo,'' albeit Thomas (1901:284) originally included ''from a hitherto unvisited part of Borneo, the Pa Bauan country in the far interior.'' Furthermore, Sclater (1901:536) elaborated well beyond Thomas (1901:284) by stating the antlers differed from ''all other known deer in being highly complicated and many-branched, with the upper portion curved forward, and the brow-tines developed into broad horizontal paddle-like structures,'' not at all like *R. unicolor*, the only large cervid that occurs on Borneo (see *Cervus brookei* Hose, 1983b). In describing Thomas' withdrawn paper, Hill (1990:31) said the antlers were ''much deformed,'' suggesting that caused Thomas to withdraw his proofs but not before Sclater perhaps had seen them and incorporated a description into his summary minutes for *Zoologischer Anzeiger*. Sclater and Thomas were close colleagues and had collaborated around the same time on their now classic, 4-volume *The Book of Antelopes*. Hill (1990:31) concluded that the name *Cervus spatulatus* ''remains available in the literature, although undiscovered.'' Under Article 50.1.1 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999), attributing *Cervus spatulatus* to Thomas is warranted if it was clearly attributed to Thomas in Sclater's publication and if Thomas previously satisfied 2 of 3 criteria of availability by offering a name (he did not), a description or indication (he did by the standards of the day), or a publication (he did—Thomas 1901; see Leslie and Sharma 2009:2–3 for a similar case involving the authority for *Tetracerus*).

Hamilton-Smith (1827a) adapted rusa, the common Malayan and Bahasan (Indonesian) name for deer (also rusa-etam), as the generic epithet, and Kerr's (1792) *unicolor* is Latin for 1 color. The common name sambar is Hindi for a vegetable stew with a mix of spices called sambar powder, which gives the stew a yellowish brown color, similar to the pelage hue of *R. unicolor* in parts of India. Because of the wide distribution of *R. unicolor*, it has many common names. In German, it is often called Aristotle-Hirsch, in reference Aristotle's knowledge of the species, or Pferdehirsch, referencing its long legs (Benirschke 2002). The large preorbital gland, everted during rut, no doubt gave rise to the Chinese vernacular name, four-eyed deer (Swinhoe 1862). Whitehead (1993:511–512) provided a comprehensive listing of common names: for example, con hai (Annamese); menjangon (Bahasa Java); payoh (Bornean); connai (Burmese); hai-lu, shui-lu, twahé (= mountain horse; Chinese); jerao, jerrow (Himalayan); sabhar, sámar (Hindi); mila, kada maan (Tamil) kadaba, kadave, kadavay, kaddama (Kanarese); kullay marn, rusa etam (Malayalam); meru, samba (Marathi); jarai (female), jarao (male; Nepalese); gona, marrei (Sri Lanka); hei-lu, hei-lu-tsze (Sichuan); cheeang, tamil (Taiwan); and kwang, kwang-paa (Thailand). *R. unicolor* has been featured on at least 23 stamps issued by 10 countries from 1894 to 1978 (Whitehead 1993).

DIAGNOSIS

All 4 species of *Rusa* (*alfredi*, *marianna*, *timorensis*, and *unicolor*—Grubb 2005) are allopatric and vary greatly in mass, forming a morphocline (Groves and Grubb 1987). *R. unicolor* can be distinguished from other species of Cervini by their ''robust, rugose antlers with a long [acutely angled—Pocock 1933] brow tine, very deep lacrimal pits, reduced auditory bullae, and dark eumelanic pelage'' (Groves and Grubb 1987:42; Fig. 1). *R. unicolor* in the western part of its range is the largest Oriental deer (Pocock 1943a), and it can be distinguished from comparably sized Eurasian red deer and North American elk (*Cervus elaphus*—Clutton-Brock et al. 1982; Geist 1998; Peek 1982; Whitehead 1972, 1993) by its 3-tined antlers, near-uniform pelage without a pronounced rump patch, and a long, dark tail.

Along with taxonomic treatments, early accounts by sportsman-naturalists contain useful descriptive information on *R. unicolor* (Baker 1855, 1898; Brander 1923; Fletcher 1911; Gilbert 1888; Glasfurd 1896; Jerdon 1874; Peacock 1933; Stebbing 1911), which also is featured in more colorful accounts of hunting ''man-eating'' predators, notably from India (Sivaramakrishnan 2008; Smith 1904). Most contemporary scientific information on wild *R. unicolor* comes from India (e.g., Johnsingh 1983; Schaller 1967) and Sri Lanka (e.g., Eisenburg and Lockhart 1972; Kurt 1978), but considerable ecological, behavioral, and physiological insight comes from research on introduced populations (free-ranging and captive) in Australia (e.g., Slee 1984) and New Zealand (e.g., Semiadi et al. 1994b, 1995a, 1995b, 1996) and on a single island off the Florida Coast in the United States (Flynn et al. 1990; Lewis et al. 1990; Shea et al. 1990). Syntheses of that information are provided to supplement missing information when likely comparable to native populations of *R. unicolor*.

GENERAL CHARACTERS

Body mass and antler length of *Rusa unicolor* are highly variable and generally decrease from west to east across its distribution (Geist 1998; Pocock 1942a). Sexes of *R. unicolor* are distinguished by larger male mass (e.g., males in India 225–320 kg; females < 225 kg—Sankar and Acharya 2004), male-only antlers on short pedicles, and generally lighter color of females and young (Blanford 1888; Brander 1923; Jerdon 1874; Lydekker 1898, 1915; Fig. 2). Across the range of *R. unicolor*, head and body length is 162–246 cm, tail length is 25–30 cm, and shoulder height is 102–160 cm (Nowak 1999).

Antlers of mature males are unique among cervids (Fig. 1), considered to exhibit an ancestral condition (Pocock 1942a), generally only 3-tined, rough, and corrugated as males age, often robust, and ''consist[ing] of an anterior more or less straight brow tine, that comes off at an acute angle (Blanford 1888:543; Pocock 1933) to the main or posterior beam, which forks [typically] but once'' (Allen 1940:1169; Jerdon 1874). The ''anterolateral tine'' tends to follow the main beam and is typically longer that the ''posteromedial'' tine (Groves 2003:351), but not always (Whitehead 1972). In exceptional cases, the brow tine can be about 50% of total length of the main beam (Brander 1923; Gilbert 1888); 10% of males can have a 4th tine on 1 antler (Ward 1896) and rarely the brow tine is bifurcate (Brander 1923). The space between antlers is V- or U-shaped, and tips of tines are often inturned (Brander 1923; Downes 1983b:figure 12; Lydekker 1898, 1915). Mean record antler length of *R. unicolor* is 109.8 cm, exceeded by only red deer–North American elk and caribou (*Rangifer tarandus*) among cervids (Clutton-Brock et al. 1980; Whitehead 1993).

Fig. 2.—Mature female and young-of-the year *Rusa unicolor* foraging on aquatic vegetation in Ranthambhore National Park, Rajasthan, northern India, January–February 2000. Photograph courtesy of James Warwick (www.jameswarwick.co.uk) used with permission.

There is considerable variation in mass and color of the various subspecies of *R. unicolor* (Geist 1998). Early general descriptions of *R. unicolor* were provided by Allen (1940), Blanford (1888), Jerdon (1874), Lydekker (1898, 1915, 1916), and Pocock (1943a, 1943b): large robust deer; pelage coarse and shaggy, particularly on males in rut and winter; coat color basically uniform around the body with considerable variation in color ranging from yellowish brown to brown or almost ''black or dark salty grey'' (Blanford 1888:543); belly often as dark as the rest of the body, or darker, but sometimes ''chestnut or whitish on the inner side of buttocks, and on the under parts'' (Lydekker 1898, 1915:73); females and young generally lighter in color and young not spotted, but very faintly spotted in Malaysia (Lydekker 1898), with a dark dorsal line (Brander 1923); sometimes inconspicuous light to rusty brown rump patch

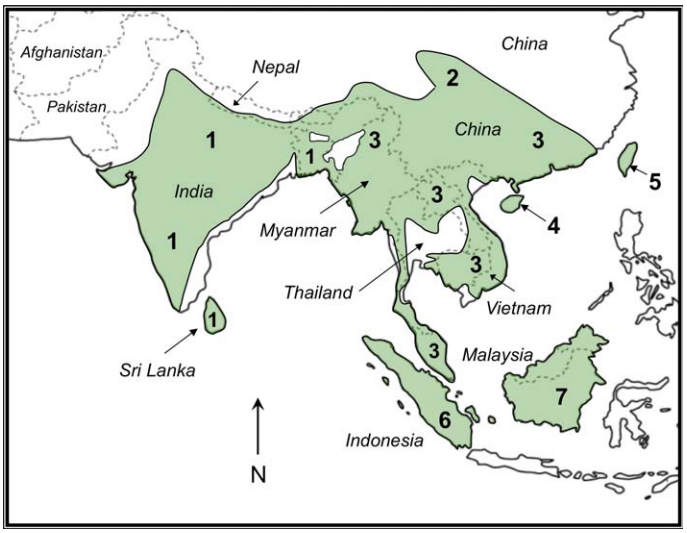

Fig. 3.—Distribution of *Rusa unicolor* in India, Sri Lanka, southern China, and southeastern Asia adapted from Ohtaishi and Gao (1990), Timmins et al. (2008), and van Bemmel (1974). The general distributions of the 7 subspecies of *R. unicolor* are: 1, *R. u. unicolor*; 2, *R. u. dejeani*; 3, *R. u. cambojensis*; 4, *R. u. hainana*; 5, *R. u. swinhoii*; 6, *R. u. equina*; and 7, *R. u. brookei*.

but not as pronounced as in other cervids (Schaller 1967) or completely absent (Swinhoe 1862); throat and neck "with unkempt ruff" of long hairs, particularly developed on males and sometimes tipped in gray (Blanford 1888; Schaller 1967:135); ears large (17.8–20.3 cm—Jerdon 1874), broad, and obovate (Brander 1923), about one-half the length of the head (Lydekker 1915) and whitish on the back at the base (Schaller 1967) and inside, resembling "the frosted terminal leaves of a young teak tree, amongst which [they] are found" (Brander 1923:169); black-tipped tail, long (30.5–33.0 cm—Jerdon 1874) compared with other cervids, rather bushy, and whitish underneath; lack of nasal scent glands (Atkeson et al. 1988); pronounced eversible (Lydekker 1898) preorbital glands and associated deep lachrymal fossa, twice the size of those of red deer (Blanford 1888; Pocock 1910, 1943b); supraorbital glands lacking; metatarsal glands with tuft of hair but sparse (Pocock 1910); caudal glands with secretion granules of 20 nm (Evgenjeva 1991); and a "sore spot" on the throat, presumably a dermal gland associated with rut (Brander 1923; Geist 1998; Peacock 1933; Schaller 1967; Thom 1937; see "Function").

DISTRIBUTION

Rusa unicolor is the most widespread deer in Asia (Corbet and Hill 1992; Fig. 3) and occurs from southern Nepal (Chesemore 1970; Dinerstein 1979, 1980; Seidensticker 1976a, 1976b), India (Menon 2009; Sankar 2008; Schaller 1967), Sri Lanka (Eisenburg and Lockhart 1972), and Burma (U Tun Yin 1967) throughout southern China (MacKinnon 2008; Ohtaishi and Gao 1990) and southeastern Asia to the Pacific Coast and the islands of Borneo, Hainan, and Taiwan (Hsu and Agoramoorthy 1997; Timmins et al. 2008; Whitehead 1972, 1993). It occurs from sea level at various places in southeastern Asia to about 3,000 m in the Indian Himalayas (Green 1985) and Burma (U Tun Yin 1967) and to about 3,500 m in Taiwan (Whitehead 1972). Largely because of excessive harvest and habitat loss (Timmins et al. 2008), *R. unicolor* is now rare in Bangladesh (Basbar et al. 2001), Thailand (Ngampongsai 1987), Laos (Timmins and Evans 1996), and Vietnam (Khun and Kan 1991).

Intentionally introduced *R. unicolor* or deer-farm escapees have established populations in Victoria, New South Wales, French Island (Victoria), Western Australia, and the Northern Territory of Australia (Bentley 1957; Downes 1983a, 1983b; Moriarty 2004; Slee 1984; Whitehead 1993; Yamada et al. 2003). More than 70,000 individual *R. unicolor* have been released or escaped in Australia since the 19th century; such activities have resulted in 8 established populations (Moriarty 2004). Similarly, introduced populations occur in New Zealand (Douglas 1983; Forsyth and Duncan 2001; Fraser et al. 2000; Harris 1971; New Zealand Department of Conservation 2005; Nugent et al. 2001; Riney 1957; Veblen and Stewart 1982); California (Hopkins 2005; Presnall 1958), Florida (Davidson et al. 1987; Lewis et al. 1990), and Texas (Ables and Ramsey 1972; Mungall 2007; Richardson 1972) in the United States; and West Cape Province, South Africa (Lever 1985). Introduced populations are mainly of Indian or Sri Lankan origin (Lever 1985). An unknown number of the Philippine deer (*R. marianna*) were introduced along with *R. unicolor* in Victoria, Australia, in the 1860s, but the current free-ranging population there is considered typical of *R. unicolor* (Downes 1983b). Similarly, some Philippine deer from Java were introduced in New Zealand, and likely interbred with *R. unicolor* (Harris 1971); literature pertaining to these populations was used only if the investigators identified *R. unicolor* as the study species. *R. unicolor* failed to establish itself after introduction in Tasmania in the early 1890s, and the status of a private herd in Rio Tietê, Brazil, is unknown since the property was liquidated in 1986 (Whitehead 1993). Given current taxonomic distinctions, references to introductions of *R. unicolor* in Guam are incorrect; the Philippine deer was introduced there in 1770s (Conry 1988).

FOSSIL RECORD

Cervidae is a species-rich family of Eurasian origin (Gilbert et al. 2006) that radiated from tropical to temperate climates in the Pleistocene (Geist 1998; Groves 2007) and contains as many as 26 fossil genera and 80 fossil species from China alone (Dong 1993). Paleomerycines (e.g., *Amphitragulus*), procervulines (e.g., *Procervulus*), and cervu-

lines (e.g., *Eostyloceros*) of the Miocene were likely precursors of species now included in the family Cervidae (Flerov 1952; Kurtén 1968; Miyamoto et al. 1990 cf. Gilbert et al. 2006), with fossil species of *Cervavitus* giving rise to tribe Cervini (Di Stefano and Petronio 2002; S. Mattioli, pers. comm.; Petronio et al. 2007). Despite a relatively recent radiation into South America during the Pliocene (Eisenberg 1987; Gilbert et al. 2006), Cervidae is mainly a family of the Northern Hemisphere (Geist 1998; Gentry 2000; Janis and Scott 1987; Webb 2000); the only cervid in Africa, *Cervus elaphus barbarus* (Barbary red deer), may have been introduced by humans from Europe along the southern Mediterranean coast as long as 8,000 years ago (V. Geist, in litt.). Despite availability of numerous cervid fossils, particularly antler parts, considerable speculation remains, much of it focused on the particularly active Plio-Pleistocene period and a transition of herbivorous species from forest to grasslands (Azzaroli et al. 1988; Di Stefano and Petronio 2002; Gilbert et al. 2006; Lister 1987, 1993).

During the upper Pliocene, rusine deer were found in Europe (Di Stefano and Petronio 2002; Lydekker 1898; van Bemmel 1974), and early lower Pleistocene forms with 3-tine antlers, such as the Philis deer (*Cervus philisi* [= *etuerarium* or *rhenanus*]), have purported affinities with living *Rusa* (Kurtén 1968; Lister 1987). *R. unicolor* is among the most ancestral of living cervids, with characteristics little changed from the late Pliocene and paralleling other Chinese pliocervines (Petronio et al. 2007). It likely evolved in southern tropical areas (Flerov 1952), perhaps from the extinct Pleistocene forms such as *Epirusa hilzheimeri* (Di Stefano and Petronio 2002; Zhdanski 1925) or *Eucladoceros* (Geist 1998; Grubb 1990; Koizumi et al. 1993). Di Stefano and Petronio (2002) proposed that *Rusa* (= *Cervus*) *elegans* branched in the mid-Villafranchian, 2.0–2.5 million years ago, giving rise to the extinct *R. hilzheimeri*, which gave rise to *R. unicolor* and the high-elevation specialist *Przewalskium albirostre* of the Tibetan Plateau (Leslie 2009; Schaller 1998).

Five rusine fossil species (*elegans*, *microta*, *stehlini*, *unicolor*, and *yunnanensis*) from the early Pleistocene have been found throughout China; *R. timorensis* apparently did not appear until the late Pleistocene (Dong 1993). A fossil *Rusa*, which was comparable but larger than extant *R. unicolor*, has been found in caves in northern Vietnam, dated from the middle Pleistocene 80,000–169,000 years ago (Bacon et al. 2004). In Sichuan, China, antlers of *R. unicolor* from the middle Pleistocene possibly were worked by humans prior to fossilization (Hooijer 1951). Bones of *R. unicolor* also occur in caves of Paleolithic origin in China (Huang et al. 1995; Si et al. 1993).

FORM AND FUNCTION

Form.—The pelage of *Rusa unicolor* is generally shaggy and coarse, and individual hairs are "not distinctly banded with different coloured rings" (Lydekker 1898:145). Hairs on *R. unicolor* are thickest on the neck, back, and abdomen; thinner on dorsal side of the tail and legs; and thinnest around the preorbital glands, temples, and gaskins (lower thighs—Sokolov et al. 1987). Guard hairs of *R. unicolor* have a mean medullary width of 186 μm and mean cortical width of 29.0 μm (Sheng et al. 1993). Measurements (μm) of axial hairs vary depending on the location on the body; ventral neck hair: cortical thickness = 15.0, medullary diameter = 75.0, root diameter = 147.0, hair diameter above the root = 93.3; ventral tail hairs: 10.6, 75.0, 166.6, 107.0; lateral gaskin hairs: 10.0, 40.0, 86.7, 66.5; lateral thigh hairs: 10.0, 37.5, 80.0, 60.0; abdomen hairs: 10.0, 75.0, 100.0, 66.6; preorbital region hairs: 10.0, 22.2, 63.3, 50.0; and forehead hairs: 12.5, 55.0, 70.0, 43.3 (Sokolov et al. 1987).

Related to the tropical origin of *R. unicolor*, development of the undercoat in young *R. unicolor* is modest or lacking; 2 of 4 captive 165-day-old (± 9.8 *SE*) *R. unicolor* did not have an undercoat, and the proportion of the undercoat relative to the total pelage weight on the other 2 young was only 0.7% (Semiadi et al. 1996). Pelage characteristics of those young *R. unicolor*, when present, were: depth of fiber undercoat, 26.8 mm; weight of fiber undercoat, 114 g/m^2; length of fiber undercoat, 20.3 mm; length of guard hairs, 44.0 mm; diameter of undercoat fibers, 18.0 μm; and diameter of guard hairs, 277.0 μm (Semiadi et al. 1996). Shedding is said to occur in "large tufts … the old hair coming away in sections" (Brander 1923:169).

Although numerous antler measurements have been published for *R. unicolor* (e.g., Downes 1983b; Lydekker 1898; Pocock 1943b; Whitehead 1993), skull measurements are less common. Nasal bones on the skull of *R. unicolor* "develop a plate at the posterior expansion, which tends to grow over the lachrymal vacuity" (Lydekker 1898:146, 1915); the vacuity is longer than in other cervids; and the skull has a robust appearance (Pocock 1943b; Fig. 4). The small auditory bullae rarely project below the basioccipital, and the preorbital "gland-pit" is large, usually exceeding the diameter of the orbit (54–64 mm in India—Pocock 1943b:27). Representative condylobasal lengths of skulls (mm, sexes combined) are 350–408 from India, 332–395 from Sumatra, 330–345 from Borneo, and 312–328 from Taiwan (Lyon 1906; Pocock 1942b, 1943b), illustrating the general decrease in size from west to east (Geist 1998). More recent representative mean skull measurements (mm ± *SD*) of *R. unicolor* include: greatest length of skull, 357.5 ± 35.0; condylobasal length, 340.5 ± 35.3; basal length, 318.6 ± 33.0; palate length, 212.0 ± 22.5; condylar breadth, 65.4 ± 7.1; rostrum length, 199.1 ± 26.7; nasal length, 104.7 ± 14.7; biorbital breadth, 139.4 ± 14.8; maximum breadth of nasals, 39.4 ± 7.4; interorbital breadth, 88.9 ± 13.5; and braincase breadth, 86.7 ± 7.5 (n = 27–30, males and females combined—Meijaard and Groves 2004).

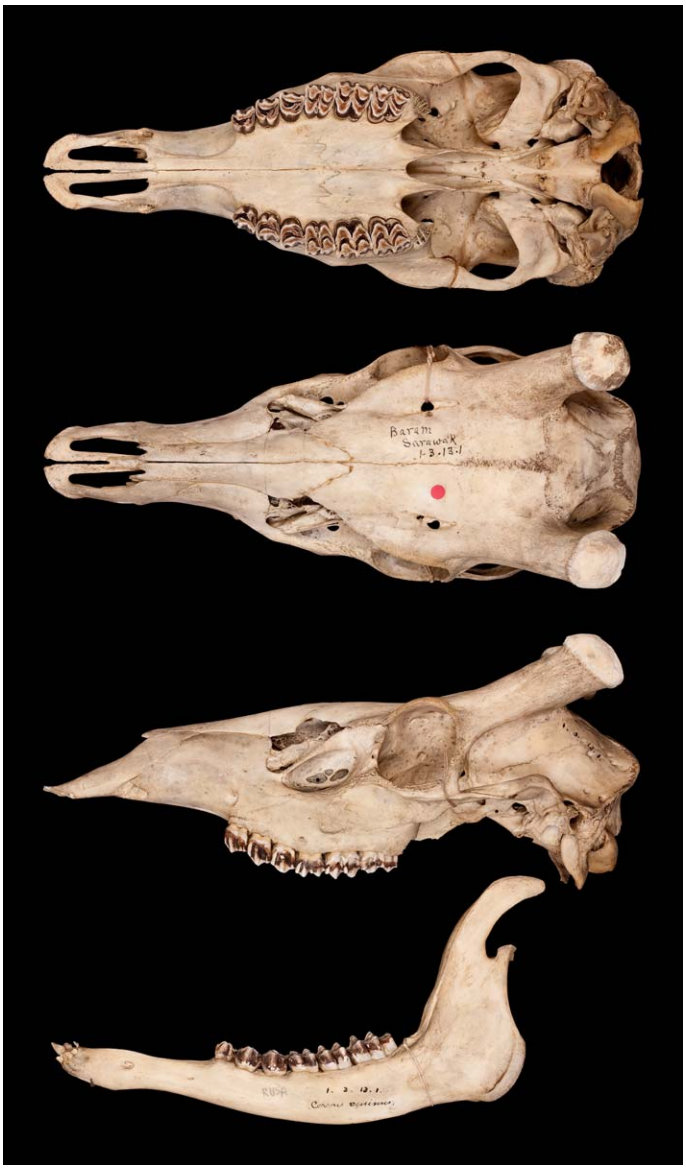

Fig. 4.—Ventral, dorsal, and lateral views of skull and lateral view of mandible of male *Rusa unicolor brookei* (British Museum [Natural History], specimen 1.3.13.1) with pedicels after antler shedding, collected in Sarawak, northwestern Borneo. Greatest length of skull is 354 mm.

Unlike New World deer, new antlers of Old World deer such as *R. unicolor* begin to grow immediately after the previous antlers are shed (Geist 1998). During growth, antlers are covered in modified skin, or velvet, that nourishes the growing bone (Bubenik 1993); developing antlers and velvet of various cervids are prized in Asian medicine (Peacock 1933; Thom 1937) and grown commercially for that market (Luick 1983). Early anecdotal accounts suggested that *R. unicolor* did not replace its antlers annually (Baker 1898; Fletcher 1911; Gilbert 1888; Phythian-Adams 1951), but this is not the case and is probably related to the lack of a pronounced breeding season and observations of males in various stages of antler growth and ossification throughout much of the year (Brander 1923; Putman 1988; Schaller 1967; Thom 1937)—a pattern that persists even if males are transplanted to more temperate areas (Lao 1968).

Unlike other cervids, particularly northern boreal species, antler bone of *R. unicolor*, as well as that of primitive species of *Axis* and *Rucervus*, has a very thick cortex suggesting rapid building processes of the osteon; a tubular cavity of 8 mm in diameter, apparently a blood sinus suggesting that the some bone remains alive after shedding of velvet; and concave seals in young males changing to flat seals in prime males (Acharjyo and Bubenik 1983). Males can be grouped into general age classes $\leq$ 6 years of age based on their antler characteristics (Downes 1983b). Length and mass of antlers increase with age but most notably in a male's 7th year; thereafter, length and mass change little (Downes 1983b), although Baker (1898) contended that maximum antler size (and mass) may not be achieved until a male is about 10 years old. Yearling males have a single spike antler, and 2- to 3-year-old males have a brow tine and main beam; both tend to have smooth antlers. By 4 years of age, males have "roughly corrugated" antlers with the typical 3 tines (Brander 1923:171; Downes 1983b). Yearling and adult females can be differentiated based on body mass, but no external characteristics are useful for aging adult females.

The dental formula of adult *R. unicolor* is typical of cervids: i 0/3, c 1/1, p 3/3, m 3/3, total 34 (c1 incisiform). Upper canines may be absent; only 2 of 83 *R. unicolor* skulls had them in Sariska Tiger Reserve, India (K. Sankar, pers. comm.). Eruption of the 1st permanent teeth (m1–M1) begins at about 1 month, followed by m2–M2 at about 8 months and then i1–I1 at about 11 months; all permanent teeth are present by about 2.5 years (Slee 1984)—a pattern useful for aging (Humphries and Rowler 1976). Molars are notably hypsodont with "small accessory columns" (Blanford 1888:543); 2 or 3 cusps occur on the occlusal surfaces of the premolars and molars forming sharp lingual crests; and incisors are "hockey stick like" in shape (Shalini et al. 2004a:1102). Representative tooth measurements (mean $\pm$ *SE*, cm) of an adult *R. unicolor* are crown length: p1 = 0.60 $\pm$ 0.01, p2 = 1.36 $\pm$ 0.01, p3 = 1.30 $\pm$ 0.04, m1 = 1.66 $\pm$ 0.11, m2 = 1.83 $\pm$ 0.02, and m3 = 1.95 $\pm$ 0.04; and crown width: p1 = 0.56 $\pm$ 0.03, p2 = 0.77 $\pm$ 0.5, p3 = 0.73 $\pm$ 0.05, m1 = 1.06 $\pm$ 0.03, m2 = 1.32 $\pm$ 0.01, and m3 = 1.42 $\pm$ 0.02 (Shalini et al. 2004a).

Tooth eruption-wear and cementum annuli of *R. unicolor* in Gir National Forest, India, were highly correlated (r^2 = 0.974—Berwick 1974), but irregular layering of cementum was reported in *R. unicolor* from Ruhuna National Park, southern Sri Lanka, making interpretation of age more difficult (Ashby and Santiapillai 1986). Patterns of growth layers in dental cementum of the 1st mandibular

molar of *R. unicolor* relative to age have been investigated in New Zealand and are comparable to those of red deer (Douglas 1970; Slee 1984). Flynn et al. (1990) noted that it was difficult to age *R. unicolor* from tooth eruption and wear alone; estimates could be off by 12 months.

Anatomy of the 4-chambered stomach, particularly the rumenoreticulum, and poorly developed papillae on the roof of the rumen suggest that *R. unicolor* should be a grass-roughage feeder (Stafford 1995). Various attributes of each chamber are rumen: volume = 9–20 l; reticulum: volume = 0.2–1.0 l, wall thickness = 1.5–4.0 mm; omasum: volume = 0.2–1.1 l, mass = 360–568 g, wall thickness = 2.0–2.75 mm; and abomasum: volume = 0.4–1.2 l, length = 25–35 cm (9 male and 4 female *R. unicolor*, aged 1–5 years—Stafford 1995). Lengths (cm) of lower digestive organs of *R. unicolor* are: small intestine, male 480 and female 360; large intestine, male 450 and female 360; and cecum, male 45 and female 35 (Stafford 1995). Compared with other ruminants, those lengths are very short, and the near 50:50 ratio of small to large intestinal length of *R. unicolor* is in contrast to that of the red deer, a true grass-roughage feeder, which has a ratio of about 75:25 (Dryden 2008; Stafford 1995). Combined, intestinal characteristics of *R. unicolor* suggest a species capable of efficiently digesting diets of grasses and browse, or an intermediate feeder. Morphology of the scapula (Sarma et al. 2003), atlas (C1 vertebra), and axis (C2—Shalini et al. 2004b) of *R. unicolor* also has been described.

The reproductive tract of female *R. unicolor* generally is comparable to that of other cervids (Plotka 1999). *R. unicolor* has a bicornuate uterine horn with 3 mesometrially located caruncles, and the 3 associated cotyledons, in each horn; the 6 placental cotyledons are large (late gestation: 300–320 g and 5 by 9 cm); and the placenta implants on the 3 mesometrial caruncles of both horns (Benirschke 2002). A single corpus luteum was noted per pregnancy in 5 females from Perak, Malaysia (Khan and Khan 1968). The uterus of a near-term female *R. unicolor* from the San Diego Zoo was 130 cm long, and the placenta was epithelio-chorial without invasion into the maternal tissue (Benirschke 2002). The 7-cm umbilical cord in that gravid female was not spiraled, contained 4 blood vessels, and had a large, highly vascularized allantoic duct (Benirschke 2002).

Mean (± *SD*) testicular and semen characteristics of 15 male *R. unicolor* from Taiwan include: single testicular volume, 126.9 ± 72.7 cm^3; scrotal circumference, 23.5 ± 5.5 cm; semen volume, 1.4 ± 0.7 ml; spermatozoa concentration, 557 ± 344.8 × 10^6/ml; spermatozoa motility, 75.5% ± 9.3%; and normal spermatozoa morphology, ≥80% (Wu et al. 2002). Mean (μm ± *SD*) lengths of individual spermatozoa include: total length, 65.4 ± 1.7; head length, 9.3 ± 0.5; midpiece length, 12.9 ± 0.7; and tail length, 43.2 ± 1.8 (Wu et al. 2002). Fetal testes of *R. unicolor* have binucleated trophoblastic cells on the villi and histological characteristics that suggest a lack of active fetal gonadotropins (Benirschke 2002).

***Function.*—**Mean (± *SD*) hematological values of *Rusa unicolor* are: hematocrit, 37.7% ± 3.2%; red blood cells, 5.70 ± 0.22 × 10^6 cells/ml; hemoglobin, 13.0 ± 0.9 g/dl; mean corpuscular volume, 66.0 ± 3.2 μm^3; white blood cells, 4.79 ± 1.18 × 10^3 cells/ml; eosinophils, 2.58% ± 2.75%; basophils, 1.43% ± 1.68%; and monocytes, 1.82% ± 0.76% (n = 3 adults—Peinado et al. 1999a). Representative mean (± *SD*) blood chemistry and serum values of *R. unicolor* are: aspartate aminotransferase, 24.4 ± 4.1 IU/l; alanine aminotransferase, 28.7 ± 4.7 IU/l; creatinine phosphokinase, 205.0 ± 122.0 IU/l; lactic dehydrogenase, 452 ± 49 IU/l; gamma glutamyl transpeptidase, 38.1 ± 19.6 IU/l; alkaline phosphatase, 197 ± 74 IU/l; glucose, 8.50 ± 1.32 mmol/l; urea, 6.94 ± 2.77 mmol/l; uric acid, 29.1 ± 10.7 mmol/l; creatinine, 238 ± 23 mmol/l; cholesterol, 1.49 ± 0.42 mmol/l; triglycerides, 0.13 ± 0.05 mmol/l; protein, 7.45 ± 0.34 g/dl; albumin, 71.9% ± 5.7%; albumin–globulin ratio, 2.6 ± 0.7; and osmolality, 289 ± 6 mOsm/kg (n = 3 adults—Peinado et al. 1999b).

Unique among cervids, reproductively active male *R. unicolor*, females during late pregnancy and lactation, and even young-of-the-year can have a ''sore spot'' of 10–15 cm (Davar 1938; Geist 1998; Kurt 1978; Peacock 1933; Schaller 1967; U Tun Yin 1967) on their throats, ventrally halfway down the neck (Evans 1912). This spot is apparently glandular, centered in a whorl of hair, and often, but not always, exuding ''whitish-looking oily or watery substance'' from a blood-red spot (Davar 1938; Evans 1912; Morris 1938; Phythian-Adams 1951; Thom 1937:315). Thom (1937:313–317) summarized the colorful early speculation on the cause or function of the sore spot, which included disease (e.g., leprosy in Thailand), consumption of ''wild olives,'' ticks or some other parasite (Davar 1938; Evans 1912; Peacock 1933; Whitehead 1972), irritation from rubbing or moving through thick coarse grass, or a wound from an attack by a marten, likely *Martes flavigula*. The sore spot apparently does not occur (or has not been observed) on *R. unicolor* in Sri Lanka (Kurt 1978), among introduced populations on St. Vincent Island, Florida (Shea et al. 1990), and Australia (Downes 1983b), or under some captive conditions (Evans 1912; Mary and Balakrishnan 1984; Thom 1937; U Tun Yin 1967). Richardson (1972:58) noted that all sexes and ages of introduced *R. unicolor* in Texas had a ''whirl of hair'' on the throat that was ''relatively bare,'' but he did not notice any secretions or blood. Perhaps this ''gland'' does not manifest itself when densities are relatively high or group size is large, as in Sri Lanka or under confinement, suggesting a role in communication (scent dispersal—Mary and Balakrishnan 1984; Schaller 1967), particularly during breeding and at low densities (Geist 1998). The sore spot is associated with the breeding season in

some places in India (Johnsingh 1980), but it does not bleed or secret any substance, even during breeding, in western or northern India (K. Sankar, pers. comm.).

Muscle tissues of *R. unicolor* vary (mean ± *SD*) in their composition: longissimus dorsi, 74.40% ± 0.29% moisture, 2.93 ± 0.41 g fat/100 g dry weight, 21.99 ± 0.34 g fat/100 g wet weight, 101.30 ± 0.39 g cholesterol/100 g dry weight, and 4.73% ash, and biceps femoris, 74.52% ± 0.42% moisture, 4.06 ± 0.41 g fat/100 g dry weight, 21.83 ± 0.11 g fat/100 g wet weight, 79.52 ± 0.21 g cholesterol/100 g dry weight, and 2.35% ash (Dahlan and Norfarizan-Hanoon 2008). Detailed information on fatty acid profiles in muscles of *R. unicolor* was provided by Sinclair et al. (1982) and Dahlan and Norfarizan-Hanoon (2007).

During captive feeding trials with <14-month-old *R. unicolor* on an ad libitum diet of chaffed alfalfa (*Medicago sativa*) hay and with a voluntary intake of 58.7 and 55.9 g/kg body weight$^{-0.75}$/day in summer and winter, respectively, numbers of eating and ruminating bouts, and their duration, were about equally distributed during the day (0600–1800 h) and night (1800–0600 h) in both seasons (Semiadi et al. 1994a). Captive *R. unicolor* fed for 6.4 h in summer and 4.2 h in winter and ruminated for 9.2 h in summer and 9.1 h in winter (Semiadi et al. 1994a). Metabolizable energy for maintenance was 474 kJ/kg body weight$^{-0.75}$/day; nitrogen retentions (h) as a percentage of intake on 26.6–47.3 and 33.7–44.4 g N/day were 15.1–31.7 and 15.3–29.4, respectively (Semiadi et al. 1998). Similar captive experiments showed that young *R. unicolor* responded to low-quality diets by lowering voluntary food intake, increasing chewing activity, and conserving nitrogen compared with young red deer (Howse et al. 1995; Semiadi et al. 1994a). The modulus of fineness (Poppi et al. 1980) of fecal particle size from digesta residue suggests that *R. unicolor* is an intermediate feeder (modulus of fineness = 2.21); percentage of fecal particles passing through various sieve sizes are: 4-mm sieve, 0.33%; 2-mm sieve, 1.15%; 1-mm sieve, 5.36%; 0.25-mm sieve, 16.74%; and <0.125-mm sieve, 44.32% (Clauss et al. 2002). Additional insight on fecal particle size during captive feeding trials was provided by Semiadi et al. (1994a).

During experiments with four 165-day-old (± 9.8 *SE*) *R. unicolor* in metabolic chambers at 5°C and 20°C without and with wind (6 km/h), respectively, mean heat production (kJ/kg body weight$^{-0.75}$/day) was 615, 659, 460, and 490 (Semiadi et al. 1996). When ambient temperature was dropped from 20°C to 5°C, heat production increased 34% without wind and 44% with wind; lower critical temperature was 11.6°C without wind and 14.0°C with wind (Semiadi et al. 1996). Compared with young red deer (Semiadi et al. 1996), metabolic responses of young *R. unicolor* suggested that, given their tropical affinities, they need more shelter and food during cold weather, not unlike Crandall's (1964) observations that adults of *R. unicolor* seek shelter during cold weather at the New York Zoological Park.

ONTOGENY AND REPRODUCTION

In the wild, female *Rusa unicolor* probably experience puberty at 18–24 months (Plotka 1999; Sheng and Ohtaishi 1993). Age of sexual maturity of 7 captive female *R. unicolor* in New Zealand was 7–19 months; mean (± *SE*) length of the luteal cycle was 17.2 ± 3 days; 6 of the 7 females were anestrus in November–February; and they displayed no seasonal patterns in prolactin secretion, suggesting little to no response to photoperiod (Asher et al. 1997). Mean birthing interval was 329 days ± 29.7 *SD* for 6 captive females in New Zealand (Semiadi et al. 1994b). A captive female in India reached sexual maturity at 18 months of age and gave birth at 26 months of age (Acharjyo and Misra 1971). Despite translocation of *R. unicolor* from its native tropical latitudes to temperate latitudes, lack of seasonal reproduction is demonstrated by births throughout the year (Asher et al. 1997; Duke of Bedford and Marshall 1942; Lao 1968; Zuckerman 1953). Gestation is about 8 months (Brand 1963; Hayssen et al. 1993), although some reports suggest that it can be longer (Plotka 1999; Sheng and Ohtaishi 1993). Among 525 birth records from 210 semidomesticated adult female *R. unicolor* in Taiwan, mean length of the estrous cycle was 18.2 days ± 0.5 *SE* (n = 56), mean length of gestation was 258.6 days ± 0.3 *SE* (n = 160), and mean birth interval was 369.9 days ± 2.3 *SE* (n = 122—Chan et al. 2009).

Estimates of productivity suggest that either females bred every other year, as was reported in Sri Lanka (Eisenburg and Lockhart 1972), mortality of young is high (Berwick 1974), low observability of offspring (Fig. 2) biases estimates of productivity (Shea et al. 1990), or some combination of all 3 (Schaller 1967). In Perak, Malaysia, only 9 of 23 females were pregnant when collected throughout the year (Khan and Khan 1968). The number of young-of-the-year per 100 females is typically <50:100, even where introduced: 11–44:100 (Johnsingh 1983), 16–43:100 (Berwick 1974), 17–24:100 (Varman and Sukumar 1993), 33.7:100 (Schaller 1967), 38.2:100 (Bagchi et al. 2008), and 55:100 (Berwick and Jordan 1971) in India; 50:100 in Nepal (Seidensticker 1976b); 43.3:100 in Thailand (Ngampongsai 1977); and 22.3:100 in Florida (Flynn et al. 1990). Female offspring may remain with their mothers as yearlings, but males leave their mothers after about 1 year (Lewis et al. 1990).

Timing of the breeding and birthing seasons of *R. unicolor* has been discussed widely because of the variability in parturition dates and antler growth and shedding across the species' substantial latitudinal and longitudinal range (Baker 1898; Fletcher 1911; Lydekker 1898; Schaller 1967). To explain variable antler growth throughout the year,

Comber (1904) suggested that 2 distinct breeding seasons occurred in India, but such variation more likely represents an opportunistic strategy, perhaps based on nutrient availability in varied locations across the species' range relative to antler growth, changing hormone levels, and photoperiod. In Chitwan National Park, Nepal, male *R. unicolor* can be observed in hard antler during any month of the year, reaching a low of 12–14% in July–August and a maximum of 81–92% in December–March; males without antlers occur in December and February–August (Mishra 1982 [not seen, cited in Putman 1988]). Similar patterns of variable antler development have been noted among captive males in New Zealand (Semiadi et al. 1994b).

Twining in *R. unicolor* is uncommon, although Evans (1912:144) stated "sometimes two at birth." Hayssen et al. (1993) give the average litter size of *R. unicolor* as 1.05. Only 2 (0.6%) of 320 births were twins among semidomesticated *R. unicolor* in Taiwan (Chan et al. 2009); only 1 (2.4%) of 41 births was twins at the New York Zoological Park (Crandall 1964); and only 1 (1.5%) of 66 births was twins among introduced *R. unicolor* in Florida (Flynn et al. 1990). Neonates in Australia are 5–6 kg at birth (Slee 1984). Measurements of 8 *R. unicolor* born in captivity throughout the year in New Zealand were: mass, 5.5–8.5 kg; body length, 36.0–43.1 cm; shoulder height, 44.4–55.0 cm; and body circumference, 44.2–54.3 cm (Semiadi et al. 1993); birth weights did not differ between sexes (Semiadi et al. 1994b). A near-term female fetus from the San Diego Zoo weighed 8.3 kg with a crown-to-rump length of 66 cm (Benirschke 2002). In captivity, neonates lick soil at 2–5 days, nibble on dead forage at 5–14 days, eat fresh forage at 13–23 days, browse lightly at 16–26 days, defecate without stimulation at 4–7 days, and begin to ruminate at 30–42 days (Semiadi et al. 1993).

ECOLOGY

Population characteristics.—Despite the widespread distribution of *Rusa unicolor* in southern Asia and use of many different habitat types, it is no longer abundant throughout most of its native range, except in some protected areas (Sankar and Acharya 2004; Timmins et al. 2008). Because of its predominantly crepuscular to nocturnal behavior, small group size, and general shyness, it is difficult to census accurately (Eisenburg and Lockhart 1972; Schaller 1967). Observed densities of *R. unicolor* are generally low but vary depending on season and related grouping behavior, habitat conditions in native and introduced areas, competition, predation, and degree of protection. Representative densities are: 0.24–10.70 individuals/km^2 in moist and dry deciduous tropical forests in India (Bagchi et al. 2003b; Balakrishnan and Easa 1986; Berwick and Jordan 1971; Biswas and Sankar 2002; Jathanna et al. 2003; Karanth and Sunquist 1992, 1995; Khan et al. 1996; Kurt 1978; Varman and Sukumar 1993); 0.70–1.17 individuals/km^2 in lowland dry-zone scrub jungle in Sri Lanka (Eisenberg and Lockhart 1972); 2.0–11.5 individuals/km^2 in riverine and *Shorea* forests and tall-grass habitats in Nepal (Seidensticker 1976b); 1.9–4.2 individuals/km^2 in dry tropical forests in Thailand (Srikosamatara 1993); 0.62–1.42 individuals/km^2 in lowland rain forest in Sumatra, Indonesia (O'Brien et al. 2003); and 1.76–6.01 individuals/km^2 in feral populations in Florida (Flynn et al. 1990). Relative abundance indices of *R. unicolor* in Bukit Barisan Selatan National Park, Sumatra, Indonesia, are 5.6 times higher in areas of low human density (0–9 villages/area) than areas of high human density (16–30 villages/area—O'Brien et al. 2003).

Longevity records in captive subspecies include 6 years, 7 months for a male *R. u. brookei*, 7 years, 11 months for a male *R. u. swinhoii*, 26 years, 5 months for a female *R. u. equina*, and 28 years, 5 months for a female *R. u. unicolor* (Manville 1957; Weigl 2005). Based on life-table analyses, a typical wild *R. unicolor* dies before about 12 years of age in Gir National Forest, India (Berwick 1974). Mean life expectancy of wild *R. unicolor* in Ruhuna National Park, southern Sri Lanka, was about 10 years, with no difference between sexes; maximum life expectancy was 24 years; and somewhat surprisingly, mortality of individuals < 2 years old was only about 6%/year (Ashby and Santiapillai 1986). Maximum life span of exotic *R. unicolor* in New Zealand is estimated at 12 years for males and 17 years for females (Forsyth and Duncan 2001).

Age structures from populations in India suggest relatively low productivity and male-biased mortality: 43–45% adult females, 5–11% yearling females, 16–19% adult males, 11% yearling males, 19–20% young-of-the-year (n = 242 [Karanth and Sunquist 1992], n = 674 [Karanth and Sunquist 1995]); 51.4%, 9.8%, 15%, 3.5%, 20.4% (n = 363—Schaller 1967); and 58%, 7%, 21%, 2%, 12% (n = 1,242—Varman and Sukumar 1993). In Gir Lion Sanctuary, India, average age structure in 1987–1989 was 57.6% adult females, 31.4% adult males, 3.7% yearlings, and 7.1% young-of-the-year, suggesting very low recruitment (Khan et al. 1995). Schaller (1967) contended that about 50% of young *R. unicolor* in central India die before reaching 1 year of age; similarly, Berwick (1974) observed high mortality of young in Gir National Forest in western India.

Adult sex ratios of *R. unicolor* favor females, sometimes remarkably: 6 males : 100 females (Ngampongsai 1977); 16–50:100 (Johnsingh 1983); 26–53:100 (Berwick 1974; Berwick and Jordan 1971); 27:100 (Varman and Sukumar 1993); 28:100 (Mohammad Ali 1982); 29:100 (Schaller 1967); 54:100 (Khan et al. 1995); and 83:100 (Bagchi et al. 2008). Comparison of sex ratios from kills by Indian tigers (*Panthera tigris tigris*—120 males : 100 females) and from direct observations (30:100) in Kanha National Park, central India, suggests differential predation on young and adult males (Schaller 1967). Where major predators are rare or

lacking, male numbers seem to be higher; for example, Eisenburg and Lockhart (1972) noted an usually high male-dominated sex ratio of 123 males : 100 females in Sri Lanka, and Flynn et al. (1990) noted 73 males : 100 females in Florida where *R. unicolor* was introduced.

A typical adult male *R. unicolor* is solitary throughout much of the year, and its low observability may bias estimates of sex ratios. Nevertheless, high rates of mortality are common for male ungulates in general, and disparate sex ratios of *R. unicolor* could be the result of rutting mortality among mature males. Combat between mature males in rut has been described as antler-to-antler "pushing matches," but "often severe wounds are inflicted by the [pronounced and lethally angled] brow antler;" Fletcher (1911:346) observed a likely lethal blow by the victorious male to the abdomen of the fleeing vanquished, which he shot. Phythian-Adams (1951:7) noted that mature males "fight desperately" and found 2 dead males with their antlers interlocked. Although mature males give the "impression of harmony" in captivity, deaths have been reported from rutting injuries (Semiadi et al. 1994b:82). Such mortality is difficult to quantify in the wild, but for related North American elk, rutting mortality may be more common than once thought (Leslie and Jenkins 1985).

Space use.—Although *Rusa unicolor* is remarkably flexible in its habitat affinities, it prefers areas relatively free from human disturbance (Kushwaha et al. 2004; O'Brien et al. 2003). It mainly prefers forested landscapes (Sankar and Acharya 2004). In India, it occurs "wherever there are hilly ranges covered with jungle" and has an affinity for the tall-grass ecotone between dense forest and open grasslands (Fletcher 1911:333; Lydekker 1916; Ngampongsai 1977) where it finds food and protective cover. In Nepal, *R. unicolor* uses dense climax sal forests, where it may have a competitive advantage (Dinerstein 1979, 1980). In Thailand, *R. unicolor* tends to preferentially bed where forest canopy cover is >90% with north and east aspects (Brodie and Brockelman 2010). *R. unicolor* is nonmigratory over much of it range, but in mountainous areas, it may leave higher elevations during winter (Green 1987). *R. unicolor* is rather sedentary, although movements become more extensive during rut (Schaller 1967).

Size of home range of deer varies depending on habitat quality and conditions (Putman 1988), and given the vast geographical distribution of *R. unicolor*, its home-range size is probably quite variable, although few studies have been conducted in its native habitat. In Sariska Tiger Reserve, India, mean annual home ranges (ha) were 1,500 for males and only 300 for females (Sankar 1994 [not seen, cited in Sankar and Acharya 2004]). Where *R. unicolor* has been introduced in coastal Texas, annual home ranges (ha) from direct observations of known individuals were larger for males (69–124, $n = 4$) than females (38–51, $n = 2$); smallest seasonal home ranges occurred in winter (4 for females and 10–86 for males—Richardson 1972). On St. Vincent Island, Florida, mean annual home ranges (ha) of radiocollared individuals were 201.2 for females and 406.6 for males; seasonally, home ranges of females (summer, 36.8; autumn, 45.4; winter, 83.0; spring, 59.8; $n = 4$) were smaller than those of males (summer, 81.2; autumn, 23.7; winter, 106.2; spring, 189.3; $n = 3$), except in autumn (Shea et al. 1990). Home-range size in New Zealand is comparable to that in Florida (Lo 1985 [not seen, cited in Shea et al. 1990]). Reflecting a generally sedentary nature of *R. unicolor*, introduced populations in New Zealand dispersed only 0.64 km/year from the time of release, the lowest level of 9 exotic translocated ungulates (maximum 8.64 km/year for chamois [*Rupicapra rupicapra*]—Caughley 1963).

Fig. 5.—Mature female *Rusa unicolor* browsing from her hind legs, a common position of the species but relatively uncommon in other cervids, Kheoladeo National Park, Bharatpur, Rajasthan, northern India, February 2006; note the relatively long tail. Males also assume this position to mark branches as high 3 m at "stomping grounds," used repeatedly during rut. Photograph courtesy of Lee Dalton (http://www.leedaltonphotography.com) used with permission.

Diet.—*Rusa unicolor* is a herbivorous ruminant with great variation in dietary selection depending on forage availability (Geist 1998; Schaller 1967). Lewis et al. (1990) provided a cogent review of the food habits of *R. unicolor*

and noted that its ability to consume a wide variety of grass and browse (Fig. 5), while meeting nutritional needs, is correlated with its wide geographical range (Timmins et al. 2008) and success when translocated to alien continents (Fraser et al. 2000; Harris 1971; Kelton and Shipworth 1987; Lewis et al. 1990). Although the size of *R. unicolor* suggests that it could favor grasses and herbs, it is an intermediate feeder and consumes a great variety of shrubs and trees (Khan et al. 1994; Schaller 1967; Srivastava et al. 1996)—not unlike the larger North American elk in temperate coastal forest in the Pacific Northwest (Leslie et al. 1984).

Dietary selection of *R. unicolor* varies considerably depending on season, location, habitat variety and its effect on forage availability and quality, competitive interactions, and human activities (Kushwaha et al. 2004), whether in native habitat (Bagchi et al. 2003a; Johnsingh and Sankar 1991; Khan 1994; Padmalal et al. 2003; Schaller 1967; Shukla and Khare 1998) or introduced locations (Kelton and Skipworth 1987; Shea et al. 1990; Stafford 1997). In India, *R. unicolor* consumes a greater variety of plants than any other ungulate (Schaller 1967), often uses cultivated areas, and is not deterred by fences as high as 2 m (Baker 1898; Brander 1923).

Rusa unicolor is 1 of 3 primary consumers of the fleshy fruits of *Choerospondias axillaris*, a large tropical canopy tree in Thailand, but it deposits most of its seeds under the female canopy trees where regeneration is low (Brodie et al. 2009). Low crude protein and low plant cell-wall contents of *R. unicolor* feces in November–December suggest that fruits were important dietary constituents in the Indian Himalayas (Green 1987). Although *R. unicolor* ate fleshy and dry seeds in Nepal, it was not considered an important seed disperser (Dinerstein 1989).

Limited information exists on the nutritional ecology of *R. unicolor*, but as with most dietary generalists, it is presumed that nutritional needs are met by varying dietary selection throughout the year. Using fecal nitrogen and other fecal constituents (e.g., Leslie et al. 2008; Leslie and Starkey 1985), Green (1987) demonstrated that *R. unicolor* in the Indian Himalayas obtained the highest dietary quality, relative to crude protein, in spring and summer and that high ash content in spring, summer, and autumn suggested ingestion of soil, perhaps as a buffer to presumed high levels of ingested volatile oils common in woody species. In Horton Plains National Park, Sri Lanka, nitrogen in feces of *R. unicolor* suggested highest nutrient availability in May–June (Padmalal et al. 2003). Similar to North American elk in temperate rain forests (Leslie et al. 1984), *R. unicolor* in the Indian Himalayas consumed significant qualities of ferns (about 40% of the diet) in winter, as well as bamboo and woody browse (Green 1987:figure 10). Despite deficiencies of copper and selenium in soils in New Zealand, introduced populations of *R. unicolor* obtain sufficient amounts of dietary selenium (>850 nmol/kg in 22 liver samples) and vitamin B12 (>220 nmol/kg), but often insufficient amounts of copper (<100 μmol/kg—Stafford 1997).

Fig. 6.—Mature male *Rusa unicolor* wallowing in the muddy wetland in Ranthambhore National Park, Rajasthan, northern India; note the acutely angled brow tine, approaching 50% of the main beam. Photograph by Chris Brunskill (www.ardea.com) used with permission.

Rusa unicolor regularly drinks water (Hose 1893a; Peacock 1933; Thom 1937; Whitehead 1972) and usually is not far from free water (Brander 1923; Sankar and Acharya 2004; Fig. 6). In Sri Lanka, temporary aggregations of *R. unicolor* occur at dusk around regularly used water sources (Eisenburg and Lockhart 1972). During feeding trials, forage intake by captive *R. unicolor* in India decreased from about 400 bites/day, with ad libitum water, to <200 bites/day after 3 days of water deprivation (Berwick 1974). Related Javan rusa (*R. timorensis russa*) in captivity in Australia tolerated saline water of 1,000–6,000 mg/kg of total dissolved salts with little effect on food intake, food digestibility, and nitrogen balance, but when salinity reached 8,500 mg/kg, they showed signs of stress such as rapid breathing, head shaking, and swelling of the preorbital gland (Yape Kii and Dryden 2005). *R. unicolor* occurs near estuaries and ocean coasts (Geist 1998; Whitehead 1972), and it may have a similar tolerance of salty water. In Florida, however, *R. unicolor* prefers freshwater habitats and avoids saltwater habitats (Flynn et al. 1990), which may reflect preferences for forage growing in such areas rather than intolerance of salt water.

Mineral licks are used regularly by *R. unicolor* (Brander 1923; Matsubayashi et al. 2007a; Schaller 1967), particularly at night (Matsubayashi et al. 2007b; Peacock 1933). In tropical rain forests of Borneo, lactating female *R. unicolor* use natural mineral licks more frequently during the wet season than the dry season, and both sexes visit such licks more often at night (85% of visits) than during daylight (15% of visits—Matsubayashi et al. 2007b). Water associated with

mineral licks in Borneo provides substantially more macronutrients (mean ± *SD*, μg/ml) than control water from local ponds and streams: calcium, 83.4 ± 50.0 versus 13.8 ± 8.5; magnesium, 21.4 ± 9.8 versus 2.7 ± 1.0; potassium, 14.4 ± 12.6 versus 1.6 ± 0.6; and sodium, 801.8 ± 1,173.5 versus 6.9 ± 2.4 (Matsubayashi et al. 2007a).

Diseases and parasites.—No infectious diseases or disease agents have been reported to cause substantial population declines of *Rusa unicolor* (Presidente 1978, 1984a, 1984b; Slee 1984), but foot-and-mouth disease in Sri Lanka (Brooksby 1973) and India (37 of 104 individuals affected—Barman et al. 1999), sarcocystotic cysts with associated pathology of a bluetonguelike disease in India (Acharjyo and Rao 1988; Gangadharan et al. 1992), erythrocyte sickling in Borneo (Dunn 1964; Undritz et al. 1960), and mucosal disease virus, malignant catarrhal fever, and, rarely, infectious bovine rhinotracheitis in Australia (Presidente 1984a; Slee 1984; Slee and Presidente 1981) have been reported. Diseases, or disease-related deaths, have been reported in captive individuals: chronic (erosive) arthritis, tuberculosis, and arteriosclerosis (Fox 1939); foot-and-mouth disease (Kar et al. 1983; Presidente 1984a; Sarma et al. 1983); malignant catarrhal fever (Semiadi et al. 1994b); and bovine tubercule bacilli (Datta 1954). Intestinal rupture and resulting acute peritonitis, perhaps from a parasitic infection, was reported in a wild pregnant female *R. unicolor* in India (Bhattacharjee 1986).

By the mid-1980s, 18 endoparasites (9 nematode species, 6 flukes, 2 protozoans, and 1 tapeworm) and 40 ectoparasites (35 tick species, 2 sucking lice, 2 keds, and 1 flea) had been reported in native, feral, and captive populations of *R. unicolor* (Presidente 1984a). Parasites of free-ranging *R. unicolor* in native habitat include the nematodes *Bunostomum*, *Haemonchus*, *Oesophagostonmum*, *Strongyloides*, and *Trichuris* in India (Bhat and Manickam 1998; Hiregoudar 1976) and *Ashwortius sidemi*, *Rinadia andreevae*, and *Spiculopteragia houdemeri* in Vietnam (Drozdz 1965, 1973), and trematodes *Calicophoron microbothrioides* in Malaysia (Lee et al. 1987), and *Fischoederius elongates*, *Homologaster poloniae*, *Paramphistomum explanatum* (Patnaik and Acharjyo 1970; Rao and Acharjyo 1969), and *Gastrothylax crumenifer* in India (Agrawal and Ahluwalia 1980). Feral and captive populations of *R. unicolor* also harbor a variety of internal parasites including nematodes *Gongylonema pulchrum* (Chakrborty 1994) and cestode cysts *Coenurus gaigeri* (Varma et al. 1994) in India; *Spiculopteragia asymmetrica* in New Zealand (Andrews 1973) and Australia (Presidente 1984a); trematodes *Ceylonocotyle streptocoelium* in Australia (Keith and Keith 1969) and *Paramphistomum explanatum* in India (Rao and Acharjyo 1984); and protozoans *Theileria aristotelis* (Levine 1971) and *Toxoplasma gondii* in India (Ippen et al. 1981).

External parasites of native and feral *R. unicolor* include ticks *Haemaphysalis ramachandrai* and *H. davisi* in India and Nepal (Dhanda et al. 1970; Hoogstraal et al. 1970); *H. anomala* and *H. papuana* in southeastern Asia (Hoogstraal et al. 1965, 1967); *H. davisi* in Malaysia (Hoogstraal and El Kammah 1971); *H. mjoebergi* in Borneo and Sumatra (Hoogstraal and Wassef 1982); and *Dermacentor variabilis* in Florida (Davidson et al. 1987). Captive *R. unicolor* in eastern India, and no doubt wild populations elsewhere, are affected by the hematophagous flies (*Tabanus rubidus*, *T. striatus*, *Stomoxys calcitrans*, *Haematobia irritans exigua*, and *Musca crassriostris*) that can transmit trypanosomiasis and other diseases (Veer et al. 2002). When flying parasites are most active (e.g., humid, rainy seasons), larger than normal groups of *R. unicolor* are seen often in open areas and near or submerged in water (Prater 1980).

Interspecific interactions.—Because of the extensive native range of *Rusa unicolor* in southern Asia (Fig. 3), it can be sympatric with many other large herbivores (e.g., Schaller 1967), with which competitive interactions for food may exist (Sankar et al. 2007). In India, for example, *R. unicolor* can be sympatric with axis deer or chital (*Axis axis*), hog deer (*A. porcinus*), barasingha (*Rucervus duvaucelii*), red muntjac (*Muntiacus muntjak*—Kushwaha et al. 2004), blackbuck (*Antilope cervicapra*), chinkara (*Gazella bennettii*), chowsingha (*Tetracerus quadricornis*—Leslie and Sharma 2009), nilgai (*Boselaphus tragocamelus*—Leslie 2008), gaur (*Bos gaurus*), water buffalo (*Bubalus bubalis*—Berwick 1974; Jathanna et al. 2003; Karanth and Sunquist 1992), Asian elephants (*Elephas maximus*—Shoshani and Eisenberg 1982), and Indian rhinoceroses (*Rhinoceros unicornis*—Laurie et al. 1983). Significant dietary overlap of *R. unicolor* and livestock can occur locally (e.g., Shukla and Khare 1998; Srivastava et al. 1996). In extreme eastern Asia and Taiwan, *R. unicolor* can be sympatric with the smaller sika deer (*Cervus nippon*—Feldhammer 1980; MacKinnon 2008). In southern China, the distributional range of *R. unicolor* could overlap with red deer, forest musk deer (*Moschus berezovskii*), tufted deer (*Elaphodus cephalophus*), red muntjac, Reeves' muntjac (*M. reevesi*), Chinese water deer (*Hydropotes inermis*—MacKinnon 2008), and white-lipped deer (*P. albirostre*—Leslie 2009), but habitat affinities and decimated populations likely limit direct interactions in most areas (Timmins et al. 2008).

Typically, some degree of habitat (Bagchi et al. 2003a, 2003b; Berwick 1974; Dinerstein 1979; Kushwaha et al. 2004) and dietary (Berwick 1974; Khan 1994; Shukla and Khare 1998) differentiation occurs among *R. unicolor* and other ungulates. In Ranthambhore National Park, India, *R. unicolor* and chital form a "cervid guild" that prefer *Anogeissus–Grewia* forests, and nilgai and chinkara form a "bovid guild" and select *Acacia–Butea* habitats during summer and winter; unlike the cervids, nilgai were tolerant of livestock grazing and associated degradation of grass cover (Bagchi et al. 2003a, 2003b). In contrast, high dietary overlap of 90–93% was noted among *R. unicolor*, chital, and nilgai in the semiarid Sariska Tiger Reserve, northwestern

India (Sankar et al. 2007). In the Himalayas of northern India, *R. unicolor* is sympatric with Himalayan musk deer (*Moschus chrysogaster*), serow (*Capricornis sumatraensis*), and goral (*Nemorhaedus goral*—Mead 1989); competitive interactions are avoided by inverse relationships of habitat use and diet, but diets of *R. unicolor* and serow were most similar in autumn (Green 1985, 1987). In Nepal, *R. unicolor* uses riverine forests (80% of its time) with muntjac (78%) and chital (75%) but not hog deer (<5%—Mishra 1982 [not seen, cited in Putman 1988]). On St. Vincent Island, Florida, *R. unicolor* and white-tailed deer (*Odocoileus virginianus*—Smith 1991) partition habitat and food resources; in particular, *R. unicolor* uses freshwater habitats and associated aquatic vegetation (11.1–56.2% aquatic vegetation in seasonal diets; Figs. 2 and 6) to a much greater extent than white-tailed deer (1.5–4.4%—Shea et al. 1990).

Cattle egrets (*Bubulcus ibis*; Fig. 7) and Indian, or rufous, tree-pies (*Dendrocitta vagabunda*) associate with and forage on *R. unicolor*, respectively. Bharucha (1987) observed a female *R. unicolor* standing awkwardly with a rear leg raised up and away from her body to accommodate an Indian tree-pie that was apparently removing parasites from her groin area.

The endangered Indian tiger preys extensively on *R. unicolor* (Mazák 1981; Ramesh et al. 2009; Schaller 1967; Wang and Macdonald 2009) and, anecdotally, is said to mimic the call of *R. unicolor* to deceive it while hunting (Whitehead 1972). In Nagarahole, southern India, tigers prey preferentially on male *R. unicolor* (43 kills: adult males, 40.0%; adult females, 30.6%; yearling males, 5.7%; yearling females, 5.7%; 122 scats: young-of-the-year, 18.0%) and take more young individuals (58.6%) than prime (34.5%) or old (6.9%) individuals (Karanth and Sunquist 1995). *R. unicolor* constitutes 30.5% of prey items in tiger scats and 36.8% of tiger kills in Bandipur Tiger Reserve, southern India (Johnsingh 1983), and 24.9% and 28.6% in Nagarahole National Park, southern India (Karanth and Sunquist 1995, 2000). Frequency of occurrence of *R. unicolor* in tiger scats is 59.8% in Mudumalai Tiger Reserve, southern India (Ramesh et al. 2009); 51.4% in Sariska Tiger Reserve, northwestern India (Sankar and Johnsingh 2002); 36.9% in Ranthambhore National Park, northern India (Bagchi et al. 2003b); 14.6% in Pench National Park, central India (Biswas and Sankar 2002); and 27.6% in Nagarjunasagar Srisailam Tiger Reserve, south-central India (Reedy et al. 2004). Seidensticker (1976a) considered *R. unicolor* a primary prey species of tigers in Royal Chitwan National Park, Nepal, as did Wang and Macdonald (2009) for tigers in Jigme Singye Wangchuck National Park, central Bhutan. The Sumatran tiger (*P. t. sumatrae*) in Bukit Barisan Selatan National Park, Sumatra, Indonesia, also preys on *R. unicolor* (O'Brien et al. 2003).

Rusa unicolor, primarily fawns, constitutes 14% of prey items in scats and 5% of the kills of the leopard (*Panthera pardus*) in Bandipur Tiger Reserve (Johnsingh 1983) and

Fig. 7.—Male *Rusa unicolor* and cattle egret (*Bubulcus ibis*) foraging together in wetland in Ranthambhore National Park, Rajasthan, northern India. Photograph by Chris Brunskill (www.ardea.com) used with permission.

13.5% and 9.6% in Nagarahole National Park, southern India (Karanth and Sunquist 1995, 2000). In southern India, frequency of occurrence of *R. unicolor* in leopard scats is 29.0% in Mudumalai Tiger Reserve (Ramesh et al. 2009), 9% and 11.7% on the Mundanthurai Plateau and in the Mudumalai Wildlife Sanctuary, respectively (Ramakrishnan et al. 1999), and 5.9–7.8% in Sigur and Thalamalai reserve forests (Arivazhagan et al. 2007). Scats of leopards in Wolong Reserve, Sichuan, China, have only 0.5–1.6% frequency of occurrence of *R. unicolor* (Johnson et al. 1993). In Sri Lanka, only 1 of 29 identified prey items of leopards was *R. unicolor* (Eisenberg and Lockhart 1972). *R. unicolor* comprised 14.8% of 142 kills by highly endangered Asiatic lions (*Panthera leo persica*—Haas et al. 2005) in Gir Forest, India (Berwick 1974; Chellam and Johnsingh 1993).

Frequency of *R. unicolor* in scats of the group-hunting dhole (*Cuon alpinus*—Cohen 1978; Earle 1987) was 14.7% in

Mudumalai Wildlife Sanctuary in southern India (Cohen et al. 1978), and elsewhere in India, comprised 9–15% of the dhole diet (Arivazhagan et al. 2007). In Bandipur Tiger Reserve, fawns of *R. unicolor* (31.4%) were about 3 times as frequent in dhole scats as adults (10.6%—Johnsingh 1983). In Nagarahole National Park, southern India, 10.2% of prey items in dhole scats and 3.0% of prey kills were *R. unicolor* (Karanth and Sunquist 1995, 2000). Composite samples of scats from large carnivores, primarily dhole and leopards, in Huai Kha Khaeng Wildlife Sanctuary, Thailand, contained only 1.2–6.4% *R. unicolor* (Rabinowitz and Walker 1991). In Khao Yai National Park, Thailand, *R. unicolor* was the most common prey found in dhole scats (Austin 2002). The highest reported frequency of occurrence of *R. unicolor* in dhole scats was 60.9% in in Jigme Singye Wangchuck National Park, central Bhutan (Wang and Macdonald 2009).

In India, *R. unicolor* has not been reported as prey of the endangered Indian wolf (*Canis lupus pallipes*) or the striped hyenas (*Hyaena hyaena*—Arivazhagan et al. 2007), as have other species (Leslie 2008). Green (1985) found small amounts of hair of *R. unicolor* in scats of red fox (*Vulpes vulpes*) in Kedernath Sanctuary in the Indian Himalayas, believed to be from fawns or scavenged animals.

HUSBANDRY

Rusa unicolor adapts readily to captivity and is well represented in zoos, private ranches, and research facilities throughout the world (Crandall 1964; Semiadi et al. 1993, 1994b, 1995a, 1995b, 1998; Weigl 2005). *R. unicolor* is reared in captivity in New Zealand (e.g., Semiadi et al. 1993), Malaysia (Dahlan and Norfarizan-Hanoon 2007, 2008), and Bangladesh (Basbar et al. 2001). Some of these captive populations involve research and production of meat and other by-products, and others are focused on restoration of wild populations (Basbar et al. 2001). Some described *R. unicolor* as very alert and nervous in captivity (Semiadi et al. 1994b), but Crandall (1964) suggested otherwise.

In New Zealand, 6 of 8 neonatal *R. unicolor* were reared successfully on commercially available sheep milk replacer, containing 38.5% lactose, 27% milk fat, 4.6% nitrogen, and 23.6 kJ/g dry matter, and a liquid vitamin replacement; 2 neonates died because of bloat and severe diarrhea (Semiadi et al. 1993). Milk intake peaked early at week 3 when neonates consumed $<$400 g dry matter/day and declined thereafter until self weaning at about 10 weeks (Semaidi et al. 1993). They consumed 312 g dry matter/day and gained 241 g/day $\pm$ 99.6 *SE* from birth through their 1st week of age, 387 $\pm$ 46.9 g/day in weeks 1–4, and 322 $\pm$ 34.0 g/day thereafter (n = 8—Semiadi et al. 1993). Neonatal mortality from adult aggression, presumably by unrelated individuals, has been noted in captivity (Semiadi et al. 1994b).

To minimize births in captivity, chemical contraceptives have been successfully applied: melengestrol acetate as a feed additive (Raphael et al. 2003) and injections of porcine zonae pellucidae vaccine, albeit the later resulted in health problems to neonates if their mother was inoculated while pregnant (Kirkpatrick et al. 1996). Because of conservation concern and possible need for captive breeding, semen cryopreservation has been investigated for *R. u. swinhoii* in Taiwan (Cheng et al. 2004). *R. unicolor* can be tranquilized for handling with a variety of drugs: 0.07–0.14 mg succinylcholine chloride/kg of body weight, but doses $\geq$ 16.0 mg/kg resulted in mortality (Lentz et al. 1986); a combination of 1 mg ketamine/kg of body weight and 0.75 mg xylazine/kg of body weight, which can be reversed by yohimbine (Ibrahim 1998); and oral doses of diazepam (Thomas et al. 1967), although capture myopathy has been reported (Presidente 1978).

Rusa unicolor–Cervus elaphus and *R. unicolor–R. timorensis* hybrids have been reported (Idris and Moin 2009; Muir et al. 1997; New Zealand Department of Conservation 2005; Slee 1984; van Mourik and Schurig 1985). *R. unicolor–R. timorensis* hybrids at 10 months old attain the same weight as pure *R. timorensis* at 20–24 months old, and male hybrids are fertile with pure *R. timorensis* females, as are female hybrids with pure *R. unicolor* males (Slee 1984).

BEHAVIOR

Grouping behavior.—Kurt (1978:233) described the social and reproductive systems of *Rusa unicolor* as varying, depending on habitat, from "non-seasonal, alternatingly territorial" in stable rain forest to "seasonal, synchronized territorial" in varied deciduous forest and "solitary, aggregational" in stable grass jungles. Unlike most comparably sized cervids characterized by large groups (Geist 1998), *R. unicolor* typically occurs in small groups, most often a single female that dominates the group, her young-of-the-year, and perhaps her female yearling; mature males $>$ 6 years old are typically solitary, with young males grouping together, close to females, or as satellites to solitary mature males (Eisenberg and Lockhart 1972; Khan et al. 1995; Schaller 1967). In some areas (e.g., Sri Lanka—Kurt 1978), *R. unicolor* occurs with regularity in groups of 30–40, usually related to more abundant patches of forage and water availability (Geist 1998).

Maximum group size of *R. unicolor* in Gir National Forest, western India, was 5 individuals (Berwick 1974), and in Gir Lion Sanctuary, there were no seasonal differences in group size (Khan et al. 1995). Group sizes were 1–10 individuals in Nagarahole, southern India: 52% of the groups, 1 individual; 44%, 2 or 3 individuals; and 4%, 4–10 individuals (Karanth and Sunquist 1992). Group sizes were 1–16 individuals in Bandipur Tiger Reserve, southeastern India: 39% of the groups, 1 individual; 27%, 2 individuals;

21%, 3 or 4 individuals; 7%, 5 or 6 individuals; 3%, 7–9 individuals; 3%, 10–16 individuals (Johnsingh 1983:figure 6). In Mudumalai Wildlife Sanctuary, southern India, group size averaged 3.1 individuals but varied seasonally: maximum dry-season group size was 19 individuals and maximum wet-season group size during 2 years was 44 and 50 individuals (Varman and Sukumar 1993). Mean summer and winter group sizes in Ranthambhore Tiger Reserve, India, were 4.2 and 3.4 individuals, respectively (Bagchi et al. 2008). In Sri Lanka, group size was 2–8 individuals, and 60% of 230 individuals were solitary (Eisenberg and Lockhart 1972). Group size is often largest near water holes (Johnsingh 1980, 1983).

Reproductive behavior.—Downes (1983b:36) described the mating system of *Rusa unicolor* as ''polygamous male dominance … in dispersed facultative meeting-territories.'' Reproductive behavior of *R. unicolor* is ''primitive with unique elements'' (Geist 1998:76); males do not establish harems (Brander 1923; Schaller 1967). At the beginning of the breeding season, male and female *R. unicolor* ''suddenly [begin] to wander widely, even at mid-day, becoming highly conspicuous in sharp contrast to their usual elusiveness,'' and appear ''nervous, as if looking for something'' (Schaller 1967:144).

The following description of reproductive behavior was synthesized from Brander (1923), Downes (1983b), Fletcher (1911), Geist (1998), Prater (1980), Schaller (1967), and Thom (1937). During rut, mature males establish nonexclusive breeding territories to attract females and from which they challenge competitors of comparable rank; younger males often occupy peripheries of such territories. Mature males in rut have swollen necks, strong odor, and everted preorbital glands and appear aggressive, often thrashing vegetation. They are usually coated with mud from regular wallowing in wet spots (Fig. 6), accentuating their generally dark pelage, and frequently rub their muddy necks on tree trunks and vegetation while patrolling their territories for receptive females and competing males. Females are said to wallow but less frequently than males (Peacock 1933). Males paw and stomp the ground, and thereby create areas as large as 3–13 m in diameter, devoid of vegetation; ''stomping grounds'' may occur in dense forest or in the open atop hills. Often such areas are below an overhanging branch 2.3–3.3 m off the ground; male ''preach'' at these sites by standing erect on their hind legs and rubbing their scent-soaked preorbital glands and antlers on the branch (a behavior not observed among introduced *R. unicolor* in Florida). Males copiously spray themselves, even their faces, with urine from their mobile penis, the structure of which is unique among cervids.

Aggressive behavior between competing males includes head-up and head-down displays, pawing and thrashing, and head-to-head pushing matches, with tail cocked up and mane and back hairs erected, until the weaker gives up. Geist (1998:76) noted that, unlike any other deer species but goat-like, male *R. unicolor* will ''rise on their hind legs and clash downward into one another.'' Females also rise on their hind legs and hit each other on the head with their forelegs, resulting in a ''noise [that] resounds through the jungle;'' the same behavior is used against predators (Brander 1923:177).

Fig. 8.—Mature male *Rusa unicolor* mounting a female in Ranthambhore National Park, Rajasthan, northern India, January–February 2000. Photograph courtesy of James Warwick (www.jameswarwick.co.uk) used with permission.

Sexual behavior of *R. unicolor* has not been described in detail, but accounts by Brander (1923), Geist (1998), and Schaller (1967) provide some insight. Females actively seek or court adult males, moving widely among breeding territories; courtship is based on pair-bonding without serious vocal advertisement; males do not clasp females during mounting, front legs hang loosely (Fig. 8); and intromission is a ''copulatory jump'' (Geist 1998:76). Schaller (1967) observed mature males sniffing and licking females' vulvae. Another male trotted after a female in a low-stretch display with his neck parallel to the ground and preorbital glands everted. Satellite males assist dominant males by ''warding off lesser rivals'' and may breed if >1 receptive female enters the dominant male's territory (Geist 1998:77).

No published observations of parturition of wild *R. unicolor* were found. Presumably, females separate themselves from other individuals, seek secluded places to give birth, and hide their neonates. Neonates may rest alone, hidden, for much of their first 3 months of life, with their mother returning at regular intervals (Eisenberg and Lockhart 1972; Shea et al. 1990).

Communication.—Brander (1923) noted that eyesight of *Rusa unicolor* was only moderately developed, but Peacock (1933) contended that all senses were highly developed. Along with highly developed scent-marking routines and persistent acrid odor, particularly among males in rut (see

"Reproductive behavior"), foot stomping by female *R. unicolor* is used to alert (and summon) neonates and conspecifics of threats (Brander 1923; Mason 1994). Despite their size, *R. unicolor* can move quietly (Stebbing 1911) and with stealth through dense forest; mature males, when moving rapidly "enclose their necks and shoulders" with their antlers by "carrying their heads thrust out before them" (Brander 1923:182). Ever alert and a "high-stepper" stomping its forelegs when alarmed (Stebbing 1911:59), *R. unicolor* makes "sharp, short 'pooks,'" "tits," or "honks" (= "sharp, high notes") when disturbed (Brander 1923:180; Lydekker 1916; Mason 1994:23; Peacock 1933:126; Thom 1937). Brander (1923:180–181) described 2 other call types: a "loud metallic bellow" of rutting males and a "death cry" consisting of "a prolonged hoarse scream."

Miscellaneous behavior.—*Rusa unicolor* is largely crepuscular to nocturnal depending on location (Brander 1923; Fletcher 1911; Peacock 1933), but it can be active throughout the day in areas with minimal human disturbance (Johnsingh 1983; O'Brien et al. 2003) and in introduced locations such as Texas (Richardson 1972). Anecdotally, the Malayan form may be more nocturnal than Indian forms (Evans 1912), but Peacock (1933:125) described *R. unicolor* in Burma as "very nocturnal … ordinarily seek[ing] heavy cover with the first light at dawn and not leave[ing] the same till dusk." U Tun Yin (1967) contended that nocturnal habits of *R. unicolor* in Burma were related to continual human harassment.

Much like the moose (*Alces alces*—Franzmann 1981), *R. unicolor* is 1 of the few deer that will readily face wild predators (e.g., leopards and dholes) and hunting dogs defensively (Brander 1923; Geist 1998; Johnsingh 1980; U Tun Yin 1967). Females defend their young in a low-head posture, "barking loudly" and stomping front legs, with tail and ears erect and mane hairs flared; if several females are present, they stand rump-to-rump, facing outward toward the threat (Geist 1998:75)—reminiscent of muskoxen (*Ovibos moschatus*—Lent 1988) and the wild yak (*Bos mutus*—Leslie and Schaller 2009). If the threat is minimal (e.g., a single dhole), they may not react at all (Divyabhanusinh 1988). Brander (1923) recounted an incident when a female *R. unicolor* aggressively defended its young from a leopard who successfully carried the offspring 3 m up into a tree; when a hunter arrived on the scene, the leopard dropped the young, which ran off with its mother. Females can be "savage" while protecting their neonates in captivity (Crandall 1964:569). When perceiving or facing a threat, *R. unicolor* will not typically run off but often stands motionless, its dark pelage blending into the surrounding vegetation; alternately, it may creep off in a "semicrouch trot" with its neck held horizontally (Schaller 1967).

Rusa unicolor readily swims with its body fully submerged and only its head above the water (Prater 1980; Fig. 9), often to avoid insects and to forage (Richardson 1972; Shea et al. 1990; Shukla and Khare 1998). When ambient temperatures approach freezing, *R. unicolor* may lie in water that is warmer than the air (Brander 1923; Prater 1980).

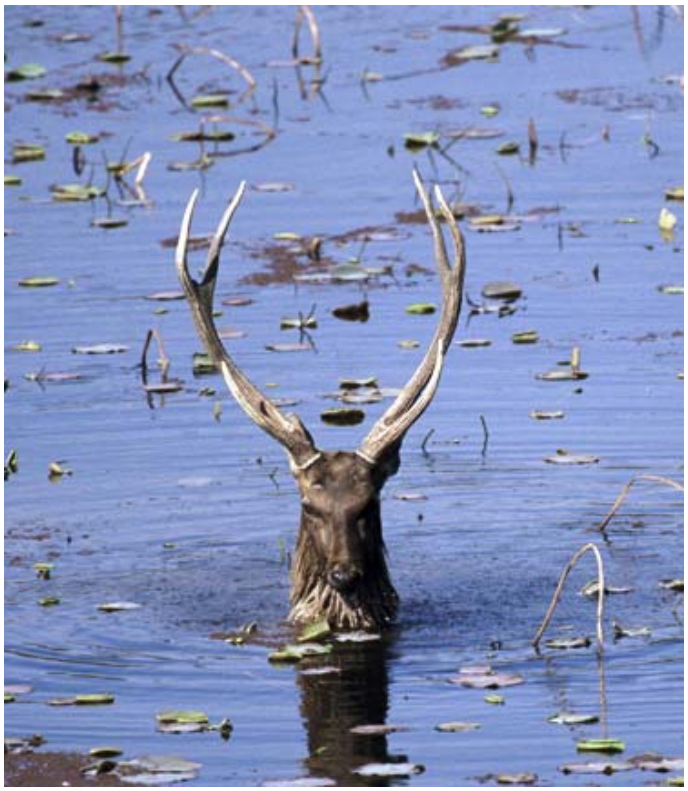

Fig. 9.—Mature male *Rusa unicolor* swimming through wetland in Ranthambhore National Park, Rajasthan, northern India, January–February 2000. Photograph courtesy of James Warwick (www.jameswarwick.co.uk) used with permission.

GENETICS

Diploid number (2n) of *Rusa unicolor* varies, apparently among subspecies, from 56 in New Zealand specimens originally from Sri Lanka and India (Muir et al. 1997) to 58 in India (Chandra et al. 1967) and 62 in southwestern China (Wang and Du 1982) and Malaysia (Idris and Moin 2009); fundamental number (FN) is 70; there are 44–64 acrocentric autosomes and 2–14 meta- and submetacentric autosomes (Bonnet-Garnier et al. 2003:table 1; Groves and Grubb 1987:table 2). The X chromosome is acrocentric, and the Y chromosome is acro- or submetacentric (Bonnet-Garnier et al. 2003; Chandra et al. 1967; Groves and Grubb 1987). Seven Robertsonian translocations have been identified in *R. unicolor* (Bonnet-Garnier et al. 2003).

Chromosomal evidence suggests that *Rusa* is sister to a clade consisting of *Przewalskium* and *Rucervus* (Groves and Grubb 1987). *R. unicolor* forms a clade closest to *R. timorensis* from Java and the Timor islands (e.g., Emerson

and Tate 1993), followed by the critically endangered *Rucervus eldi* from India, and their speciation was proposed by Bonnet-Garnier et al. (2003) to have occurred from monobrachial centric fusions (Baker and Brickham 1986). Ongoing interest in the molecular systematics of Cervidae (e.g., Cronin 1991; Di Stefano and Petronio 2002; Liu et al. 2003; Miyamoto et al. 1990; Pitra et al. 2004; Randi et al. 2001) led Groves (2006:21) to note that conspicuous external features (e.g., antler configurations of males, rump patch) that have led to taxonomic affiliations are more likely convergent, caused by shared ''climatic-related lifestyle factors'' rather than phylogeny. Although some evidence suggests that rusine deer split from other cervids about 5 million years ago, the validity of *Rusa* as a monophyletic genus is still debated by morphologists (Meijaard and Groves 2004) and molecular systematists (Hernández-Fernández and Vrba 2005; Randi et al. 2001).

Characteristics of the mitochondrial 16S rRNA gene have been used forensically to differentiate *R. unicolor* from sympatric species such as nilgai, chital, and blackbuck (Guha and Kashyap 2005). Electrophoretic analysis of mitochondrial DNA fragments also have been used to differentiate *R. unicolor* from other ungulates (Cronin et al. 1991). Five exclusive monomorphic random amplified polymorphic DNA markers of 150–520 base pairs have been identified for *R. unicolor* from Malaysia (El-Jaafari et al. 2008).

CONSERVATION

Conservation challenges for *Rusa unicolor* are daunting because it is so widespread geographically and affected by numerous local customs, national laws, and even civil unrest (e.g., Sri Lanka and Myanmar—Timmins and Evans 1996; Timmins et al. 2008). *R. unicolor* was elevated by the International Union for Conservation of Nature and Natural Resources from no status in 2006 to ''Vulnerable'' in 2008 because of >50% decline over the past 3 generations in many populations, with probable local extinctions, notably in Vietnam, Laos, Thailand, Cambodia, Myanmar, Malaysia, Bangladesh, Borneo, and Sumatra (Timmins et al. 2008). Populations of *R. unicolor* in Taiwan, India, and Nepal are more stable, mostly in protected or remote areas (Hsu and Agoramoorthy 1997; Timmins et al. 2008). *R. unicolor* is considered ''Lower Risk, Schedule III'' in India with an estimated population size of >100,000 countrywide (Sankar 2008), although nowhere is it abundant (Sankar and Acharya 2004). Even a century ago, game wardens and sportsman expressed concern that Indian and Burmese wildlife, including *R. unicolor*, was being overexploited for subsistence and sport and to minimize depredation of agricultural areas (Glasfurd 1903; Peacock 1933; Stebbing 1911; Wang et al. 2006). Well ahead of their time, Glasfurd (1903) and Stebbing (1911) commented that fire suppression caused forest encroachment into grasslands and diminished important habitat of *R. unicolor* and other large herbivores.

Rusa unicolor is a preferred meat throughout southeastern Asia (Duckworth et al. 1999; Gardner 1993), although some historic local taboos have existed; Evans (1918:194) noted that among the Sakai of Malaysia ''women and children may not eat, cook, or touch deer's flesh, or go near the body of a dead deer.'' Nevertheless and despite strict laws against hunting in India and elsewhere, exploitation for subsistence and marketing of meat and antlers are the most important ongoing problems facing *R. unicolor* throughout southeastern Asia (Datta et al. 2008; Duckworth et al. 1999; Khan and Khan 1968; Sammaiah et al. 2008; Steinmetz et al. 2006; Timmins et al. 2008). Timmins et al. (2008) noted that expanding urban wealth and increasing demand for exotic meat and ''medicines,'' rather than rural poverty, are having the greatest pernicious impacts on declining populations of *R. unicolor* and other fauna in southeastern Asia. Other conservation challenges recently summarized by Timmins et al. (2008) include fragmentation and loss of forested habitats through indiscriminate logging for wood products or conversion to agriculture (Johnsingh 1983; Kumara et al. 2004; Kushwaha et al. 2004), associated loss of or access to specialized habitats such as salt licks (Matsubayashi et al. 2007a, 2007b), mining and energy development, urban expansion, and roads and associated human traffic (Griffiths and van Schaik 1993). Improved education and partnerships with local communities and conservation initiatives that work together to identify critical wildlife issues are useful to enhance local buy-in and forward-thinking conservation action (Steinmetz et al. 2006).

Few comprehensive ecological studies of *R. unicolor* have been conducted within its native range, and much of what is known comes from demographic assessments of *R. unicolor* as prey for highly endangered and charismatic species such as the Indian tiger or the Asiatic leopard. Studies of introduced populations provide some insight (e.g., Downes 1983b; Lewis et al. 1990), but clearly, more basic information on status, ecology, and behavior of native populations is needed to assure adequate conservation of southeastern Asia's largest and most ecologically generalized cervid. Without such knowledge, *R. unicolor* may indeed ''be, like the Hog Deer and Eld's Deer are already, almost absent from South-east Asia'' (Timmins et al. 2008:19).

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