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8 **MAMMALIAN SPECIES 54(101X):00–00**

9 ***Lycaon pictus* (Carnivora: Canidae)**

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17

18 **Abstract:** *Lycaon pictus* Temminck, 1820, the African wild dog, is a moderately sized
19 carnivore with dog-like appearance and irregularly mottled black, yellow-brown, and
20 white pelage. *Lycaon pictus* has a head–body length of 76–112 cm, tail length of 30–41
21 cm, shoulder height of 61–78 cm, and body weight of 17–36 kg. *L. pictus* has four toes
22 on each foot, differentiating it from other canids; is the only extant species within the
23 genus with no subspecies; and is unlikely to be confused with any other canid. *L. pictus*
24 was once widespread throughout sub-Saharan Africa inhabiting nearly all environments
25 and now inhabit grasslands, montane savanna, and open woodlands. *L. pictus* is

26 recognized as endangered by the U.S. Fish and Wildlife Service and the International
27 Union for Conservation of Nature.

28

29 **Key words:** Africa, African wild dog, wild canid, carnivore, endangered

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38 ***Lycaon* Brookes, 1827**

39 *Hyaena*: Temminck, 1820:54. Part, not *Hyaena* Brisson, 1762.

40 *Canis*: Desmarest, 1822: 538. Part; not *Canis* Linnaeus, 1758.

41 *Lycaon* Brookes in Gray, 1825:339. Nomen nudum.

42 *Lycaon* Brookes, 1827:151. Proposed as a subgenus of *Canis* Linnaeus, 1758; type

43 species *Lycaon tricolor* Brookes, 1827 (= *Hyaena picta* Temminck, 1820), by
44 monotypy.

45 *Cynhyaena* F. Cuvier, 1829:454. Type species *Hyaena picta* Temminck, 1820, by
46 monotypy.

47 *Hyenoides* Boitard, 1842:214. Type species *Hyenoides picta* Boitard, 1842 (= *Hyaena*
48 *picta* Temminck, 1820), by monotypy.

49 *Kynos* Rüppell, 1842:163. Type species *Kynos (Canis) pictus* Rüppell, 1842 (= *Hyaena*
50 *picta* Temminck, 1820), by monotypy.

51 *Hyenoides* Gervais, 1855:53. Incorrect subsequent spelling of *Hyenoides* Boitard, 1842.

52

53 CONTEXT AND CONTENT. Order Carnivora, suborder Caniformia, family Canidae,
54 subfamily Caninae, tribe Canini. *Lycaon* is monotypic.

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56

57 ***Lycaon pictus* (Temminck, 1820)**

58 African Wild Dog

59 *Canis aureus*: Thunberg, 1811:302. Not *Canis aureus* Linnaeus, 1758.

60 *Hyaena picta* Temminck, 1820:54, plate XXXV. Type locality “à la côte de
61 Mosambique” (= coast of Mozambique).

62 *Hyaena venatica* Burchell, 1822: 456. Type locality “Northeast of Asbestos Range, upper
63 Orange River.”

64 *Canis pictus*: Desmarest, 1822:538. Name combination.

65 *Lycaon tricolor* Brookes, 1827:151. Type locality “Cape of Good Hope.”

66 *Cynhyaena picta*: F. Cuvier, 1829:454. Name combination.

67 *Lycaon typicus* A. Smith, 1833:91. Type locality “South Africa.”

68 *Lycaon pictus*: A. Smith, 1833:91. First use of the current name combination.

69 *Hyenoides picta*: Boitard, 1842:214. Name combination.

70 *Kynos (Canis) pictus*: Rüppell, 1842:163. Name combination.

71 *Lycaon venaticus*: Gray, 1868:497. Name combination.

- 72 *Lycaon pictus venaticus*: Thomas, 1902:438. Name combination.
- 73 *Lycaon pictus lupinus* Thomas, 1902:439. Type locality “Nyuki River Swamp, in the Rift
74 Valley on Equator. Altitude 2000 m.”
- 75 *Lycaon pictus somalicus* Thomas, 1904:98. Type locality “Central Somaliland.”
- 76 *Lycaon pictus zuluensis* Thomas, 1904:98, footnote. Type locality “Pongola River,”
77 Zululand, KwaZulu-Natal, South Africa.
- 78 *Lycaon pictus sharicus* Thomas and Wroughton, 1907:375. Type locality “Maui, Shari
79 River Chari] River,” Chad.
- 80 *Lycaon pictus prageri* Matschie, 1912:311. Type locality “vom Nzoia-Flusse auf dem
81 Guasso-Ngischu-Hochlande südlich des Elgon” (= Nzoia River on Guasso
82 Ngischu Uplands south Elgon).
- 83 *Lycaon lalandei* Matschie, 1915:313. Type locality “aus der Gegend zwischen der Algoa-
84 Bucht und dem Keiskama-Flusse” [= between Algoa Bay and the Keiskama
85 River],” Cape Province, South Africa.
- 86 *Lycaon rüppelli* Matschie, 1915:315. Type locality “der Umgebung der Bajuda-Steppe
87 stammt” [= area around Bajuda steppe],” northeastern Africa.
- 88 *Lycaon lademanni* Matschie, 1915:315. Type locality “Mbarangandu in der Nähe der
89 Staße Songea-Liwale in Deutsch-Ostafrika” (= Mbarangandu near the Songea-
90 Liwale road in German East Africa [= Tanzania]).
- 91 *Lycaon ssongaeae* Matschie, 1915:317. Type locality “bei Ussangire, 14 km
92 westsudwestlich von Ssongae im Quellgebiete des Rovuma, Deutsch-Ostafrika (=
93 near Ussangire, 14 km west-southwest of Songae in the headwaters of the
94 Ruvuma River, German East Africa [= Tanzania]).

- 95 *Lycaon hennigi* Matschie, 1915:320. Type locality “Makangaga, ungefähr 40 km
96 westsüdwestlich von Kilwa (= Makangaga, about 40 km west-southwest of Kilwa
97 [= Tanzania]).
- 98 *Lycaon stierlingi* Matschie, 1915:323. Type locality “Rijuni, einem Nebenflusse des
99 oberen Rovuma im Bezirke Songea, Deutsch-Ostafrika, ungefähr 30 km von den
100 Quellen des Mbarangandu-Luwegu” (= Rijuni, a tributary of the upper Ruvuma
101 River in Songea district, German East Africa [= Tanzania], about 30 km from the
102 springs of Mbarangandu-Luwegu).
- 103 *Lycaon huebneri* Matschie, 1915:326. Type locality “Kibwesi an der Uganda-Bahn [=
104 Kibwesi on the Uganda Railway],” Kenya.
- 105 *Lycaon ruwanae* Matschie, 1915:328. Type locality “der Ruwana-Steppe nordöstlich von
106 der Speke-Bucht des am Viktoria -Nyansa in Deutsch-Ostafrika” (= Ruwana-
107 steppe northeast of Speke Bay in Lakeon the Victoria Nyanzain German East
108 Africa [= Tanzania]).
- 109 *Lycaon kondoa* Matschie, 1915:331. Type locality “Bubu bei Kondoa-Irangi in Deutsch-
110 Ostafrika” (= Bubu River at Kondoa-Irangi in German East Africa [= Tanzania]).
- 111 *Lycaon langheldi* Matschie, 1915:333. Type locality “Njawa in Ussomgo, nordöstlich
112 von Ussongo Tabora in der westlichen Wembaeäre-steppe, Deutsch-Ostafrika” (=
113 Najwa in Ushomgo, south northwest of Ussongo Tabora in the western
114 Wembaeäre-steppe, German East Africa [= Tanzania]).
- 115 *Lycaon dieseneri* Matschie, 1915:336. Type locality “Myombo-Walde zwischen Usinsa
116 und OstUssuwi im Süden am des Viktoria Nyansa in Deutsch-Ostafrika” (=

117 Myombo forest between Usinsa and east Ussuri on the south of Lake Victoria in
118 German East Africa [= Tanzania]).

119 *Lycaon gansseri* Matschie, 1915:340. Type locality “Bezirke Tabora [Tabora districts],”
120 Tanzania.

121 *Lycaon taborae* Matschie, 1915:344. Type locality 1/2 stunde von Tabora” [= one-half
122 hour south of Tabora],” Tanzania.

123 *Lycaon wintgensii* Matschie, 1915:347. Type locality “m Luegere-Fluß an der Kungue-
124 Bucht des Ostufers de Tanganjika in Deutsch-Ostafrika” (= on the Luegere River
125 on Kungue Bay on the east bank of the [Lake] on Tanganyika in German East
126 Africa [= Tanzania]).

127 *Lycaon richteri* Matschie, 1915:350. Type locality “Daressalam [= Dar es-Salaam],”
128 Tanzania.

129 *Lycaon styxi* Matschie, 1915:352. Type locality “Mpapua in Deutsch-Ostafrika [German
130 East Africa],” Tanzania.

131 *Lycaon luchsingeri* Matschie, 1915:355. Type locality “Edaballa, Mulla, nahe dem
132 Hauasch im Danakil-Lande [=Edaballa, Mulla, near the Awash River in the
133 Danakil Desert],” Ethiopia.

134 *Lycaon zedlitzi* Matschie, 1915:358. Type locality “Scetel-Flusse in der Buschsteppe,
135 ungefähr 800 m über dem Meere erlegt ... östlichsten Quellfluß des Barka
136 südöstlich von Agordat” (= Scetel River in the bush steppe, about 800 m above
137 sea level ... easternmost source river of the Barka [River] south-east of Agordat
138 [Eritrea]).

- 139 *Lycaon takanus* Matschie, 1915:360. Type locality “Landschaft Taka [= Taka Mountain
140 landscape, Sudan, northeastern Africa].
- 141 *Lycaon manguensis* Matschie, 1915:364. Type locality “Djannaga nördlich von Sansanne
142 Mangu unweit des Oti in Togo” (= Djannaga north of Sansanneé-Mango near Oti
143 in Togo).
- 144 *Lycaon mischlichii* Matschie, 1915:366. Type locality “nördlichen Teile des Bezirkes
145 Kete-Kratschi in Togo, wahrscheinlich bei Bimbila, der Hauptstadt von Nanumba,
146 zwischen dem Oti und Daka [= northern part of district Kete-Kratschi in Togo,
147 possibly near Bimbila, the capital of Nanumba, between Oti and Daka].”
- 148 *Lycaon ebermaieri* Matschie, 1915:369. Type locality “aus der Grasländern am Tschad-
149 See, wahrscheinlich aus der Gegend von Dikoa” (= grasslands of Lake Chad,
150 probably from Dikwa area [= northeastern Nigeria]).”
- 151 *Lycaon fuchsia* Matschie, 1915:371. Type locality “Rio Cubal in Benguella” (= Cubal
152 River in Benguella [= western Angola]).
- 153 *Lycaon cacondae* Matschie, 1915:373. Type locality “Caconda in Benguella” (= Caconda
154 in Benguella [= western Angola]).
- 155 *Lycaon gobabis* Matschie, 1915:373. Type locality “Gobabis in Deutsch Südwestafrika”
156 (= Gobabis of German Southwest Africa [= Namibia]).
- 157 *Lycaon krebsi* Matschie, 1915:376. Type locality “Bavians Revier- Fluß im Kaplande” (=
158 Baviaans territory in [Eastern] Cape [South Africa]).
- 159 *Lycaon windhorni* Matschie, 1915:378. Type locality “Rustenburg, in Transvaal [now
160 North West Province, South Africa].”
- 161

162 CONTEXT AND CONTENT. Context as for genus. Recent DNA analysis and research
163 revealed are no subspecies of *Lycaon pictus*, only geographical variants (Sillero-Zubiri
164 2009).

165

166 NOMENCLATURAL NOTES. The generic name *Lycaon* can be traced to Greek mythology.
167 *Lycaon* was a king who was turned into a wolf because he insulted a god. *Lycaon*,
168 however, is not the word for “wolf” in Greek; it is “lycos” (Borrer 1960). The specific
169 epithet *pictus* is from Latin meaning “painted or variegated,” aptly describing the painted
170 coat of *L. pictus*. Other common names include Cape hunting dog (Skinner and
171 Chimimba 2005) and painted hunting dog (Sillero-Zubiri 2009:355).

172

173

DIAGNOSIS

174 *Lycaon pictus* is the only extant species in the genus (Nowak 1991; Girman and
175 Wayne 1997). Compared with the other canids within its distribution (African golden
176 wolf [*Canis lupaster*], side-striped jackal [*Lupulella adustus*], black-backed jackal [*L.*
177 *mesomelas*], and bat-eared fox [*Otocyon megalotis*]—Burgin et al. 2020), *L. pictus* is the
178 largest and lightly built with large, rounded ears (Nowak 1991). *Lycaon pictus* has four
179 toes on each foot, differentiating it from other canids, and legs are long and slender (van
180 Lawick 1970; Nowak 1991). Each *L. pictus* has a unique coat coloration of irregularly
181 mottled black, yellow-brown, and white that can be used to identify individuals (Fig. 1;
182 Wilson and Mittermeier 2009).

183

184

GENERAL CHARACTERS

185 *Lycaon pictus* has a head–body length of 76–112 cm, tail length of 30–41 cm,
186 shoulder height of 61–78 cm, and body weight of 17–36 kg (Kingdon 1977, 2015). The
187 second and third molars are reduced and smaller than the paracone (antero-external cusp)
188 of the first molar. Palatal width between carnassials is greater than one-half the palate
189 length measured from anterior edge of the canines (Meester and Setzer 1971). The skull
190 is large (length >180 mm) and robust, and teeth are adapted for holding and slicing rather
191 than grinding. Zygomatic arch is heavily built with a width > 120 mm (Meester and
192 Setzer 1971; Skinner 2005; Fig. 2). The pollex (i.e., big toe) is absent (Meester and
193 Setzer 1971).

194 Morphological and genetic differences occur in populations of *L. pictus* from
195 eastern and southern Africa, indicating genetic differentiation and population structure
196 throughout its geographic distribution. Although sizes and weights vary among
197 populations (Haltenorth and Diller 1980; Girman et al. 1993), genetic differences indicate
198 recent (< 100 years) interrupted gene flow between eastern and southern populations but
199 not enough to identify distinct clades corresponding to subspecies (Girman and Wayne
200 1997). There are no noticeable differences between sexes other than a 3–7% difference
201 in skeletal and musculature characteristics (Girman et al. 1993; Creel and Creel 2002).
202 Differences in back length and chest girth of males and females are positively correlated
203 with prey density (back length: males, $r = 0.33$, $P < 0.001$; females, $r = 0.46$, $P = 0.002$
204 and chest girth: males, $r = 0.23$, $P = 0.026$; females, $r = 0.24$, $P = 0.123$ —McNutt and
205 Gussett 2012).

206 Pelage of *L. pictus* is irregularly mottled black, yellow-brown, and white (Van der
207 Merwe 1959; Meester and Setzer 1971; Nowak 1991; Wilson and Mittermeier 2009) and

208 is unique to individuals (Skinner and Chimimba 2005). Tip of the tail is almost always
209 white, forehead is generally white, and muzzle is dark (Kingdon 1977, 2015; Nowak
210 1991; Skinner and Chimimba 2005). Ears are large, round, and covered with short dark
211 hairs with tufts of light hair on the inside (Nowak 1991; Skinner and Chimimba 2005).
212 Hair on the body is short and sparse, and there is no undercoat (Skinner and Chimimba
213 2005).

214

215

DISTRIBUTION

216 *Lycaon pictus* was once widespread throughout sub-Saharan Africa (Skinner and
217 Chimimba 2005), inhabiting nearly all environments except rain forests (Fanshawe et al.
218 1991) and the driest deserts (Schaller 1972). *L. pictus* have been reported from Mount
219 Kilimanjaro (Thesiger 1970) to deserts in central Sahara (Monrod 1928; Lhote 1946).
220 Historically, a relict population in Algeria suggests that arid lands might have been
221 inhabited by *L. pictus* (Fanshawe et al.1997). They have been virtually extirpated from
222 western Africa and reduced in central and northeastern Africa. Botswana, Tanzania, and
223 Zimbabwe provide habitat for nearly one-half of the remaining wild *L. pictus*. Other
224 populations occur in Central African Republic, Ethiopia, Kenya, Mozambique, Namibia,
225 South Africa, Sudan, and Zambia, with potential populations of < 100 individuals in
226 Cameroon, Chad, Senegal, and Somalia (Fig. 3; Wilson and Mittermeier 2009).

227 There are about 6,700 *L. pictus*, with about 1,400 mature adults, distributed
228 throughout Africa (Woodroffe and Sillero-Zubiri 2012, 2020). Populations throughout
229 northern, eastern, and western Africa are low density; they are patchy in central Africa,
230 and the majority of individuals occur in southern Africa (Fanshawe et al. 1997). A

231 survey of 43 African countries reported 17 countries with viable or potentially viable
232 populations of *L. pictus* (Angola, Bein, Botswana, Burkina Faso, Central African
233 Republic, Chad, Ethiopia, Kenya, Malawi, Mozambique, Namibia, Senegal, South
234 Africa, Sudan, Tanzania, Zambia, and Zimbabwe), 11 countries with extirpated (Burundi,
235 Cameroon, Egypt, Eritrea, Eswatini, Gabon, Gambia, Ghana, Mauritania, Rwanda, and
236 Sierra Leone), 7 countries with nearly extirpated populations (Democratic Republic of the
237 Congo, Côte d'Ivoire, Guinea-Bissau, Mali, Nigeria, Togo, and Uganda), 6 countries
238 having no verifiable records of *L. pictus* (Djibouti, Equatorial Guinea, Lesotho, Liberia,
239 Mauritania, and Western Sahara), and 2 countries with uncertain presence (Algeria and
240 Guinea—Fanshaw et al. 1997; Woodroffe and Sillero-Zubiri 2020).

241

242

FOSSIL RECORD

243 The fossil record for *Lycaon pictus* is sparse, and the earliest known indisputable
244 *L. pictus* fossil is from the mid-Pleistocene in Africa (Savage 1978). Identification of
245 early *L. pictus* fossils has been difficult because of their similarity to the early Pleistocene
246 wolf, *Canis africanus* (Macolm 1979). Whether late Pleistocene (Kurtén 1968) and
247 European *L. pictus* fossils are *Canis* is debated (Thenius 1972). *L. pictus* probably
248 proliferated in Africa 2–3 million years ago (Savage and Russell 1983), with major
249 radiations occurring north and south of the miombo woodland belt (Creel and Creel
250 2002).

251

252

FORM AND FUNCTION

253 Feet of *Lycaon pictus* are digitigrade and reduced, with the four toes on each foot
254 allowing for improved cursorial ability (Girman et al. 1993). The only common pelage
255 characteristic generally shared by all individuals is a white tip on the tail that might serve
256 to keep individuals together when the pack is moving through dense, tall vegetation
257 (Estes and Goddard 1967). Dental formula is $i\ 3/3$, $c\ 1/1$, $p\ 3/4$, and $m\ 3/3$, total 21; m_3
258 is vestigial (Van Valkenburgh 1989).

259 The praeputial sebaceous glands of male *L. pictus* secrete their contents directly
260 into the praeputial lumen or the hair shaft, which indicates urine is mixed with glandular
261 secretions before released. Secretions from the anal sacs and sebaceous glands (that
262 occur over the entire body) might be useful in scent-marking, with deposition of the scent
263 accomplished through anal-dragging behavior (van Heerden 1981). During non-mating
264 periods, subordinate females had higher levels of estrogen and estrogen:progesterone ratios
265 indicating ovulation suppression (Creel et al. 1997b), and subordinate males had
266 increased glucocorticoid secretion (Van Heerden and Kuhn 1985; Creel et al.
267 1996).

268 Hematological and biochemical values of the peripheral blood in six captive male
269 and 7 female *L. pictus* from a zoo in the Czech Republic did not differ at the 5% level
270 except for the erythrocyte count ($P = 0.031$) and sodium level ($P = 0.044$ —Pospíšil
271 1987). Mean erythrocyte counts ($10^{12}/l$) were 9.86 for females and 8.45 for males, and
272 mean leukocyte counts ($10^9/l$) were 13.03 for females and 12.88 for males (Pospíšil
273 1987).

274

275

ONTONGENY AND REPRODUCTION

276 **Ontogeny.**—Newborn *Lycaon pictus* are altricial and weigh about 300 g at birth.
277 Eyes open after about 13 days, but young remain in the den for up to 3 weeks when they
278 begin to take solid food regurgitated by other pack members. Young begin following the
279 pack by 3 months of age and can kill prey by 11 months, although they remain inefficient
280 at hunting until 12–14 months after birth. Social restrictions can mask the age at which
281 *L. pictus* is first capable of copulating, but 21-month-old males and 22-month-old females
282 have copulated successfully (Frame et al. 1979).

283 **Reproduction.**—Estrus in *Lycaon pictus* gradually builds during the weeks prior
284 to copulation, at which time the vulva becomes swollen with a bloody discharge. The
285 bond between the alpha pair develops and becomes more overt (Creel and Creel 2002).
286 Early attempts by the male to mount the female are rejected until she is ready and stands
287 “firmly with her tail averted to one side as the male mounts” (Creel and Creel 2002:204).
288 Copulations occur over 3–7 days but not all attempts end in copulation. The copulatory
289 lock (i.e., bulbis glandis of the penis enlarges preventing the pair from disengaging—van
290 Lawick 1970; Reich 1981) can last 5–6 min (van Lawick 1970; Frame et al. 1979;
291 Malcolm 1979; Creel 2002) during which the pair is highly vulnerable (Skinner and
292 Chimimba 2005).

293 Gestation lasts 71–73 days, and young are born in underground dens, usually an
294 abandoned burrow (Sillero-Zubiri 2009). Females have 12–14 mammae (van Lawick
295 1970). Young suckle for up to 12 weeks. In one case, pack members raised a litter of 5-
296 week-old young whose mother had died; thus, continued suckling might not be a
297 necessity (Nowak 1991).

298 Females produce litters every 12–14 months, but this interval can be reduced if a
299 litter is unsuccessful (Frame et al. 1979). Average litter size is 10 young (range = 6–16
300 young—Nowak 1991). *L. pictus* copulates seasonally at latitudes from 7–25°S generally
301 producing a single litter per year within a pack, coinciding with peak prey abundance and
302 cooler temperatures (Malcolm 1979; Reich 1981; McNutt et al. 2019). Reproduction is
303 aseasonal at latitudes < 2° (McNutt et al. 2019). In Kruger National Park (KNP), young
304 were born in April–September, peaking in late May and early June (Reich 1981).
305 Inbreeding has occurred in KNP (Reich 1978). In Selous Game Reserve, peak birthing
306 occurred in July during the driest part of the year when ungulates congregated at water
307 sources (Creel and Creel 2002). On the Serengeti Plains, peak birth rates occurred during
308 the rainy season in March–June when ungulates underwent annual migration (Schaller
309 1972; Frame et al. 1979). Births occurred on average on 3 and 4 June corresponding to
310 conception dates of 23 and 24 March in Botswana and Zimbabwe, respectively (McNutt
311 et al. 2019). In northern Botswana, 96.3% of litters were born in May–July (McNutt
312 1996). Intervals between births are 12–14 months if young survive but can be as short as
313 6 months if they do not (Frame et al. 1979; Malcom 1979). Captive populations averaged
314 11.7 months between litters (Van Heerden and Kuhn 1985).

315 In some packs of *L. pictus*, sex ratio of male and female offspring at birth is
316 skewed toward males (Frame et al. 1979), but it is equal in others (Creel et al. 1995;
317 Somers et al. 2008). Although many authors cite a male-biased sex ratio at all ages
318 (Fuller et al. 1992), there is extensive regional variation, and it is unclear if a skewed sex-
319 ratio is a distribution-wide characteristic or an artifact of certain populations. In northern

320 Botswana, sex biases were most prominent in young females in smaller packs rather than
321 older females in larger packs (McNutt and Silk 2008).

322

323

ECOLOGY

324 ***Population characteristics.***— Survival estimates of young *Lycaon pictus* vary
325 widely among and within populations, ranging from 0.14 to 0.73 (Fuller et al. 1992) with
326 most averaging less than 0.50 (e.g., 0.43 in McNutt and Silk 2008). Survival of young
327 was 24% in the Serengeti and 73% ($n = 5$ litters) in Maasai Mara National Reserve,
328 Kenya (Frame et al. 1979; Malcom 1979; Fuller et al. 1992). Possible causes of high
329 mortality of young include disease, predation by spotted hyena (*Crocuta crocuta*) and
330 lion (*Panthera leo*), and hypothermia as a result of den flooding (Burrows 1995).
331 Competition between dominant and subdominant mothers might also affect survival rates
332 of young. Survival to 1 year was dependent on sizes of the pack and litter, ages of
333 breeding females, and proportion of adult males in the pack in northern Botswana
334 (McNutt and Silk 2008).

335 Young and yearling survival probabilities are lower than survival probabilities of
336 adults and influenced by pack size and food availability (Fuller et al. 1992). Survival was
337 0.35 for young-of- the-year and 0.45 for yearlings in KNP, 0.54 and 0.74 in Botswana,
338 and 0.75 and 0.84 in Selous Game Reserve, Tanzania (Creel et al. 2004). Higher
339 probabilities of survival and production of young are associated with larger pack sizes
340 and increasing survival of adults because of balancing energetic costs of leaving an adult
341 to protect young rather than to hunt (Courchamp et al. 2002). Survival and production of
342 young decrease with increasing pack size because of infanticide (Creel and Creel 2015).

343 A helper provides increased care of young and increases survival probabilities of
344 young by tending to and protecting them at the den when they are unable to travel with
345 the pack (Kühme 1965; Malcolm and Marten 1982). In Zimbabwe, packs of *L. pictus*
346 needed to contain at least five individuals for a helper to be left to guard young
347 (Courchamp et al. 2002).

348 Annual probability of survival for adult *L. pictus* ranged from 0.65 to 0.85, with
349 annual finite rates of increase ranging from 0.83 to 1.77, and it is affected by numerous
350 factors including human-related mortality and disease (Fuller et al. 1992). Adult survival
351 is highly variable across populations, e.g., 0.4–0.67 for adults and 0.77 for 2–4-year-old
352 females in Botswana (Fuller et al. 1992), 0.5 for adults > 5 years old in Selous Game
353 Reserve (Creel et al. 2004), and > 0.72 in KNP (Reich 1981). A greater proportion of *L.*
354 *pictus* in Selous Game Reserve, however, were aged > 5 years old (Creel et al. 2004).
355 Advantages of larger pack size to adult survival are increased predator vigilance, larger
356 hunting groups, larger numbers during pack conflicts, older and injured individuals are
357 tolerated and fed, and the ability for pack take-overs and establishment of new packs
358 (Courchamp and McDonald 2001).

359 Female *L. pictus* were more likely than males to emigrate because of the presence
360 of a breeding female; furthermore, female emigrants never joined an existing pack with a
361 breeding female. In northern Botswana, on average, females covered greater distances
362 than males for all movement statistics calculated, but differences in distances moved
363 were not statistically different than movements of males (Cozzi et al. 2020). On the
364 Serengeti Plains, nearly one-half of the young-of-the-year male offspring are recruited
365 into their natal pack, whereas young-of-the-year females were almost certain to emigrate

366 (Frame and Frame 1976). Females in Selous Game Reserve were twice as likely to
367 emigrate as males (Creel et al. 1997b), but this did not appear to be the rule across
368 populations. In Botswana, all *L. pictus* dispersed in the presence of their same sex parent;
369 however, males waited longer, dispersed in larger groups, and moved greater distances
370 than females (McNutt 1996). Females and males emigrate in nearly equal numbers, and it
371 is rare for individuals of either sex to remain in their natal pack (Fuller et al. 1992;
372 McNutt 1996; Girman et al. 1997; Woodroffe et al. 2020). In Maasai Mara National
373 Reserve, all yearlings dispersed (Fuller et al. 1992), but not all yearlings dispersed in
374 KNP. A yearling female replaced her mother as the dominant breeding female in the pack
375 in KNP (Reich 1981). Populations in which females emigrate at a higher rate tend to
376 have male-skewed sex ratios (Creel et al. 1997b). Mixed-sex dispersal groups occur
377 (Creel and Creel 2002).

378 Dispersal usually occurs in single-sex sibling groups, with males often forming
379 larger groups and traveling farther than females (Frame et al. 1979; McNutt, 1996).
380 Males also appear to delay emigration longer than females: median age of dispersal was
381 28 months for males but only 21 months for females in northern Botswana (McNutt
382 1996). These sex-biased trends are an outcome of competition for mates in populations
383 with male-biased sex ratios (McNutt 1996). Alternatively, subordinate males have more
384 opportunities to reproduce than subordinate females and thus are more likely to postpone
385 emigration (Creel et al. 1997b). Emigrants leave their natal pack between 1–3 years of
386 age (Frame et al. 1979). Dispersing females typically settle closer to their natal range
387 than do males (McNutt 1996; Girman et al. 1997). In northern Botswana, 13 of 14
388 successful female emigrant groups established home ranges adjacent to or overlapping

389 their natal range (McNutt 1996). Molecular data indicated an increased degree of
390 relatedness between adjacent packs (Girman et al. 1997). This kinship might partially
391 explain the lack of intraspecific aggression between packs with highly overlapping
392 ranges. Twenty-one unrelated neighboring packs of *L. pictus* in southern Africa had low
393 levels of overlap, restricted to peripheral regions of their areas of use, but related
394 neighbors had significantly more overlap. Pack size did not influence overlap (Jackson et
395 al. 2017).

396 *Lycaon pictus* packs can disperse up to 35 km in 4 h (\bar{x} = 17 km, range = 8–35
397 km) and up to 54 km in 24 h (\bar{x} = 35 km, range = 11–54 km—Cozzi et al. 2020). In
398 northern Botswana, dispersal distances were up to 42 km in 24 h (Pomilia et al. 2015).
399 Dispersers do not avoid water bodies, but resident *L. pictus* tends to avoid them (Cozzi et
400 al. 2013), raising concern that barriers to movement might be overestimated if only
401 measuring movements of resident packs (Cozzi et al. 2013, 2020; Jackson et al. 2016;
402 Abrahms et al. 2017). Human density and activities, land-use practices, vehicle traffic,
403 and active killing are barriers to movements (Mesenga et al. 2016; Cozzi et al. 2020). In a
404 recent study in northern Botswana, *L. pictus* selected roads when traveling, avoided them
405 when resting, and ignored roads when running at high speeds (Abrahms et al. 2015).

406 Long-distance dispersal events from Botswana included a 345-km journey in 9
407 days that ended in Zimbabwe and a 5-day journey of 154-km that ended on the Namibian
408 border (Cozzi et al. 2020). Long-distance dispersals are important for gene flow and
409 connectivity and thus are important in conservation (Barton et al. 2019).

410 Individuals might emigrate more than once during their life (Frame et al. 1979).
411 Groups of same-sex siblings leave together, and lone individuals undergo “secondary

412 emigration.” One form of secondary emigration is pack fission in which at least one pair
413 of opposite-sex, unrelated subdominants (e.g., brother of the alpha male and sister of the
414 alpha female) emigrate together from the pack. They might be joined by others resulting
415 in one pack dividing to form two separate breeding units (Frame et al. 1979).
416 Observations of segregation of a pack into male and female groups that were joined by
417 other like groups were not uncommon (Reich 1981; Creel and Creel 2002).

418 After dispersing, emigrants die, form new packs with an unrelated group of
419 emigrating siblings, or aggressively take over an existing pack. In Selous Game Reserve,
420 risk of mortality was higher for dispersing individuals than those in stable packs (Creel et
421 al 1997b). Dispersal was 1.5 times more dangerous for females than males because of
422 the amount of time spent in small groups dispersing; however, dispersal is 1.6 times more
423 dangerous to males because of risks associated with fighting with pack members during
424 attempted immigration (Creel and Creel 2002). Aggressive takeovers are more common
425 in male emigrant groups, especially when they outnumber males in an existing pack
426 (Frame et al. 1979). Unsuccessful emigrants infrequently return to their natal pack
427 (Frame et al. 1979; McNutt 1996; Creel and Creel 2002). Occasional long-distance
428 dispersal, most commonly by males, and formation of new packs through fusion of
429 unrelated sibling groups help minimize inbreeding and promote gene flow (Girman et al.
430 1997). The system of dispersal discourages mating of close relatives, but even when
431 presented with the opportunity, individuals do not appear to mate with related individuals
432 (McNutt 1996).

433 The opportunity to mate with unrelated individuals could be the ultimate cause of
434 emigration, but several proximate causes have also been proposed. Subdominants might

435 disperse because of a change in pack leadership and are no longer related to either
436 individual in the alpha pair, thus they receive no inclusive fitness benefit from helping
437 raise related offspring (Girman et al. 1997). Preferential access is also given to pups and
438 yearlings of the alpha pair, and competition for food might trigger emigration among
439 older offspring and subordinate adults, especially in large packs (McNutt 1996).

440 Some individuals avoid emigration and remain within their natal pack, usually
441 individuals whose opposite sex parent has been killed or displaced. This avoidance is
442 more common among males (Creel et al. 1997b; Frame et al. 1979; McNutt 1996).
443 Remaining individuals might avoid costs of emigration while also gaining an opportunity
444 to breed with an unrelated individual (McNutt 1996). Male bias toward delayed
445 emigration might also result from the relatively lesser degree of reproductive dominance
446 asserted by alpha males, allowing for increased reproductive opportunities among beta
447 males (Creel et al. 1997b). Beta males and females have low rates of reproduction; only
448 10% of young that survive to 1 year of age with a father other than the alpha male and
449 8% with a mother other than the alpha female (Girman et al. 1997).

450 ***Space use.***— *Lycaon pictus* inhabits grasslands, montane savanna, and open
451 woodlands and tends to avoid dense forest (Meester and Setzer 1977; Fig. 4). It requires
452 vast areas (thousands of ha) with minimal disturbance (i.e., human villages and activities)
453 to support viable, self-sustaining populations (Cozzi 2020). In the Serengeti–Maasai
454 Mara region of Tanzania and Kenya, *L. pictus* selects open grasslands over other
455 available vegetation (Fuller and Kat 1990; Burrows 1995), but in southern Africa, it
456 inhabits areas of dense brush and woodland (Mills and Biggs 1993). The wide range of

457 environments currently or historically occupied suggests *L. pictus* is fairly flexible in
458 selecting habitat, at least relative to climate and physiognomy.

459 Annual home-range size varies widely among regions with estimates from 150
460 km² to 3,900 km² (e.g., Fuller et al. 1992; Creel and Creel 2002; Woodroffe 2011).
461 Home range is influenced by vegetation, prey density and availability, presence of
462 neighboring packs, pack size, presence of young-of-the-year, and reserve size (Fuller et
463 al. 1992). Home ranges are smaller in preferred vegetation and larger in less preferred
464 vegetation (Creel and Creel 2002). Vegetation preferences varied by location; short- to
465 medium-length grasses were preferred by *L. pictus* in Maasai Mara National Reserve
466 (Fuller and Kat 1990), and deciduous woodland was preferred in Selous Game Reserve
467 (Creel and Creel 2002). In KNP, *L. pictus* has an affinity for wooded hills (Mills and
468 Gorman 1997).

469 *Lycaon pictus* also has smaller home ranges in areas with stable or abundant prey
470 sources (Mills and Gorman 1997; Andreka et al. 1999). Home-range size tended to
471 increase when densities of *L. pictus* were low and other packs did not restrict movement
472 (Fuller et al. 1992). In Zambia, larger packs have larger home ranges (Leigh 2005).
473 Home range decreases during the 2–4-month denning period and is centered on the den
474 because young are not able to keep up with far ranging adults (Reich 1981; Burrows
475 1995; Frame et al. 1979; Leigh 2005). *L. pictus* outside of protected reserves had more
476 conflicts with humans and higher mortality rates because of persecution (i.e., poisoning
477 and shooting of adults) than those whose home ranges did not extend outside large
478 reserves (Woodroffe and Ginsberg 1999).

479 Home ranges of adjacent packs can overlap by 35% in KNP (Reich 1981) and as
480 much as 80% in the Serengeti (Frame et al. 1979), and conflict over boundaries is
481 infrequent. Generally, within the home range, a central core area is used the most and is
482 heavily defended by packs (Mills and Gorman 1997; Reich 1981). In northern Kenya,
483 packs overlapped by 22.3%, but packs were still territorial and avoided other packs
484 (Woodroffe, 2011). Of 8 packs tracked during nearly three years in KNP, only two packs
485 met and then only once (Mills and Gorman 1997). In Selous Game Reserve, direct pack
486 encounters occurred more frequently, which might have resulted from higher density of
487 *L. pictus* (Creel and Creel 2002). During encounters, small packs fled before direct
488 contact was made, but if direct contact was made, a chase or fight always occurred
489 (Frame et al. 1979; Creel and Creel 2002). Eighty-four percent of the time, a larger pack
490 attacked a smaller pack that would flee (Frame et al. 1979; Creel and Creel 2002). Packs
491 of equal size both fled. Aggressive interactions (i.e., fights) between packs usually
492 occurred between members of the same sex.

493 Eleven packs in the Okavango Delta, Botswana were studied from November
494 2011 to February 2015 to examine interactions between packs of *L. pictus* (Jordan et al.
495 2017). On average, packs encountered another pack every 7 weeks and met neighbors
496 (i.e., packs with overlapping 95% kernel utility distributions) twice each year. Injuries
497 occurred in < 15% of encounters. Packs winning the encounters were defined as those
498 that remained closest to the encounter site 1 h following the encounter; 73.3% of
499 encounters were won by residents (Jordan et al. 2017). Inter-pack encounters are low risk
500 and did not influence long-term movement or ranging of *L. pictus* (Jordan et al. 2017).

501 In marking territorial boundaries, captive *L. pictus* use urine-marking, body
502 rubbing, and secretions from anal sacs to mark areas (Van Heerden 1981). The urine of *L.*
503 *pictus* contains about 1,000 chemical components and at least 10 of the components are
504 pair-specific to dominant individuals (Jordan et al. 2016). Packs showed interested in
505 scent marks of other packs by sniffing, urinating, defecating, and, in the case of large
506 packs, following a scent trail (Creel and Creel 2002). One hundred and three organic
507 compounds from urine, feces, anal glands, and preputial glands of *L. pictus* have been
508 identified: aliphatic acids were the dominant class of compounds in all materials (Apps et
509 al. 2012). Free-ranging *L. pictus* communicates where its residence is using scent marks
510 (Jackson et al. 2012; Jordan et al. 2013), by the presence of a mated pair (Jordan et al.
511 2014), and by sending messages to other species (Apps et al. 2019).

512 **Diet.**—*Lycaon pictus* kills prey primarily through disembowelment (Estes and
513 Goddard 1967); it is also capable of killing prey much larger than itself with a traditional
514 stranglehold (more commonly associated with cats). Daily hunting activity and other
515 daily activities tend to be bimodal, with a period of inactivity at 1200–1400 h; most kills
516 occur in early morning (0700–0900 h) and early evening (1800–2000 h— Estes and
517 Goddard 1967; Fuller and Kat 1990; Hayward and Slotow 2009).

518 Thomson's gazelles (*Eudorcas thomsonii*) are the primary prey of *L. pictus* in
519 southern Kenya and northern Tanzania, accounting for up to 70% of all kills (Estes and
520 Goddard 1967; Fuller and Kat 1990). In South Africa, impala (*Aepyceros malampus*) and
521 nyala (*Tragelaphus angassi*) made up 76% of the diet of translocated *L. pictus* (Vogel et
522 al. 2018). In Zimbabwe, impala accounted for 74% of all kills and kudu (*Tragelaphus*
523 *strepsiceros*) for 22% of kills (Pole et al. 2004). *L. pictus* is most successful hunting

524 immature gazelle, with success rates > 90% when fawns and immature individuals are
525 hunted (Fanshawe and Fitzgibbon 1993). Grant's gazelle (*Gazella granti*) is a secondary
526 prey species in parts of Tanzania, making up about 10% of the diet. Impalas are a
527 secondary prey item in Kenya, but in South Africa, they can make up 90% of the diet of
528 *L. pictus* (Reich 1981). When present, migratory wildebeest (*Connochaetes* spp.) are an
529 important prey item for some populations of *L. pictus*, with calves making up the
530 majority (61–85%) of wildebeest killed (Fuller and Kat 1990).

531 Except for South African populations that specialize on impala, populations of *L.*
532 *pictus* throughout southern Africa consume a wider variety of species than do populations
533 in eastern Africa. Prey species in Zambia, Zimbabwe, and South Africa include
534 bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), impala, reedbuck
535 (*Redunca arundinum*), Lichtenstein's hartebeest (*Alcelaphus lichtensteini*), kudu, and
536 eland (*Taurotragus oryx*— Malcolm and van Lawick 1975; Estes and Goddard 1967).
537 Some packs of *L. pictus* in the Serengeti specialize on plains zebra (*Equus quagga*
538 *burchellii*). In other areas, zebra will harass and pursue *L. pictus* (Estes and Goddard
539 1967; Malcolm and van Lawick 1975). Smaller prey including insects and several
540 species of hare are eaten occasionally (Creel and Creel 2002). *L. pictus* recolonized an
541 area in central Kenya and preyed on dik-dik (*Madoqua kirkii*) reducing the population by
542 33% (Ford et al. 2015); their diet consisted of 70% dik-dik (Woodroffe et al 2007).

543 *Lycaon pictus* does not prey extensively on livestock (Fanshawe et al. 1991).
544 Outside of protected areas in northern Kenya, depredation on livestock by *L. pictus* was
545 uncommon when wild prey remained (even at low densities). When wild prey was
546 depleted, *L. pictus* killed livestock regularly (Woodroffe et al. 2005). Throughout the

547 distribution of *L. pictus*, economic effects of depredation on livestock was negligible, but
548 locally it could be severe (Woodroffe et al. 2005).

549 Variation in predation of prey across locations occurs within a bimodal body mass
550 range (16–32 kg and 120–140 kg) because these sizes are available and not likely to
551 cause injury to *L. pictus* when hunted (Hayward et al. 2006). Large and potentially
552 threatening species tend to be avoided by *L. pictus* (i.e., giraffe [*Giraffa* spp.], ostrich
553 [*Struthio camelus*], African savannah elephant [*Loxodonta africana*], black rhinoceros
554 [*Diceros bicornis*], white rhinoceros [*Ceratotherium simum*], hippopotamus
555 [*Hippopotamus amphibius*], yellow baboon [*Papio cynocephalus*], common warthog
556 [*Phacochoerus africanus*], bushpig [*Potamochoerus larvatus*], or gemsbok [*Oryx*
557 *gazella*]—Hayward et al. 2006).

558 *Lycaon pictus* hunts cooperatively for certain prey species and individually for
559 others. Individuals are more likely to pursue immature prey, whereas groups will focus
560 on larger adult prey (Fanshawe and Fitzgibbon 1993). Group hunting allows *L. pictus* to
561 take a wider variety of prey species than an individual could, and groups are better able to
562 defend kills from competitors, such as spotted hyena, and are more energetically
563 efficient. Group size does not have an effect on the time required for a hunt, and groups
564 are not more successful than individuals (Fanshawe and Fitzgibbon 1993). Hunting
565 success increased as pack size increased, chase distances decreased even though the
566 number of chases per day increased, and medium pack sizes were the most energetically
567 efficient hunting groups (Creel and Creel 2002). *L. pictus* rarely scavenges (Creel and
568 Creel 2002).

569 *Lycaon pictus* coexists with hyenas, cheetahs (*Acinonyx jubatus*—Krausman and
570 Morales 2005), leopards (*Panthera pardus*—Stein and Hayssen 2013), and lions
571 (*Panthera leo*—Hass et al. 2005). Spotted hyenas (*Crocuta crocuta*—Hayssen and
572 Noonan 2021) are their main competitors, and daily times of activity significantly overlap
573 but not with the other three major predators (Hayward and Slowtow 2009). Where *L.*
574 *pictus* is sympatric with spotted hyenas, lions, and leopards in Zimbabwe, there is > 70%
575 overlap in their diets, with impala being the most frequent prey among them (Mbizah et
576 al. 2012). Presence of spotted hyenas might have excluded *L. pictus* from parts of its
577 former distribution (Estes and Goddard 1967), and other competitors and declining prey
578 might contribute to declining populations of *L. pictus* (Mbizah et al. 2012). In some
579 areas, spotted hyenas are present at nearly every *L. pictus* kill and can steal a carcass if
580 few *L. pictus* are present. When most of a pack of *L. pictus* is at the kill, hyenas are
581 usually unable to appropriate the carcass until *L. pictus* is done feeding (Fanshawe and
582 Fitzgibbon 1993; Fig. 5). When hyena density is low, hyenas rarely try to obtain kills
583 from *L. pictus*.

584 Although *L. pictus* might be able to defend kills from hyenas, they cannot do so
585 against lions. Lions kill adult and juvenile *L. pictus* (Mills and Biggs 1993), and lion
586 predation can represent a significant cause of mortality of *L. pictus* (Creel and Creel
587 1996). Lions caused 8.9% of *L. pictus* deaths in Selous Game Reserve and 33.3% of
588 deaths in KNP (van Heerdan 1995). *L. pictus* generally does poorly in areas with high
589 densities of hyenas and lions, probably a result of competition for food and direct,
590 agonistic encounters (Creel and Creel 1996). As a mechanism to prevent

591 kleptoparasitism, *L. pictus* minimizes its activity patterns to not coincide with lions and
592 hyenas (Hayward and Slowtow 2009).

593 **Disease and parasites.**—Anthrax, canine distemper virus (CDV), canine hepatitis,
594 canine herpes, parvovirus, rabies, rickettsia, and *Toxoplasma* affect *L. pictus* (Creel et al.
595 1995; Creel et al. 1997c; Vander Merwe 1959). Captive *L. pictus* ($n = 87$) examined in
596 South Africa from 1983 to 1995 died from exposure ($n = 37$), septicemia and pulmonary
597 lesions ($n = 13$), aggression and siblicide ($n = 13$), and lesions of lungs, kidneys, heart,
598 pancreas, uterus, intestines, and skin ($n = 4, 6, 3, 3, 5, 5,$ and 2 , respectively—Van
599 Heerden et al. 1996).

600 In the Samburu-Laikipia Districts, Kenya, *L. pictus* had higher rates of disease
601 leading to mortality than in all other studies combined (44.4% mortality vs. 1% mortality
602 in other studies—Woodroffe et al. 2007). Rabies and CDV have had the largest effect on
603 population declines in different packs of *L. pictus* across its distribution. All *L. pictus*
604 died and disappeared in the Serengeti from 1985 to 1991 (Gascoyne et al. 1993); the
605 pathogen might have been rabies but was never unequivocally determined (Creel 1992;
606 Macdonald 1992; Creel et al. 1995). Rabies killed 21 of 23 individuals in a pack in
607 Maasai Mara National Reserve during the same time period (Kat et al. 1995). Two
608 outbreaks occurred in Madikwe, South Africa: seven adult *L. pictus* were diagnosed with
609 rabies after a rapid die-off in 1997 and 83.3% of eight-month-old young died due a
610 second outbreak during a reintroduction in 2000, despite vaccination against the virus. In
611 both cases, black-backed jackals were reported to be the primary vector because domestic
612 dogs were not present in the area (Hofmeyr et al. 2000, 2004).

613 Rabies also contributed to the failure of three attempted re-introductions of *L.*
614 *pictus* in Etosha National Park, Namibia, when four individuals died of rabies (Scheepers
615 and Venzke 1995). Overall, about 9% of *L. pictus* populations contracted rabies
616 compared with other known diseases (Lembo et al. 2008). Older *L. pictus* and those in
617 unprotected areas were more likely to contract rabies than those in protected reserves
618 (Prager et al. 2012). Vaccines provide two years of immunity. Thirty to 40% of a small
619 population should be vaccinated every 1–2 years; smaller percentage of individuals can
620 be vaccinated in larger populations; and young should be vaccinated every year (Vial et
621 al. 2006). Rabies isolates taken from dead *L. pictus* in Kenya were identical to virus
622 isolates taken from rabid domestic dogs in the region (Kat et al. 1995).

623 Distemper could be a cause of die-offs of *L. pictus* in the Serengeti-Mara
624 ecosystem and elsewhere, but CDV has only recently been isolated and verified to cause
625 death in *L. pictus* in Kenya (Creel et al. 1997c). In the 1970s and earlier, mortality
626 attributed to CDV was based on field observations of ecological, development, and social
627 relationships (Schaller 1972; Malcom 1979). The first confirmed case of CDV was from
628 a single carcass after 83.3% of *L. pictus* died in northern Botswana (Alexander et al.
629 1996). Mortality due to CDV has been confirmed in a number of other packs. The CDV
630 pathogen was responsible for 94.2% mortality rate in captive *L. pictus* in an outbreak in
631 2001 in Mkomazi Game Reserve, Tanzania (van de Bildt et al. 2002). In October 2007,
632 60.5% of pack members died from CDV in an area northeast of the Serengeti boundary.
633 The CDV pathogen isolated was closely related genetically to CDV found in domestic
634 dogs in Ngorongoro Conservation Area, Tanzania, in 1994, in captive *L. pictus* in
635 northeastern Tanzania in 1994, and in lions, spotted hyenas, and bat-eared foxes in the

636 Serengeti in 1993–1994 (Goller et al. 2010). In Selous Game Reserve, 59% of *L. pictus*
637 tested positive for CDV, and 45% of those lived about 2 years post sero-sampling,
638 indicating that CDV does not appear to be an important limiting factor in that population
639 (Creel and Creel 2002).

640 Anthrax was isolated from *L. pictus* in Luangwa Valley, Zambia, and caused
641 several deaths; 80% of carcasses tested positive (Turnbull et al. 1991). In Selous Game
642 Reserve, only two deaths of young in one pack were the direct result of anthrax (Creel
643 and Creel 2002). Unlike the novel variants of rabies that appear to have arisen among
644 domestic dogs (Kat et al. 1995) or diseases such as distemper that have only recently
645 become widespread throughout Africa (Alexander et al. 1992), the bacterium causing
646 anthrax has occurred within the distribution of *L. pictus*. Thus, host-pathogen
647 coadaptation between *L. pictus* and the bacterium might result in reduced pathogenicity.
648 Anthrax might therefore be less of a threat to the persistence of populations of *L. pictus*
649 than CDV or rabies (Creel et al. 1995).

650 Four of six *L. pictus* tested positive for parvovirus antibodies in one pack in the
651 Serengeti (Fuller et al. 1992). In Selous, 68% of *L. pictus* tested positive for parvovirus
652 (Creel and Creel 2002). Parvovirus occurred in 25% of *L. pictus* tested from 19 packs in
653 the Laikipia District, Kenya (Woodroffe et al. 2012), and 43% of individuals tested
654 positive in KNP (Maddock and Mills 1994).

655 Tick-borne pathogenic infections (e.g., *Amblyomma marmoreum*, *Babesia*, and
656 *Hepatozoon*—Van Heerden et al. 1995; Matjila et al. 2008) and tick-borne parasites
657 (Flacke et al. 2010) are not widely distributed in populations of *L. pictus* except the
658 gastrointestinal parasite *Sarcocystis* that was reported in 12 of 13 *L. pictus* in Zambia.

659 Additional gastrointestinal parasites were detected in wild (i.e., Taeniid, *Ancylostoma*,
660 *Spirometra*, *Giardia*, Coccidia, and *Filaroides*) and captive *L. pictus* (i.e., *Giardia* and
661 *Spirometra*—Ash et al. 2008; Ash 2011). Other parasites (e.g., *Isospora*, $n = 1$;
662 *Spirometra*, $n = 1$; Taenidae, $n = 3$) were obtained from ingesting infected prey
663 (Berensten et al. 2012). Ixodid ticks were collected from six *L. pictus* in KNP and the
664 Madikwe Nature Reserve: *Amblyomma herbraeum*, *Rhipicephalus simus*, *R. turanicus*,
665 and *R. zambeziensis* (Horak et al. 2000).

666 ***Interspecific interactions.***—Lions are a primary risk for *Lycaon pictus*; the risk
667 of extirpation for *L. pictus* increased to nearly 100% when lion populations exceeded
668 moderate densities (i.e., $\sim 110\text{--}140/1,000\text{ km}^2$ —Vucetich and Creel 1999). High
669 densities of *L. pictus* (i.e., 40 adults/1,000 km²) have been associated with weak
670 competition from lions and spotted hyenas. In Selous Game Reserve because of the
671 limited number of competitors, predation of *L. pictus* was 13% compared to 33–50% in
672 KNP where competition was stronger (Creel and Creel 1968; McNutt 1995; Van Heerden
673 et al. 1995). Interspecific competition among *L. pictus*, lions, and hyenas can limit
674 recruitment of *L. pictus* (Creel and Creel 1998).

675 *Lycaon pictus* responds to its competitors by moving, specific den selection, and
676 changing hunting times. *L. pictus* reportedly moved away from simulated lion roars; they
677 stood their ground when hyena “whoops” were played or moved off in random directions,
678 perhaps indicating that threats from lions represented a higher risk than from hyenas
679 (Webster et al. 2012). When lion movements were restricted by fences, *L. pictus* used
680 areas on the lion-free side of the fences more than on areas occupied by lions (Cozzi et al.
681 2013). Den-site selection by *L. pictus* is designed to avoid predators and increase

682 probability of escape by selecting closed woody vegetation in rugged terrain so detection
683 by lions and hyenas is reduced (Van der Meer et al. 2013; Darnell et al. 2014; Jackson et
684 al. 2014; Davies et al. 2016).

685 *Lycaon pictus* is also able to vary hunting times, which was reported to reduce
686 temporal encounters with humans by 64% but increased the potential for interactions with
687 hyenas by 70% and lions by 37%. Thus, *L. pictus* makes clear tradeoffs among risks
688 (Rasmussen and McDonald 2012).

689

690

HUSBANDRY

691 *Lycaon pictus* occurs and can usually breed and produce young in zoological
692 parks around the world (Dekker 1968, Thomas et al. 2006). Copulation and production of
693 young fails when there are social problems within packs. More commonly, difficulties
694 arise in managing *L. pictus* in zoos because they are capable of rapidly increasing and
695 exhausting available holding spaces. As a result, most zoos have a single adult female
696 and one or more adult males (Thomas et al. 2006). Successful copulation and birth of
697 litters in zoos has been attributed to designing captive facilities with burrows like those in
698 the wild, that can limit male access, and that are not regularly cleaned by humans (Brand
699 and Cullen 1967)—factors that cause stress leading to females killing and eating some or
700 all of their litters. Dens were designed in Petoria Zoo to resemble natural burrows with a
701 floor 0.9 m below ground level and a 0.6- x 0.6-m entrance (Brand and Cullen 1967). *L.*
702 *pictus* was housed in the Bronx Zoo in 4 interconnected chambers made from shipping
703 crates, and an outdoor yard; two larger rooms were 41.5 m², and the others were 29.3 m²
704 and 23.7 m²; and the outdoor yard was 150 m² (Thomas et al. 2006). With advances in

705 animal husbandry for *L. pictus* and continued success in productivity, more individuals
706 will be able to be housed in zoos and available for translocation programs.

707 *Lycaon pictus* is fed a nutritionally complete raw meat-based diet in zoos. Diets
708 consist of 1.0–1.36 kg of raw meat/adult/day supplemented with knuckles, ribs, and
709 shank-bones 1–2 times/week and carcasses of pigs, deer, cows, and horses; captive *L.*
710 *pictus* fast from the meat diet 1 day/week and are provided bones (Langan and Jankowski
711 2019).

712 Low genetic diversity has important conservation implications, and most *L.*
713 *pictus* in captive populations are of southern African descent (Girman et al. 1993). Thus,
714 reintroduction of captive-bred individuals into eastern Africa would create the problem of
715 mixing lineages and might jeopardize persistence of the eastern subpopulation. Although
716 augmentation programs could become important as populations of *L. pictus* continue to
717 decline and disappear, it might be necessary to create additional captive populations with
718 eastern African founders (Girman et al. 1993).

719

720

BEHAVIOR

721 **Grouping behavior.**—*Lycaon pictus* lives in packs of up to 26 individuals, with a
722 mean size of 11 individuals including young-of-the-year and yearlings (Frame et al.
723 1979; Fuller et al. 1992; Davies-Mostert et al. 2015). Average number of adults in packs,
724 excluding yearlings, were 4–11, with an average of 6 (Fuller et al. 1992; Davies-Mostert
725 et al. 2015). Alpha females typically retain their status for life, but alpha males are often
726 (> 60% of the time) displaced by a subdominant sibling. Tenure of an alpha male is 1–8
727 years (Frame et al. 1979).

728 The high degree of relatedness among pack members provides an inclusive fitness
729 benefit for nonbreeding helpers that assist in raising siblings or half-siblings (Frame et al.
730 1979; McNutt 1996; Girman et al. 1997). Helpers are not always related to those they
731 help (McNutt 1996). In Botswana, a minimum of 25% of study area packs ($n = 12$)
732 contained nonbreeding adults that provided parental care for unrelated young. Caring for
733 unrelated weaned young might reduce potential conflict with mature same-sex adoptees
734 over access to mates in the future (McNutt 1996). The number of adult helpers and
735 number of young raised are positively correlated (Girman et al. 1997). Subdominant
736 individuals occasionally gain direct breeding opportunities, although this accounts for <
737 50% of their overall reproductive success, most of which is accrued indirectly (Girman et
738 al. 1997).

739 When hunting, a designated leader chooses prey and leads the chase, but there are
740 no other levels of hunting hierarchy (Estes and Goddard 1967). A couple of *L. pictus*
741 follows the leader within a few hundred meters during the chase, but other members of
742 the pack take a circuitous route to intercept prey (Estes and Goddard 1967). Packs do not
743 make kills in the same manner; generally, after prey is captured, members often
744 cooperate in taking it down. Habitat also plays a part in hunting. In the grass plains of
745 East Africa, *L. pictus* hunt with high levels of collaborative endurance pursuit (Taylor et
746 al. 1971; Estes and Goddard 1967), but *L. pictus* inhabiting mixed woodland savannah in
747 northern Botswana hunt with multiple short-distance hunting attempts (Hubel et al.
748 2016a). The individual kill rate of *L. pictus* is 15.5% in northern Botswana with higher
749 energy expenditure than collaborative endurance pursuits (Hubel et al. 2016b), but there
750 is a high group feeding rate to share prey (Hubel et al. 2016a).

751 Competition over meat is mollified through appeasement behaviors (i.e., infantile
752 food begging) resulting in few fights (Estes and Goddard 1967). Large packs in Selous
753 Game Reserve can split and take multiple prey animals simultaneously. Packs in the
754 reserve with a larger number of adults had a higher number of multiple kills, increased
755 hunting success, decreased chase distances, and increased prey mass (Creel and Creel
756 1995). In the Serengeti, larger packs were able to take adult Serengeti white-bearded
757 wildebeest (*Connochaetes mearnsi*), but smaller packs or single individuals could not
758 successfully hunt large species. Cooperative hunting also allowed improved defense of
759 resources. Prey taken in the Serengeti were better defended against spotted hyenas in *L.*
760 *pictus* packs that had more adults (Fanshawe and Fitzgibbon 1993).

761 Packs of *L. pictus* adopt one of two behaviors when stalking prey (Fanshawe and
762 Fitzgibbon 1993). Most commonly, they simply run directly at their prey, remaining in
763 full view throughout the stalking period; alternately, they approach in a tight group, with
764 heads lowered in an attempt to remain cryptic. Although the cryptic approach allows *L.*
765 *pictus* to get closer before prey flees, it does not influence the success of the hunt or does
766 it significantly reduce the distance of the ensuing chase (Fanshawe and Fitzgibbon 1993).
767 Group cooperation has benefits for all group members through vigilance and benefits to
768 individuals via cooperative hunting (Creel and Creel 2015).

769 ***Reproductive behavior.***—Pre-estrous female *Lycaon pictus* are followed
770 constantly by their suitors and physical contact becomes increasingly common during this
771 period (Van Heerden 1981). Typical behaviors of the male include pushing the head
772 against the female's flank, nibbling, and licking the skin and genitalia of the female,
773 raising hindquarters of the female with the head, and finally mounting without actual

774 penetration (Van Lawick 1970; Frane et al. 1979; Van Heerden 1981). Typical behaviors
775 of the females included urination and anal dragging (Van Heerden 1981). When
776 mounting begins, the female is on all four feet with the male often clasping her with his
777 forelegs and his head pressing against her scapular region. During the copulatory lock,
778 the female might assume a semi-sitting position with the male locked into a sitting
779 position on the ground (Van Heerden 1981). Marking behaviors of *L. pictus* such as
780 urine marking, anal dragging, and body rubbing become increasingly common during
781 sexual attraction (Van Heerden 1981).

782 Packs of *L. pictus* generally include a dominant breeding pair that accomplishes
783 nearly all reproduction and non-breeding adults and yearlings that support the alpha
784 female rearing her young (Wilson and Mittermeier 2009). The alpha pair (usually the
785 oldest female and a male of mid-age) monopolizes reproduction in the pack through
786 aggressive behavior and ritualized displays of dominance and subordination and
787 hormonal suppression (Frame et al. 1979). During the breeding season, aggression
788 among members of the pack to attain dominance occurs (Creel and Creel 2002).
789 Suppression of reproduction in subordinates, however, is reported to be primarily
790 behavioral and not physiologically; only 1 of 15 females did not ovulate in a study of
791 hormone patterns contrasted with behavioral patterns (Van der Weyde 2015).

792 Subordinate *L. pictus* can breed and rear offspring within a pack (Fuller et al.
793 1992). In Tanzania, a subordinate female was observed with a litter and a subordinate
794 male, but paternity of the offspring was unknown (Malcolm and Marten 1982). In Selous
795 Game Reserve, 24% of subordinate females gave birth while 19% produced litters in
796 KNP (Creel et al. 1997b). Six litters were born to subordinate females in the Serengeti

797 whereas dominant females bore nine litters (Frame et al. 1979). In KNP, a subordinate
798 bred in 42.9% of cases (Mills 1993). Genetic data indicate multiple paternity within a
799 pack. Subordinate males in two packs copulated with the dominant female (Reich
800 (1981). In KNP, 10.3% of young from two packs had subordinate males as their fathers
801 (Girman et al. 1997); genetic data from the Selous Game Reserve also revealed multiple
802 paternity (Creel and Creel 2002). At times, nearly one-half of beta males and females
803 within packs bred successfully, and reproductive sharing between dominant and
804 subordinate members is significant for *L. pictus* (Spiering et al. 2010). Inbred *L. pictus*
805 had inbreeding coefficients < 0.25 , and subordinate individuals had shorter life spans than
806 outbred and dominant contemporaries; thus, there are consequences of inbreeding
807 (Spiering et al. 2011).

808 In some populations of *L. pictus*, beta females account for up to 25% of litters
809 produced (Burrows 1995; Creel et al. 1997b), but very few young born to subordinate
810 females survive one year (Girman et al. 1997). Using molecular data from a population
811 in KNP, only 8% of young reaching 1 year of age had a mother other than the alpha
812 female (Girman et al, 1997). When a subordinate female produced a litter at the same
813 time as the dominant female, the dominant female controlled access to all offspring,
814 including those of the subordinate females, and influenced provisioning rates (Frame et
815 al. 1979). Offspring of the subordinate female often suffer from reduced nutrition as a
816 result, and most litters produced by subordinate females die or are taken over by the alpha
817 female (Frame et al. 1979, Girman et al. 1997). Alpha females have reportedly killed the
818 young of subordinates (Creel et al. 1997b). This tendency of alpha females to take over

819 litters also probably explains the extremely large (16 young) litters occasionally reported
820 (Frame et al. 1979; Girman et al. 1997).

821 Prey availability is important for successful reproduction of *L. pictus*. Females
822 copulate at younger ages when pack density and availability of prey are high. Older
823 females in large packs raised the highest numbers of offspring (Marneweck et al. 2019).

824 **Communication.**--Begging and appeasement behavior by *Lycaon pictus* are
825 common and occur during nearly every contact between individuals including gatherings
826 at kills. Appeasement behavior involves flattening forequarters and head along the
827 ground while keeping hindquarters elevated and tail arched. This is usually accompanied
828 by a twittering call, often described as bird-like (Estes and Goddard 1967). Food
829 solicitation is used by pups to induce adult pack members to regurgitate and is
830 accomplished by a pup sticking its nose into the corner of an adult's mouth and licking or
831 biting at the lips. A ritualized form is used by adults as an appeasement behavior (Estes
832 and Goddard 1967; Fanshawe and Fitzgibbon 1993).

833 The greeting ceremony of *L. pictus* usually occurs as the pack is becoming active
834 after a period of rest. The ceremony consists mainly of face-licking and ritualized food-
835 solicitation behavior (Estes and Goddard 1967). Either one or both individuals involved
836 might assume a submissive, crouched posture. A ritualized stalking behavior in which
837 individuals hunch the neck and shoulders and hang the tail and head can precede the
838 greeting ceremony. The greeting ceremony is often a precursor to hunting and might
839 synchronize and stimulate hunting behavior (Estes and Goddard 1967). Nasal exhalations
840 (i.e., sneezes) are used by *L. pictus* in Botswana before moving away from resting spots
841 (Walker et al. 2017). The probability of a rally success (i.e., departure of the pack) is

842 predicted by the minimum number of audible rapid sneezes ($\bar{x} = 7.48 \pm 1.49 SE$). Rally
843 success is higher (76.5%) when sneezes are initiated by alpha members of the pack than
844 by subordinate members (27.3%—Walker et al. 2017).

845 When a kill is made, individuals at the front of the pack immediately begin
846 consuming the carcass (Estes and Goddard 1967). Behavior at the kill is a free for all, at
847 least until the young arrive and receive exclusive access to the kill, regardless of whether
848 the adults have finished feeding. Young monopolize the kill through appeasement
849 behavior (Estes and Goddard 1967) or through the mediation of the dominant adult pair
850 (Creel and Creel 1995). If present, yearlings also receive preferential access to kills
851 (McNutt 1996). Individuals that are unable to participate in the kill due to injury, illness,
852 or old age are also allowed to eat from the carcass when they arrive (Estes and Goddard
853 1967).

854 Vocalizations of *L. pictus* in Hwange National Park, Zimbabwe, have about equal
855 numbers of low- and high-frequency calls, with 11 vocal classes and 19 subclasses
856 (Hartwig 2005). The 11 classes are twitters, begging, yelps and squeals, whimpers,
857 whines, moans, rumble, growl, barks, hoo, and a pack call. Twitters are the most
858 common and used during social interactions, play, pursuit, and warning. Begging cries
859 are emitted during greeting ceremonies, food solicitation, or distress of an individual.
860 Yelps and squeals are submission calls, and whimpers are emitted during social greetings
861 and during approaches by other individuals. Whines indicate solicitation or frustration,
862 as do moans. Growls can serve as pack warnings or during aggressive encounters. Barks
863 can indicate alarm or threat and are emitted during aggressive interactions. Vocalizations
864 by young minimize conflicts (Robbins and McCrerry 2003). The hoo is a contact call

865 described as a bell-like hoo (Estes and Goddard 1967:55) and emitted during periods of
866 separation or times of distress. Acoustic identification in *L. pictus* can be a non-invasive
867 method of tracking individuals (Hartwig 2005).

868

869

GENETICS

870 *Molecular genetics.*—*Lycaon pictus* like other canids has 78 chromosomes
871 arranged in 39 pairs (Graphodatsky et al. 2008). Packs generally consist of unrelated
872 alpha male and alpha female, subdominant close relatives, and offspring of the alpha pair.
873 Timing of dispersal and the destination of dispersal are related to patterns of relatedness.
874 When relatedness to the alpha pair is low, individuals disperse and establish territories
875 near close relatives. Genetic variability is obtained by occasional long-distance migration
876 and pack structure that inhibits inbreeding (Girman et al. 1997). Emigration of non-
877 breeding individuals from their natal pack is the primary mechanism by which *L. pictus*
878 minimizes inbreeding. Mitochondrial DNA variability of *L. pictus* is not unusually low
879 (i.e., 1% divergence in mtDNA) relative to other large carnivores, but mitochondrial
880 variability is not indicative of nuclear DNA variability (Girman et al. 1993). *L. pictus* (n
881 = 168) is genetically depauperate at the major histocompatibility complex relative to
882 other canids (Marsden et al. 2009).

883 Genetic and morphological studies suggest that populations of *L. pictus* in eastern
884 and southern Africa are distinct subspecies (Campana et al. 2016), but these have not
885 been formally recognized. *L. pictus* underwent two or more effective population size
886 reductions in the last 1,000,000 years resulting in individual-specific regions of low
887 diversity (Campana et al. 2016). It is not certain if the low-diversity regions are

888 characteristic of the entire population. Campana et al. (2016) also reported that positive
889 selection was evident on the mitochondrial genome of *L. pictus*, and candidate genes (i.e.,
890 ASIP, MITF, MLPH, PMEL) might play a role in the characteristic pelage of *L. pictus*.

891 **Population genetics.**—Reintroductions of captive-bred *L. pictus* can result in
892 positive growth, lower inbreeding and mean kinship, and increase genetic diversity
893 (Frantzen et al 2001). Unfortunately, there are few successful long-term reintroductions
894 into southern Africa using captive-bred *L. pictus* because of a lack of collaboration
895 between captive breeding and nature conservation institutions (Frantzen et al. 2001).
896 There are, however, increasing cooperative ventures to enhance conservation of *L. pictus*
897 (Tensen et al. 2019). With adequate habitat and prey and low levels of human
898 persecution, populations should be able to sustain robust genetic diversity (Beker et al.
899 2012). *L. pictus* will benefit from avoiding inbreeding, but with their rapid population
900 decline, extinction could advance rapidly before inbreeding depression is observed
901 (Becker et al. 2012). Increased gene flow via habitat corridors, increased survival in
902 unprotected areas (Tensen et al. 2016), and metapopulation management with
903 translocations can achieve population growth. The future of *L. pictus* probably depends
904 on genetic diversity of extant populations (Tensen et al. 2019).

905

906

CONSERVATION

907 *L. pictus* is among Africa's most endangered carnivores (Cozzi et al. 2020) and is
908 recognized as one of the most endangered canids in the world (Ginsberg and Macdonald
909 1990; Woodroffe et al. 2005). It is approaching extinction (Ginsberg and Macdonald
910 1990) with only about 6,000 free-ranging individuals remaining in a few isolated

911 subpopulations (Cozzi et al. 2020). Based on continued loss of habitat and the decline in
912 numbers over the past 20 years, *L. pictus* is recognized as endangered by the U.S. Fish
913 and Wildlife Service since 1894 (49 FR 2779; [https://www.govinfo.gov/content/pkg/FR-
914 1984-01-23/pdf/FR-1984-01-23.pdf#page=47](https://www.govinfo.gov/content/pkg/FR-1984-01-23/pdf/FR-1984-01-23.pdf#page=47), accessed 21 June 2021) and the
915 International Union for the Conservation of Nature (IUCN—Woodroffe and Sillero-
916 Zubiri 2020). It not is listed by the Convention on International Trade in Endangered
917 Species of Wild Fauna and Flora (CITES 2021; <https://cites.org/eng/app/appendices.php>,
918 accessed 21 June 2021).

919 Human persecution of *L. pictus* is common, and populations are declining because
920 of accidental snaring; conflicts with farmers, game ranches, and human communities;
921 detrimental land-use policies including a lack of engagement in the private sector
922 involved in mining and resource extraction and use of predator proof fencing that blocks
923 dispersal and heightens risks from disease and drought; diseases; habitat loss; insufficient
924 political commitment; interspecific competition with lions and spotted hyenas;
925 irresponsible tourism and den disturbance; poisoning; prey depletion; road kills; and
926 small population size (Macdonald 1990; Creel and Creel 2015; Fanshawe et al. 1991;
927 IUCN 2015). Other threats to survival of *L. pictus* include land mines that restrict access
928 to areas and kill individuals, corruption in law enforcement agencies, and loss of
929 resilience because of climate change (IUCN 2015).

930 In Zimbabwe, *L. pictus* was considered vermin until 1975, and a minimum of
931 3,404 were shot during government control programs from 1956 to 1975 (Childes 1988).
932 Although attitudes are slowly changing (Ramnanan et al. 2013), many landowners
933 continue to view *L. pictus* as pests. Road kills are becoming increasingly common as

934 highways are built through the distribution of *L. pictus*, presenting a real threat to many
935 small populations scattered throughout national parks (Fanshawe et al. 1991). For
936 example, in Hwange National Park, Zimbabwe, from 1988 to 1993, 64% ($n = 16$) of *L.*
937 *pictus* mortalities resulted from automobile collisions, and the remainder were due to
938 shooting or trapping by humans ($n = 7$ —Ginsberg et al. 1995b).

939 In South Africa, Kenya, and Zimbabwe, human-caused mortality (i.e., road kills,
940 shooting, snaring, and poisoning) accounted for 30% of mortality of radio-collared *L.*
941 *pictus* and 52% of mortality of individually identified *L. pictus* that were not radio-
942 collared, whereas naturally occurring mortality accounted for 33 and 19%, respectively,
943 and diseases only accounted for 5 and 1%, respectively (Woodroffe et al. 2007). During
944 dispersal, Cozzi et al. (2020) reported that all mortalities were attributed to anthropogenic
945 causes (e.g., shooting, poisoning); a third of dispersing *L. pictus* ($n = 9$) that traveled
946 through human-dominated landscapes did not survive in Botswana. With changing
947 attitudes, > 50% of ranchers in South Africa are amenable to having *L. pictus* on their
948 land (Lindsey et al. 2005). *L. pictus* is an attractive draw for tourists that are willing to
949 pay to observe it in the wild (Gusset et al. 2008).

950 Genetic problems associated with having small and isolated populations, namely
951 decreased heterozygosity, and subsequent increase in susceptibility to disease and
952 parasitism have also been suggested as causes of decline (Fanshawe et al. 1991).
953 Research indicates that population declines in *L. pictus* have not resulted in a comparable
954 loss of mtDNA diversity that such steep population declines would indicate. *L. pictus*
955 occurs in low numbers with low genetic diversity (Girman et al. 2001). Thus, there is

956 conservation concern that genetic variability will decline when populations become
957 isolated due to habitat fragmentation and long-distance dispersal is prevented

958 Hunting *L. pictus* is prohibited, although some poaching does continue. Sport
959 hunting for *L. pictus* has never been popular, and there does not appear to be a demand
960 for body parts; thus there is little concern that illegal commerce is a significant factor in
961 the decline of the species (Fanshawe et al. 1991). Unfortunately, demand for illegally
962 obtained wildlife is increasing, and illicit demand might be growing (Wyler and Sheikh
963 2009). Poaching from illegal shooting, snaring, and poisoning accounted for 9%, 1%,
964 and 16% of mortality in radio-collared *L. pictus* and 16%, 8%, and 21% of mortality in
965 individually identified *L. pictus* not radio-collared, respectively (Woodroffe et al. 2007).
966 Most incidents of poaching occurred in unprotected areas where land was used for
967 livestock and game ranching (Woodroffe et al. 2007), and most *L. pictus* caught in snares
968 were caught as by-catch.

969 There have been several attempts to reintroduce *L. pictus* into formerly occupied
970 parts of its distribution. Because the only viable population of *L. pictus* in South Africa
971 occurs in KNP, a working group was established to create other viable populations (i.e.,
972 managed metapopulations) in South Africa (Davies-Mostert et al. 2009). *L. pictus* was
973 reintroduced at 12 sites in South Africa up to 2005. One hundred and twenty-seven *L.*
974 *pictus* were released during 18 release events, and 129 offspring were born from
975 reintroduced individuals. Effective reintroductions used captive-bred or translocated
976 individuals that were socially integrated, and releases were made in fenced reserves
977 unless intensive management strategies were used to reduce effects of human-caused
978 mortality (Gusset et al. 2008). Only the Tswalu Kalahari Reserve metapopulation

979 experienced an extinction event in 1998–2006 because of a distemper outbreak. Other
980 local extirpation events have been prevented through intensive management of
981 metapopulations and intervention to reduce conflicts occurring off reserve land. The
982 working group successfully established at least 9 viable free-ranging packs of *L. pictus*
983 outside of KNP to prevent stochastic events (i.e., disease—Davies-Mostert et al. 2009).

984 Three attempts to reestablish *L. pictus* in Etosha National Park, Namibia, failed
985 (Scheepers and Venzke 1995). Of the six *Lycaon pictus* released in the first attempt, each
986 individual 1 year of age died within 4 months of release due to predation by lions and
987 starvation. Five adult *L. pictus* released in a second attempt died within 3 months of
988 release from unknown causes. Eight captive bred females and five captive bred males, 1–
989 4 years of age, were released during a third attempt (Scheepers and Venzke 1995). They
990 appeared to lack group cohesion and hunting skills, relying on carcasses provided by
991 researchers. Their first kill came 5 weeks after release when they killed a young zebra.
992 They eventually became coordinated enough to successfully hunt adult springbok
993 (*Antidorcas marsupialis*), but the pack appeared to lose cohesion again after six
994 individuals were killed by lions in a series of separate incidents (Scheepers and Venzke
995 1995). The remaining *L. pictus* resorted to scavenging from tourist camps and carcasses,
996 at which point they were captured and returned to a holding facility. Within 2 weeks, all
997 remaining individuals died of rabies contracted from a black-backed jackal carcass they
998 fed on prior to the recapture (Scheepers and Venzke 1995).

999 Since 2005, translocation efforts for *L. pictus* have improved and increased with
1000 more concern for genetic variation. In KNP, high levels of genetic variation occurred in
1001 populations of *L. pictus* due to translocations. Genetic data are important for

1002 conservation management, and it can be restored via translocation (Tensen et al. 2019).
1003 Furthermore, translocations are more successful when the importance of social groups are
1004 considered in translocations (Gusset et al. 2006). Translocation planning also has been
1005 important for their continued success (Gussett et al. 2009).

1006 Radiotelemetry is the most common, practical, and effective method to study
1007 populations of *L. pictus* (e.g., Ginsburg et al. 1995; Creel et al. 1997a). Nonetheless,
1008 there was concern in the wake of massive die-offs of study packs in Serengeti National
1009 Park that immobilization and handling of *L. pictus* for the fitting of radiocollars caused
1010 stress (Burrows 1992; Burrows et al. 1994). Villiers et al. (1995), Dye (1996), Ginsberg
1011 et al. (1995b), and Kat et al. (1995) criticized this hypothesis on a variety of theoretical
1012 and empirical grounds. Most importantly, Creel et al. (1997a) and Ginsberg et al. (1995b)
1013 demonstrated that anesthesia and handling did not provoke a persistent,
1014 immunosuppressive stress response. Similarly, it cannot be concluded that handling
1015 increases susceptibility of *L. pictus* to disease (Creel 1992; Macdonald 1992; Dye 1996;
1016 Creel et al. 1997a).

1017 Conservation of *L. pictus* will require a paradigm shift that uses a more holistic
1018 approach that includes protection inside and outside of protected areas and across
1019 international boundaries and landscapes $> 10,000 \text{ km}^2$ (Woodroffe et al 1997; Cozzi et al.
1020 2020), including smaller protected areas and very small, intensively managed areas with
1021 only 1–2 packs (Woodroffe et al. 1997); standardized and regular populations surveys
1022 (Nicholson et al. 2020); serious consideration of climate change that will reduce foraging
1023 and survival of young (Woodroffe et al. 2017; Rabaiotti and Woodroffe 2019);
1024 community-based management (Measham and Lumbasi 2013) that will allocate space for

1025 *Lyacon pictus*; and translocations (Marneweck et al. 2019). Techniques are available to
1026 conserve *L. pictus*, but collaboration among national and international researchers and
1027 their institutions, government organizations, private landowners, and interest groups will
1028 be necessary for success (Cozzi et al. 2020).

1029

1030

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1607 Associate Editor was DAVID M. LESLIE, JR., and R. W. NORRIS and DAVID M. LESLIE, JR.

1608 reviewed the synonymies. Editor was MEREDITH J. HAMILTON.

1609

1610 **Figure Legends**

1611 **Fig. 1.**—Adult male *Lycaon pictus* in Karongwe Game Reserve, South Africa, June 2004.

1612 Used with permission of the photographer Kerry L. Nicholson.

1613 **Fig. 2.**—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an

1614 adult female *Lycaon pictus* (National Museum of Natural History, Smithsonian

1615 Institution # 368442) from Mabeleapudi, Botswana, Africa.

1616 **Fig. 3.**—Distribution of *Lycaon pictus* including eight categories: resident, possible

1617 occurrence, recoverable areas, transient, connecting areas, unknown, extirpated, and areas

1618 outside their distribution. Modified by K. L. Nicholson and used with permission of R.

1619 Groom (Range Wide Conservation Program for Cheetah and African Wild Dogs;

1620 <http://www.cheetahandwilddog.org>, accessed 23 June 2021).

1621 **Fig. 4.**—Components of habitat used by *Lycaon pictus* (i.e., grasslands, montane

1622 savanna, open woodlands; dense woodlands in the foreground are avoided), Makuleke

1623 Contractual Park, northern Kruger National Park, South Africa, 2004. Used with

1624 permission of photographer K. L. Nicholson.

1625 **Fig. 5.**—Confrontation between *Lycaon pictus* and spotted hyena (*Crocuta crocuta*) in

1626 the Linyanti region, Botswana, Africa. A pack of wild dogs had taken down a tsessebe

1627 (*Damaliscus lunatus*) calf and were feeding on it when two spotted hyenas arrived at the

1628 scene. Members from the pack charged the hyenas to keep them at bay while the rest of

1629 the pack continued the to eat. Confrontations between these two species are well-known
1630 in this region. Used with permission of the photographer M. Trolle.

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1632