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Tropical bats counter heat by combining torpor with adaptive hyperthermia

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Many tropical mammals are vulnerable to heat because their water budget limits the use of evaporative cooling for heat compensation. Further increasing temperatures and aridity might consequently exceed their thermoregulatory capacities. Here, we describe two novel modes of torpor, a response usually associated with cold or resource bottlenecks, as efficient mechanisms to counter heat. We conducted a field study on the Malagasy bat *Macronycteris commersoni* resting in foliage during the hot season, unprotected from environmental extremes. On warm days, the bats alternated between remarkably short micro-torpor bouts and normal resting metabolism within a few minutes. On hot days, the bats extended their torpor bouts over the hottest time of the day while tolerating body temperatures up to 42.9°C. Adaptive hyperthermia combined with lowered metabolic heat production from torpor allows higher heat storage from the environment, negates the need for evaporative cooling and thus increases heat tolerance. However, it is a high-risk response as the torpid bats cannot defend body temperature if ambient temperature increases above a critical/lethal threshold. Torpor coupled with hyperthermia and micro-torpor bouts broaden our understanding of the basic principles of thermal physiology and demonstrate how mammals can perform near their upper thermal limits in an increasingly warmer world.

1. Background

The safety margin between euthermia and lethally high body temperatures in mammals is very narrow and even minor changes can be life threatening, particularly in the tropics. Mammals obtain their body heat mainly from metabolic activities and usually regulate their body temperature within a set range of a few degrees [1,2]. They reach their thermal limits when body temperature approaches 41–44°C due to overheating or dehydration [3,4]. The maximum temperatures experienced by mammals are increasing because of extensive habitat modification [5] or more frequent and more intense heatwaves associated with global climate change [6], and these maxima can be fatal [7–11]. Indeed, heatwaves have led to several recent mass mortalities of flying foxes (*Pteropus* spp.) in Australia [10,12], with ambient temperatures (T_a) of 42°C or higher representing a critical threshold [8].

Efficient thermoregulation is essential for survival, but there are few options for downregulating body temperature near the upper limit. Radiation, convection and conduction are passive mechanisms of heat loss only used when T_a is lower than the desired body temperature [13]. When T_a exceeds body temperature, the only options are evaporative cooling or tolerating short-term hyperthermia [14]. In warm and dry environments with unpredictable or limited water availability, evaporation might be constrained by the risk of dehydration. By accumulating heat instead of dumping it and thereby tolerating an increase in body temperature, the need for evaporative cooling can be postponed or even avoided, and considerable amounts of water can be conserved [15,16]. The classic example of this adaptive hyperthermia comes from dromedary camels (*Camelus dromedarius*), which regularly cycle between 41°C in daytime and 34–35°C at night when dehydrated [17], but other mammals also allow hyperthermia

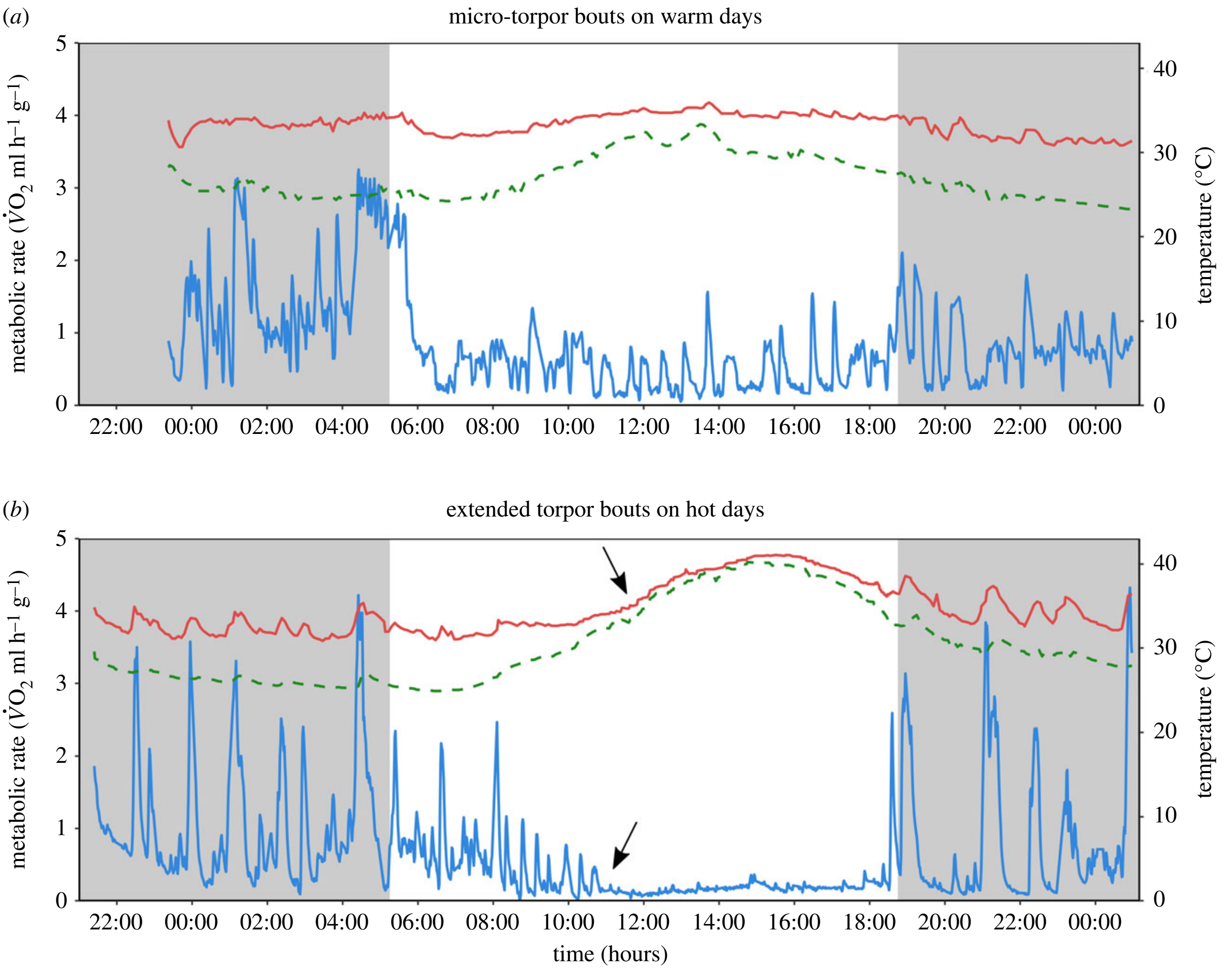

Figure 1. Two new modes of torpor in a tropical bat species. Metabolic rate as $\dot{V}O_2$ (MR, ml h^{-1} g^{-1}; blue; lower line) and skin temperature (T_{skin},°C; red; upper line) of two male individuals of the bat *Macronycteris commersoni* and the bats' ambient temperature (T_a,°C; green; dashed line). Grey shaded blocks indicate the dark phase. (*a*) The typical response on regular warm (rainy or cloudy) days. Under these conditions, bats alternated between regular resting MR and micro-torpor bouts (12.4 ± 10.5 min) over the course of their usual inactive phase (approx. 05:30–18:30 h). (*b*) The response of bats on hot days. When T_a exceeded euthermic body temperature, the bats extended their torpor bouts, which lasted until the beginning of their active phase in the late afternoon when T_a had decreased again (293.6 ± 101.2 min). The arrows highlight the decline in MR and almost simultaneous increase in T_{skin}, which passively followed T_a, during extended torpor up to 42.9°C indicating that bats tolerated hyperthermia while torpid (see electronic supplementary material, figure S1 for two examples of female bats showing the same patterns). (Online version in colour.)

during hot phases (llamas [18], elephants [19], large treeshrews [20], ringtail possums [11], bats [7,16,21]).

The most dramatic thermoregulatory response of mammals is the controlled downregulation of virtually all metabolic processes during torpor (hypometabolism) [22,23]. This is widely believed to be an adaptive response of endotherms to cold stress or food limitation during seasonal periods of scarcity. However, the last two decades have shown that torpor is also common in the tropics [24] and could negate some effects of heat [25]. A reduction of metabolic rate (MR) is accompanied by reduced water consumption through respiration, defecation, urine formation and metabolic heat dissipation [26–28], which could permit torpid animals to tolerate greater heat loads than euthermic ones. Nonetheless, how mammals perform and thermoregulate at high temperatures remains poorly understood [14,25,29–31], yet is essential to predict their responses to rising temperatures. Global warming confronts many small mammals more regularly with fatal mismatches between environmental conditions and their physiological limitations. To this end, we studied how a small tropical bat withstands heat in its natural environment and found that novel modes of torpor were a critical part of their response.

2. Short methods

We worked with the insectivorous bat *Macronycteris commersoni* (mean body mass: females = 46.3 ± 6.8 g; males = 79.6 ± 8.0 g) in a tropical dry forest in western Madagascar (Kirindy Forest/CNFEREF; S 20.06714°/E 44.65745°, 40 m) during the hottest season of the year. The bats rest alone in vegetation during the day exposed to temperature extremes and cannot necessarily expend the water required to cool their bodies below ambient temperatures. On sunny days, maximum T_a can reach over 41°C in Kirindy Forest/CNFEREF whereas relative humidity is comparatively low at 44.2 ±6.6% (29.0–53.6%). We monitored the physiological responses to regular daytime heat (73% sunny days) by measuring mass-specific MR as rate of oxygen consumption ($\dot{V}O_2$ ml h^{-1} g^{-1}) and skin temperature (T_{skin}) in 16 adult bats in their natural environment (nine females, seven males; see electronic supplementary material for a detailed description of procedures). Our

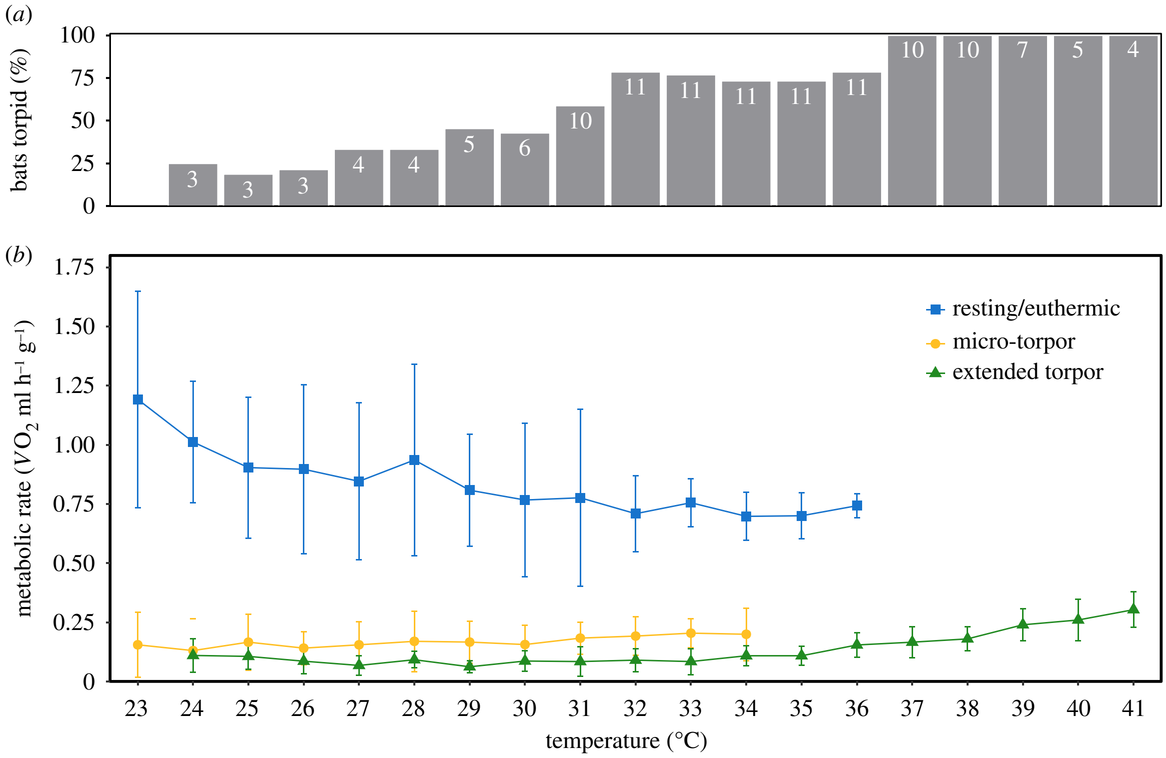

Figure 2. More bats enter torpor as ambient temperature rises. (*a*) The proportion of torpid bats at different ambient temperatures (T_a; integers indicate number of bats measured per interval). When T_a increased, more bats entered torpor and all bats were torpid above 36°C. (*b*) The mass-specific metabolic rate as $\dot{V}O_2$ (ml h^{-1} g^{-1}) of bats in the three different physiological states: resting (blue; squares), micro-torpor bouts (yellow; circles) and extended torpor bouts (green; triangles) at each temperature interval. Error bars represent standard deviation. (Online version in colour.)

Table 1. Physiological key variables of the metabolic states. Mass-specific metabolic rate as $\dot{V}O_2$ (ml h^{-1} g^{-1}) and mean maximum skin temperature (°C) of bats (n = 12) when resting and euthermic, during micro-torpor and during extended hot torpor.

	euthermia	micro-torpor	extended torpor
mean metabolic rate (ml O_2 h^{-1} g^{-1})	1.07 ± 0.41	0.24 ± 0.08	0.19 ± 0.06
mean skin temperature (°C)	36.7 ± 1.9	36.2 ± 2.1	38.1 ± 2.6

methods complied with the current ethical regulations and laws of Madagascar (see ‘Ethics’).

3. Two novel modes of torpor

Unexpectedly, all bats entered torpor on all days and we observed two unique, novel modes of torpor, regardless of sex. On warm, rainy or cloudy, days (mean max $T_a = 33.9 \pm 1.98$°C), most bats (67%) alternated between short micro-torpor bouts lasting between 3 and 53 min (mean = 12.4 ± 10.5 min; $n = 462$ bouts) and resting MR (figure 1*a*; electronic supplementary material, figure S1A). This pattern occurred throughout their resting phase from sunrise at approximately 05:30 to sunset at approximately 18:30 before nightly activity. Interestingly, micro-torpor did not lead to notable changes in T_{skin} compared to euthermia (figure 1*a*; electronic supplementary material, figure S1A). The pattern of recurring micro-torpor bouts is likely a fine balance: Individuals can save energy [32] and water [27] on the one hand, but simultaneously are still alert and responsive to any threats given the exposed roosting conditions.

On hotter, days (mean max $T_a = 37.8 \pm 1.85$°C), the bats used micro-torpor bouts only during the cooler, early morning hours (figure 1*b*; electronic supplementary material, figure S1B). However, when T_a exceeded normal body temperature, most bats (94%) stopped switching between micro-torpor and resting MR and extended their torpor bouts. This usually led to a significant increase in T_{skin} because active regulation of body temperature was suspended and thus T_{skin} approximated T_a. This pattern is contrary to the traditional view of torpor as cold response and we refer to it as ‘hot torpor’. Therewith we want to stress that the physiological underpinnings seem to be the same as in arctic species entering torpor, only the environmental conditions lead to different patterns. Individuals were torpid over the hottest time of the day and aroused at the beginning of their active phase when T_a and T_{skin} had decreased again to 33.5 ± 2.3°C and 36.0 ± 1.8°C, respectively. The extended torpor bouts lasted between 78 and 436 min (mean = 293.6 ± 101.2 min; n = 27 bouts) and T_{skin} passively increased with T_a up to a maximum value of 42.9°C. Thus, the bats applied a well-known response to cold conditions, i.e. entering torpor, while tolerating hyperthermia (figure 1*b*; electronic supplementary material, figure S1B). In contrast to adaptive hyperthermia used by e.g. camels, the bats actively depressed metabolism and bodily functions to a minimum during hottest body temperatures. This allows for negligible internal heat production and thus substantial water savings, making hot torpor an efficient

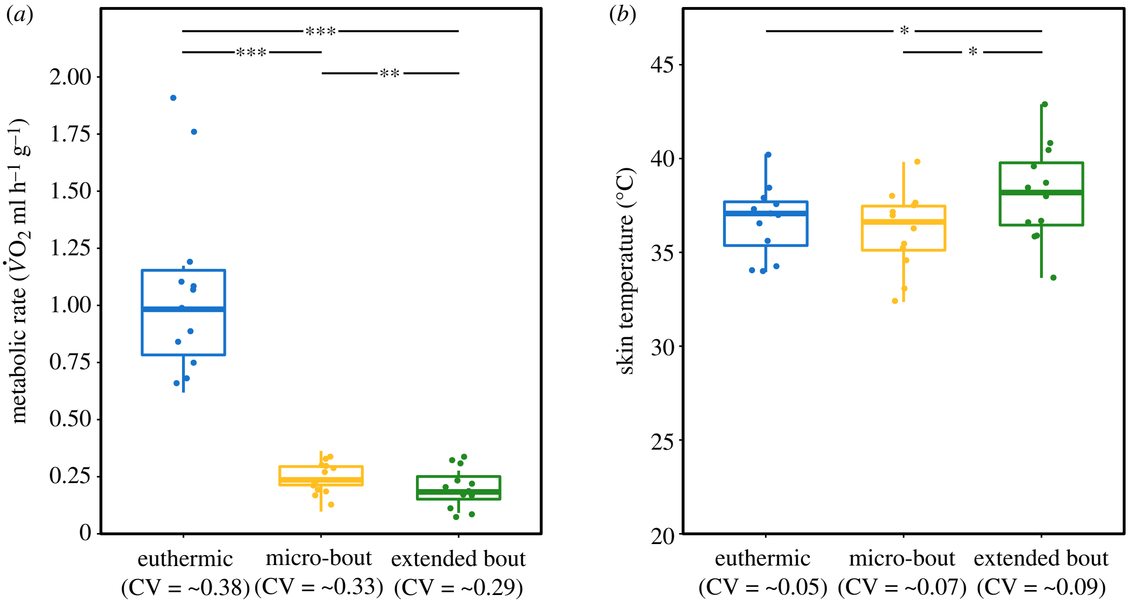

Figure 3. Depressed metabolism does not dictate skin temperature. Mass-specific metabolic rate as $\dot{V}O_2$ (MR, ml h^{-1} g^{-1}; (*a*); $n = 12$) and skin temperature (T_{skin},°C; (*b*); $n = 12$) of animals in three different physiological states: resting metabolism/euthermia (blue), micro-torpor bouts (yellow) and extended torpor bouts (green; centre line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range; points, all data included). The coefficient of variation (CV) is given in parentheses; significant differences are marked with asterisks (*$p \leq 0.05$; **$p < 0.01$; ***$p < 0.001$). (Online version in colour.)

option to withstand tropical heat. When small mammals are euthermic and confronted with T_a near the upper critical temperature, excess heat generated by metabolism or activity and the absorption of heat from the environment can quickly exceed their thermoregulatory capacities. Other tropical bats enter extended torpor, but only in the cooler morning hours and always accompanied by a reduction in body temperature, probably to save water in anticipation of responding to afternoon heat [33,34]. By contrast, *M. commersoni* entered hot torpor only under heat stress and maintained micro-bouts during cooler daytimes. This flexible response to high T_a might allow *M. commersoni* to thrive in the dry tropics in areas where buffered diurnal roosts, such as caves, are absent.

Over the inactive phase, we found that resting MR decreased with increasing T_a and plateaued between 31.9°C and 36°C (figure 2*b*). We could not determine the upper end of this plateau, because all individuals entered extended torpor above 36°C, but it is very likely to represent the thermal neutral zone of this population during the hot season (i.e. the range in which heat production and loss to the environment are balanced and no energy is needed to actively thermoregulate). In general, the warmer it became, the more individuals entered torpor (figure 2*a*). Above 36°C, thermoregulation at euthermia required excessive water consumption (see electronic supplementary material, video S1 for a thermal imaging video of a bat salivating its forearms extensively for evaporative cooling at $T_a = 36.9$°C) and we found bats to be torpid even at T_a of 41°C (figure 2*b*). Clearly, torpor was more beneficial than defending euthermia, suggesting the existence of an upper limit of tolerable euthermia.

4. High body temperature masks torpor

The magnitude of metabolic depression during torpor was high and the MR for both modes of torpor was significantly lower than resting MR, despite similar daytime temperatures (resting MR versus extended torpor: $t_{11} = 7.737$, $p < 0.001$; resting MR versus micro-torpor: $t_{11} = 7.434$, $p < 0.001$; table 1 and figure 3*a*). Although MR during extended torpor bouts was significantly lower than during micro-torpor bouts ($t_{11} = -3.427$, $p = 0.006$; table 1 and figure 3*a*), both modes of torpor resulted in a similar level of metabolic depression of 82.2 and 77.6%, respectively. This is close to the highest metabolic reductions seen during more continuous torpor in warm environments (25–84% [35–38]). By contrast, variation in corresponding T_{skin} values of these three different physiological states was less clear-cut (maximum mean difference 1.9°C; figure 3*b*). T_{skin} during micro-torpor bouts was similar to that of euthermia ($t_{11} = 1.052$, $p = 0.316$), but both were significantly lower than T_{skin} during extended hot torpor bouts (extended versus micro-torpor: $t_{11} = 2.511$, $p = 0.029$; extended torpor versus euthermia: $t_{11} = -2.425$, $p = 0.034$; table 1 and figure 3*b*). Consequently, although the reduction in metabolism during torpor was substantial, the magnitude of the MR decline did not dictate T_{skin}, regardless of torpor length.

Both modes of torpor could not have been detected with the classical temperature recordings often used in ecophysiological research because their impact on body temperature was marginal; the mean deviation of T_{skin} from euthermia was less than 2°C. Our study has identified two hitherto unknown modes of torpor, which suggest that the traditional concept of torpor needs to be re-considered. Torpor was originally defined as a substantial decline in MR and body temperature, mainly in response to low T_a [22,23]. However, a decline in body temperature is clearly not a necessity and we have shown that it may even increase when an animal is entering torpor. Thus, while a controlled depression in MR has always been a central part of torpor, a more universal definition should also specify that body temperature during torpor can be variable: it may approximate T_a in either direction (as per the traditional definition and as seen during hot torpor [24,37,39–41] or may remain stable as seen during micro-torpor bouts. Different environmental conditions can result in different patterns of torpor and study methods should recognize this. Researchers should not rely solely on traditional indicators of torpor such as body temperature and should strive to include other proxies for torpor, such as heart rate or oxygen consumption, particularly when studying endotherms in hot environments.

5. Conclusion

Our study dramatically broadens our knowledge on the fundamental concepts of thermal physiology and describes newly discovered options for mammals to cope with heat based on data from a free-living endotherm. We found that a tropical bat coped with daytime heat by using torpor (a response classically still associated with cold conditions), in novel ways: micro-torpor bouts at regular warm temperatures and hot torpor coupled with body temperature above euthermia during hot afternoon hours. This demonstrates the capacity of small mammals to survive rising ambient temperatures. Hot torpor allows *M. commersoni* to exist in habitats lacking well-buffered diurnal roosts and in regions that are even more arid. However, this response is not without risk: these bats could face lethal temperatures while in a torpid state if temperature increases too much, which would necessitate a premature re-arousal including evaporative cooling as a last resort. The inevitable upregulation of metabolic heat production during emergency arousals could easily push the individual beyond tolerable temperature maxima. Hot torpor is thus a high-risk response that relies on ambient temperature to not exceed certain maxima and cool again. Whether hot torpor occurs more widely in the dry tropics remains to be determined. Our discovery of variations of the classical pattern of torpor should spur studies of the responses of other species living near their thermal limits in an era of global warming and is also relevant for the potential use of induced torpor for medical purposes and possible future space travel near human euthermic levels.

Ethics. This study has been conducted under the 'Accord de Collaboration' between the Université d'Antananarivo (Département de Biologie Animale), Madagascar National Parks and the Universität Hamburg. We thank these authorities and the Ministère de l'Environnement, de l'Ecologie et des Forêts for support and project authorization. The research was approved by the Directeur du Système des Aires Protégées, Ministère de l'Environnement, Antananarivo (permit no. 296/17/MEEF/SG/DGF/DSAP/SCB.Re) and all described procedures comply with the current ethical regulations and laws of Madagascar.

Data accessibility. The data used for the analysis underlying the study are available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.80gb5mkpk [65].

Authors' contributions. K.H.D. and S.R. designed the study. S.R. carried out fieldwork, data analysis and wrote the first draft. K.H.D. commented, critically revised and edited the manuscript. S.R. and K.H.D. read and approved the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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