

Hibernation in pygmy lorises (*Nycticebus pygmaeus*) – what does it mean?

Ulrike Streicher^{1,3}, Julia Nowack², Gabrielle Stalder², Christian Walzer², Tilo Nadler³ and Thomas Ruf²

¹ Current address: Cascades Raptor Center, Eugene, USA

² University of Veterinary Medicine, Research Institute of Wildlife Ecology, Department of Integrative Biology and Evolution, Vienna, Austria, Savoyenstr. 1, 110 Vienna, Austria

³ Endangered Primate Rescue Center, Cuc Phương National Park, Nho Quan District, Ninh Binh Province, Vietnam
Corresponding author: Ulrike Streicher <u.streicher1612@gmail.com>

Key words: South-East Asia, primate, torpor, multiday torpor, pygmy loris, hibernation

Summary

Torpor use in primates appeared to be restricted to African species and was only recently discovered in a species from Asia, the pygmy loris (*Nycticebus pygmaeus*). This finding has considerable implications for our perception of torpor in this mammal group and demonstrates that torpor is probably more widespread in mammals than commonly thought. This article summarizes the current knowledge on the use of torpor in the pygmy loris and places it into the context of ongoing research on this topic.

Hiện tượng ngủ đông ở loài cu li nhỏ (*Nycticebus pygmaeus*) – Ý nghĩa là gì?

Tóm tắt

Hiện tượng ngủ đông ở các loài linh trưởng được cho rằng chỉ tồn tại ở một số loài linh trưởng ở Châu Phi. Gần đây hiện tượng này được khám phá ở một loài linh trưởng ở Châu Á, loài cu li nhỏ (*Nycticebus pygmaeus*). Phát hiện mới này có thể thay đổi nhận thức của chúng ta về hiện tượng ngủ đông ở nhóm thú này và nó cũng minh chứng rằng hiện tượng ngủ đông có thể phổ biến ở nhiều loài thú khác hơn những gì chúng ta thường nghĩ. Bài báo này tóm tắt những kiến thức hiện tại về việc sử dụng phương pháp ngủ đông ở loài cu li nhỏ và đặt ra những vấn đề cần tiếp tục nghiên cứu đối với hiện tượng này.

Introduction

Animals in highly seasonal habitats face severe seasonal fluctuations of climatic conditions and often of resource availability. Ambient temperatures can be substantially lower during the cold season than during the hot season, requiring higher energetic expenses for endogenous heat production to maintain a high body temperature. Whilst the conditions during the hot season often provide a surplus of food, animals have to deal with food scarcity or low-quality food resources during the cold season. To overcome these challenges, many small heterothermic mammals display states of energy conservation such as daily torpor that lasts less than 24 hours, or multiday torpor that lasts more than 24 hours, commonly called hibernation. Daily torpor and hibernation are both characterized by a reduced metabolic rate, decreased activity, and reduced body temperature (e.g. Bieber et al., 2014; Hoelzl et al, 2015; Ruf & Geiser, 2015).

Recently we have reported hibernation in the pygmy loris, which was the first description of hibernation in a primate outside of Madagascar (Ruf et al., 2015). The pygmy slow loris or pygmy loris (*Nycticebus pygmaeus*) is a small, solitary, nocturnal primate, distributed east of the Mekong in Vietnam, eastern Cambodia, Laos and the southernmost part of China. The species is listed as 'Vulnerable' on the IUCN Red list of Threatened Species, due to an estimated population decline

of more than 30% over the last two decades caused by habitat loss and poaching (Streicher et al., 2008).

Evidence of torpor in the pygmy lorises

Pygmy lorises are members of the same suborder as lemurs, and have a small body with a weight rarely exceeding 400 g, which accounts for a high rate of heat loss (Fig. 1). They live partly in habitats with distinct seasonal fluctuations in ambient temperatures and food availability. Both body size and the seasonality of their habitats have previously given cause to assume that lorises might use torpor, and anecdotal evidence suggested that pygmy lorises undergo bouts of torpor during the cold season (Ratajszczak, 1998; Streicher, 2004).



Fig.1. Pygmy loris (*Nycticebus pygmaeus*) at the Endangered Primate Rescue Center. Photo Ulrike Streicher.

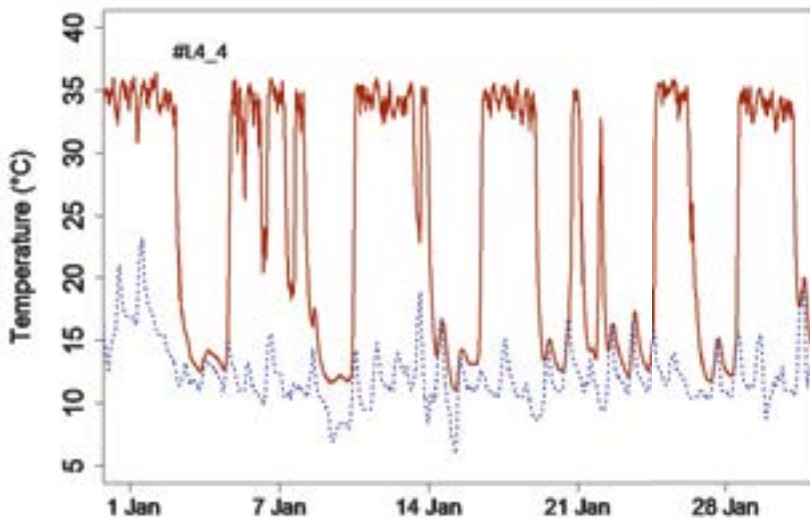
Daily torpor can be employed fairly spontaneously and often without restriction to specific seasons (Geiser, 2013); in contrast hibernation requires preparation in the form of accumulation of substantial energy reserves, usually stored in the forms of adipose tissue (Carey et al., 2003; Geiser, 2013). Pygmy lorises showed pronounced seasonal body weight changes, weighing up to 50% more in winter than during the hot summer months (Streicher, 2005), and were regularly found rigid and unresponsive during the cold winter months (Streicher, 2004). Therefore, they were an obvious candidate for a study on thermoregulatory processes.

Five individuals, housed at the Endangered Primate Rescue Center in Cuc Phuong National Park of northern Vietnam (Fig. 2), were implanted with data loggers to record their core body temperature (Ruf et al., 2015). Torpor was defined as body temperature below 30°C for at least one hour. For three individuals winter data was collected, and these three individuals all used torpor between late October and early April (Fig. 3) (Ruf et al., 2015). The recorded torpor bout durations varied

substantially, from less than 12 hours to over 24 hours (Fig. 4). The longest torpor bout recorded was 62.6 hours. This might seem relatively short, but it is longer than the maximum bout duration in four other hibernating species (including one lemur, Table 1), and comparable to the median maximum torpor bout duration in mammals, which is only 4.8 days (Ruf & Geiser, 2015). The occurrence of multiday torpor bouts, the fact that minimum body temperatures closely resembled ambient temperatures, and the weight gain and accumulation of adipose tissue prior to the cold season all identify pygmy lorises as seasonal hibernators (Ruf & Geiser, 2015).

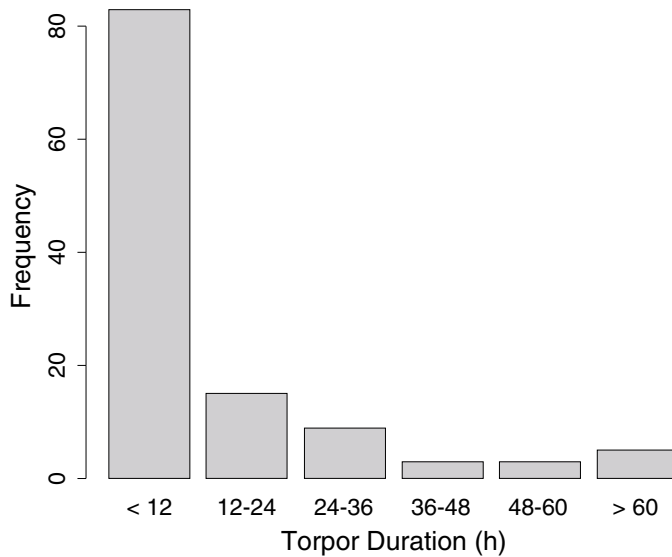


Fig.2. Outdoor enclosures for lorises at the Endangered Primate Rescue Center. Photo Ulrike Streicher.



Hibernation in pygmy loris

Fig.3. Core Tb (red line) in a pygmy slow lorises in midwinter, recorded over a four week period. The animal exhibited bouts of multiday torpor that is hibernation, interspersed with periods of euthermia and short torpor episodes. Blue line shows ambient air temperature.



Torpor duration in pygmy lorises

Fig.4. Animals (N = 3) exhibited both daily torpor (≤ 24 h) or long phases of hibernation (or multi-day torpor) (≥ 24 h).

Since study subjects were in captivity and not exposed to seasonal changes of food availability the occurrence of torpor was clearly not related to food availability. We assume torpor bout duration and frequency are even more pronounced in free-ranging individuals which experience seasonal food shortages. When provided with food *ad libitum* over winter, 'classical' hibernators such as the garden dormouse (*Eliomys quercinus*) exhibit short torpor bouts with a frequency distribution very similar to that of the pygmy loris shown in Fig. 3, with most torpor bouts lasting less than 24 hours (Daan, 1973). Torpor in the pygmy lorises was possibly triggered by ambient temperature and/or photo period, both well-known modulators of the timing of hibernation in the temperate zone (Körtner & Geiser, 2000; Malan, 1996). In contrast to many other hibernators, pygmy lorises do not retreat into burrows, but hibernate in relatively exposed locations (Streicher, 2004) and therefore are subjected to highly varying ambient temperatures during torpor. The lorises predominantly entered torpor in the late night and early morning and remained torpid until the early afternoon (Ruf et al., 2015). They returned to euthermia when there was still sunlight available and well prior to the onset of their nocturnal activity, suggesting that they use sunbathing to reduce the energetic expenses required to return to euthermia after a torpor period, similar to many other tropical heterotherms (Schmid et al., 2000). Although torpor use allows for enormous energy savings, some species only use torpor opportunistically in response to acute energetic bottlenecks. There are costly trade-offs to energy savings during torpid periods such as slowed reactions (Nowack et al., 2016; Rojas et al., 2012), and reduced sensory abilities (Nowack et al., 2016) that potentially increase the risk of predation (but see Armitage, 2004; Bieber & Ruf, 2009; Turbill et al., 2011). Species using tree hollows or underground burrows are hidden and protected during torpor and often undergo hibernation for months (e.g. *Cheirogaleus sibirii*: Blanco et al. (2013); *Glis glis*: Hoelzl et al. (2015)), but pygmy lorises rest either in dense scrub or on exposed high terminal branches of trees (Streicher et al., 2003). An increased risk of predation might explain why torpor use was only observed on the coldest days during mid-winter (Ruf et al., 2015). In addition to expressing torpor and hibernation, pygmy lorises also slightly reduced their body temperature within euthermic levels on colder days, but not to levels below 30°C. Variability of body temperature likely allows lorises to remain alert and responsive to possible predators, while still permitting for energy savings (Glanville & Seebacher, 2010).

Table 1. Primate species for which heterothermy has been reported, including the maximum torpor bout duration (TBD) within the hibernation phase (in hours; not including uninterrupted hibernation when body temperature passively tracks ambient temperature. (T/H: T= daily heterotherm, H= hibernator, n.k.: not known).

Species	Common name	TBD (h)	T/H	Citation
LEMUROIDAE				
Cheirogaleus				
<i>C. crossleyi</i>	Furry-eared dwarf lemur	168	H	Blanco and Rahalinarivo (2010)
<i>C. medius</i>	Fat-tailed dwarf lemur	288	H	Dausmann et al. (2005)
<i>C. major</i>	Greater dwarf lemur	n.k.	H	Lahann (2007)
<i>C. sibreei</i>	Sibree's dwarf lemur		H	Blanco et al. (2013)
Microcebus				
<i>M. berthae</i> (published as <i>M. myoxinus</i>)	Madame Berthe's mouse lemur	19.2	T	Ortmann et al. (1997), Schmid et al. (2000)
<i>M. griseorufus</i>	Reddish-gray mouse lemur	61	H	Kobbe and Dausmann (2009), Kobbe et al. (2011)
<i>M. lehilahytsara</i>	Goodman's mouse lemur	n.k.	H	Blanco et al. (2016) Blanco et al. (2016)
<i>M. imurinus</i>	Grey mouse lemur	26 (captivity)	H	Schmid (2000), Schmid & Speakman (2000)
<i>M. rufus</i>	Brown mouse lemur	n.k.	H	Atsalis (1999), Randrianambinina et al. (2003)
<i>M. ravelobensis</i>	Gray brown mouse lemur	n.k.	T	Lovegrove et al. (2014)
Mirza				
<i>M. coquereli</i>	Coquerel's mouse lemur	n.k.	T	Dausmann (2008)
Allocebus				
<i>A. trichotis</i>	Hairy-eared dwarf lemur	n.k.	H	reviewed by Dausmann (2014)
LORISOIDAE				
GALAGIDAE				
Galagos				
<i>G. moholi</i>	African lesser bushbaby	10.1	T	Nowack et al. (2010), Nowack et al. (2013)
LORISIDAE				
Loris				
<i>L. tardigradus</i> <i>tardigradus</i>	Slender loris	n.k.	n.k.	Pers. obs. KAI Nekaris
Nycticebus				
<i>N. javanicus</i>	Javan slow loris	n.k.	n.k.	Pers. obs. KAI Nekaris
<i>N. pygmaeus</i>	Pygmy slow loris	62.6	H	Ruf et al. (2015)

Impact of the finding

Our study (Ruf et al, 2015) demonstrated that hibernation it is not restricted to primates of Madagascar. An earlier study already found daily torpor in a small primate from the African mainland, the lesser bushbaby (*Galago moholi*) (Nowack et al., 2013). However, in contrast to lorises, bushbabies only use torpor as an emergency strategy and may be unable to undergo prolonged phases of hibernation (Nowack et al., 2013). The hibernation found in an Asian primate and the daily torpor found in African bushbabies clearly indicate that these energy saving strategies are not a

result of specific climatic conditions or evolutionary events unique to Madagascar, as was previously suggested (Dewar & Richard, 2007). On the contrary, torpor might have facilitated the colonization of Madagascar by lemurs and other terrestrial mammals (Kappeler, 2000; Martin, 1972; Nowack & Dausmann, 2015).

To date, torpor has been recorded in 12 lemur species of four genera of the same family in Madagascar (Table 1), one galago species in mainland Africa and one loris species in Vietnam. It is likely that further research will find hibernation and torpor in other primates living in seasonal habitats. There are also indications that the Javan slow loris (*Nycticebus javanicus*) and the slender loris, (*Loris tardigradus tardigradus*) might undergo states of decreased physiological activity such as torpor or even hibernation (Nekaris pers. com.). Tarsiers are another candidate for torpor (Lovegrove, 2012). Tarsiers are small (80–160 g), and exhibit the lowest euthermic body temperature (33.8°C) and basal metabolic rate (~65% of expected) of all primates (McNab, 1978). However, only a slight relaxation of euthermic body temperature regulation has been observed in this group with no evidence of pronounced torpor or hibernation (Lovegrove et al., 2014). Evidence of torpor in South American primates is entirely lacking (Alterman et al., 1995), but considering their small body sizes and variable climatic conditions further research might reveal torpor and hibernation among these primates as well.

Interestingly, torpor use in all primates seems to be restricted to the cold and dry season. It remains to be seen whether primates, as other hibernators (reviewed by Körtner & Geiser, 2000) have an endogenous circannual clock that governs the timing of hibernation or if they entirely rely on external signals such as decreasing temperature and shortening photoperiod, and if primates are able to use torpor year-round in response to unexpected events.

Conclusion

We predict that, given the availability of increasingly smaller temperature recording devices with high storage capacity, torpor or hibernation will soon be detected in other primates. Many mammals and birds that are reluctant to exhibit torpor in captivity, even when kept in outdoor enclosures, readily undergo torpor in the wild (reviewed by Ruf & Geiser, 2015). Thus, it is likely that with an increasing number of studies on free-living animals the number of species known to use hibernation or daily torpor will further increase.

References

- Alterman L, Doyle GA & Izard MK.** (1995). *Creatures of the dark. The nocturnal prosimians.* New York: Plenum Press.
- Armitage KB** (2004): Badger Predation on Yellow-bellied Marmots. *Am. Mid. Nat.* 151(2), 378-387.
- Atsalis S** (1999): Seasonal Fluctuations in Body Fat and Activity Levels in a Rain-Forest Species of Mouse Lemur, *Microcebus rufus*. *Int. J. Primatol.* 20(6), 883-910.
- Bieber C, Lebl K, Stalder G, Geiser F & Ruf T** (2014): Body mass dependent use of hibernation: why not prolong the active season, if they can? *Funct. Ecol.* 28(1), 167-177.
- Bieber C & Ruf T** (2009): Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* 96(1), 165-171.
- Blanco MB, Andriantsalohimisantatra AnA, Rivoharison TV & Andriambeloston J-B** (2016): Evidence of prolonged torpor in Goodman's mouse lemurs at Ankafoabe forest, central Madagascar. *Primatesonline* first, 1-7.
- Blanco MB, Dausmann KH, Ranaivoarisoa JF & Yoder AD** (2013): Underground hibernation in a primate. *Sci. Rep.* 3.
- Blanco MB & Rahalinarivo V** (2010): First direct evidence of hibernation in an eastern dwarf lemur species (*Cheirogaleus crossleyi*) from the high-altitude forest of Tsinjoarivo, central-eastern Madagascar. *Naturwissenschaften* 97(10), 945-950.
- Carey HV, Andrews MT & Martin SL** (2003): Mammalian Hibernation: Cellular and Molecular Responses to Depressed Metabolism and Low Temperature. *Physiol. Rev.* 83(4), 1153-1181.
- Daan S** (1973): Periodicity of heterothermy in the garden dormouse, *Eliomys quercinus* (L.). *Neth. J. Zool.* 23(3), 237-265.
- Dausmann KH.** (2008). Hypometabolism in primates: torpor and hibernation. In: Lovegrove BG & McKechnie AE (eds.): *Hypometabolism in Animals: Torpor, Hibernation and Cryobiology*, pp. 327-336. Pietermaritzburg, South Africa: Interpak Books.
- Dausmann KH** (2014): Flexible patterns in energy savings: heterothermy in primates. *J. Zool.* 292(2), 101-111.
- Dausmann KH, Glos J, Ganzhorn JU & Heldmaier G** (2005): Hibernation in the tropics: lessons from a primate. *J. Comp. Physiol.* B175(3), 147-155.
- Dewar RE & Richard AF** (2007): Evolution in the hypervariable environment of Madagascar. *Proc. Natl. Acad. Sci. USA* 104(34), 13723-13727.

- Geiser F** (2013): Hibernation. *Curr. Biol.* 23(5), R188-R193.
- Glanville EJ & Seebacher F** (2010): Plasticity in body temperature and metabolic capacity sustains winter activity in a small endotherm (*Rattus fuscipes*). *Comp. Biochem. Physiol. A* 155(3), 383-391.
- Hoelzl F, Bieber C, Cornils JS, Gerritsmann H, Stalder GL & Walzer C** (2015): How to spend the summer? Free-living dormice (*Glis glis*) can hibernate for 11 months in non-reproductive years. *J Comp. Physiol.* B185(8), 931-939.
- Kappeler PM** (2000): Lemur Origins: Rafting by Groups of Hibernators? *Folia Primatol.* 71(6), 422-425.
- Kobbe S & Dausmann KH** (2009): Hibernation in Malagasy mouse lemurs as a strategy to counter environmental challenge. *Naturwissenschaften* 96(10), 1221-1227.
- Kobbe S, Ganzhorn JU & Dausmann KH** (2011): Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *J Comp. Physiol.* B181(1), 165-173.
- Körtner G & Geiser F** (2000): The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. *Chronobiol. Int.* 17(2), 103-128.
- Lahann P** (2007): Biology of *Cheirogaleus major* in a Littoral Rain Forest in Southeast Madagascar. *Int. J. Primatol.* 28(4), 895-905.
- Lovegrove BG** (2012): The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. *Biol. Rev.* 87(1), 128-162.
- Lovegrove BG, Canale C, Levesque D, Fluch G, Řeháková-Petrů M & Ruf T** (2014): Are Tropical Small Mammals Physiologically Vulnerable to Arrhenius Effects and Climate Change? *Physiol. Biochem. Zool.* 87(1), 30-45.
- Malan A.** (1996). The origins of hibernation: a reappraisal. In: Geiser F, Hulbert AJ & Nicol SC (eds.): *Adaptations to the Cold*. Tenth International Hibernation Symposium, pp. 1-6. Armidale, New South Wales.: University of New England Press.
- Martin RD** (1972): Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London* B264(862), 295-352.
- McNab BK** (1978): The Evolution of Endothermy in the Phylogeny of Mammals. *Am. Nat.* 112(983), 1-21.
- Nowack J & Dausmann KH** (2015): Can heterothermy facilitate the colonization of new habitats? *Mammal Rev.* 45(2), 117-127.
- Nowack J, Delesalle M, Stawski C & Geiser F** (2016): Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. *Science of Nature* 103(9-10), 73.
- Nowack J, Mzilikazi N & Dausmann KH** (2010): Torpor on Demand: Heterothermy in the Non-Lemur Primate *Galago moholi*. *PLoS ONE* 5(5), e10797.
- Nowack J, Mzilikazi N & Dausmann KH** (2013): Torpor as an emergency solution in *Galago moholi*: heterothermy is triggered by different constraints. *J Comp. Physiol.* B183(4), 547-556.
- Ortmann S, Heldmaier G, Schmid J & Ganzhorn JU** (1997): Spontaneous Daily Torpor in Malagasy Mouse Lemurs. *Die Naturwissenschaften* 84(1), 28-32.
- Randrianambinina B, Rakotondravony D, Radespiel U & Zimmermann E** (2003): Seasonal changes in general activity, body mass and reproduction of two small nocturnal primates: a comparison of the golden brown mouse lemur (*Microcebus ravelobensis*) in Northwestern Madagascar and the brown mouse lemur (*Microcebus rufus*) in Eastern Madagascar. *Primates* 44(4), 321-331.
- Ratajszczak R** (1998): Taxonomy, Distribution and Status of the Lesser Slow Loris *Nycticebus pygmaeus* and Their Implications for Captive Management. *Folia Primatol.* 69 (suppl. 1 Biology and conservation of prosimians), 171-174.
- Rojas AD, Körtner G & Geiser F** (2012): Cool running: locomotor performance at low body temperature in mammals. *Biol. Lett.* 8(5), 868-870.
- Ruf T & Geiser F** (2015): Daily torpor and hibernation in birds and mammals. *Biol. Rev.* 90, 891-926.
- Ruf T, Streicher U, Stalder GL, Nadler T & Walzer C** (2015): Hibernation in the pygmy slow loris (*Nycticebus pygmaeus*): multiday torpor in primates is not restricted to Madagascar. *Sci. Rep.* 5, 17392.
- Schmid J** (2000): Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar: energetic consequences and biological significance. *Oecologia* 123(2), 175-183.
- Schmid J, Ruf T & Heldmaier G** (2000): Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. *J Comp. Physiol.* B170, 59-68.
- Schmid J & Speakman JR** (2000): Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): a small primate that uses torpor. *J Comp. Physiol.* B170(8), 633-641.
- Streicher U** (2004): Aspects of Ecology and Conservation of the Pygmy Loris *Nycticebus pygmaeus* in Vietnam. PhD thesis, Ludwig Maximilians University, Munich, Germany.
- Streicher U** (2005): Seasonal Body Weight Changes in Pygmy Lorises (*Nycticebus pygmaeus*). *Verhber. Erkr. Zootiere* 42, 292-298.
- Streicher U, Nadler T & Zinner D** (2003): Re-introduction study of Pygmy lorises in Vietnam. *Reintroduction News*. Newsletter of the IUCN Reintroduction Specialist Group, 37-40.
- Streicher U, Ngoc Thanh V, Nadler T, Timmins RJ & Nekaris A.** (2008): *Nycticebus pygmaeus* [Electronic Version]. The IUCN Red List of Threatened Species, e.T14941A4481461. downloaded Dec 12, 2016 from <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T14941A4481461.en>.
- Turbill C, Bieber C & Ruf T** (2011): Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc. R. Soc.* B278(1723), 3355-3363.