NEWS AND PERSPECTIVES



Leopard predation on wild Sichuan snub-nosed monkeys

Bin Yang¹ • James R. Anderson² • Ni-Na Gou¹ • Jun Luo³ • Bo Hong⁴ • Wei-Wei Fu¹ • Yong-Feng Chen⁵ • Wei-Feng Wang⁶ • Bao-Jia Cao⁶ • Shi-Yu Chen⁷ • Kai-Feng Wang¹ • Bao-Guo Li⁸

Received: 16 May 2023 / Accepted: 18 July 2023 / Published online: 9 August 2023 © The Author(s), under exclusive licence to Japan Monkey Centre 2023

Abstract

Predation is widely recognized as a powerful selective pressure on primate behavior and ecology, although knowledge of predator–prey relationships remains limited partly due to the rarity of directly observed attacks on primates. Here, we describe four confirmed or suspected instances of leopard (*Panthera pardus*) predation on free-ranging Sichuan (golden) snub-nosed monkeys (*Rhinopithecus roxellana*), a highly endangered colobine species endemic to China. We recorded predation events and the reactions of monkey group members. We suggest that the evolution of a multilevel society may be an adaptive response by Sichuan snub-nosed monkeys to the risk from leopards as well as other potential predators, one that balances the pressures of predation and intra-species competition and conflict.

Keywords Rhinopithecus roxellana · Panthera pardus · Predatory attacks · Alarm calls

- Shi-Yu Chen chenshiyu180236@163.com
- ⊠ Kai-Feng Wang wkf3231185@163.com
- Shaanxi Key Laboratory for Animal Conservation, Shaanxi Institute of Zoology, Xi'an 710032, Shaanxi, China
- Department of Psychology, Kyoto University Graduate School of Letters, Kyoto 606-8501, Japan
- Tianhuashan National Nature Reserve Administration of Shaanxi, Xi'an 710300, China
- Bio-Agriculture Institute of Shaanxi, Xi'an 710043, China
- Qiaobei National Forest Administration of Yan'an, Yan'an 727500, China
- Shaanxi Nature Reserve and Wildlife Management Station, Shaanxi Forestry Bureau, Xi'an 710082, Shaanxi, China
- Feline Research Center of National Forestry and Grassland Administration, College of Wildlife and Protected Area, Northeast Forestry University, Harbin 710069, China
- Shaanxi Key Laboratory for Animal Conservation, and College of Life Sciences, Northwest University, Xi'an 710069, Shaanxi, China

Introduction

Predation has long been considered to be a key selection pressure in primate behavioral evolution (Cheney and Wrangham 1987; Treves 1999; Zuberbühler and Jenny 2002; Miller and Treves 2011; Shultz et al. 2011). Group living is thought to have evolved as an anti-predator strategy in primates; it enhances collective alertness, dilutes the risk of predation for group members, and increases defensive capabilities against predators (van Schaik 1983; Isbell 1991; Boinski et al. 2000; Treves 2000; Hart 2007). In parallel, however, pressures arising from group living, such as increased competition for food and mates, and a greater likelihood of being detected by predators have also influenced the evolution of individual and social behaviors (Isbell 1991; Boinski et al. 2000; Majolo et al. 2008).

Large cats are known to prey on primates in all regions where both occur. Although immaturity and being on the ground may increase vulnerability to attacks by felids (discussed by Isbell 1994), many of the latter are excellent climbers and can also kill adults in trees. Numerous reports of predatory attacks in South America (e.g., Peetz et al. 1992; Ludwig et al. 2007; Matsuda and Izawa 2008; Santos et al. 2014) and Africa (e.g., Busse 1980; Boesch 1991; Tsukahara 1993; D'Amour et al. 2006; Isbell et al. 2018; Matsumoto-Oda 2015; McLester et al. 2019; Lin et al. 2020) testify to the danger posed to extant primates by felids. In



590 Primates (2023) 64:589–594

Asia, nonhuman primates are preyed upon by tigers (*Panthera tigris*, Karanth and Sundquist 1995; Støen and Wegge 1996; O'Brien et al. 2003), leopards (*Panthera pardus*, Seidensticker 1983; Naha et al. 2018), snow leopards (*Panthera uncia*, Lyngdoh et al. 2014), and clouded leopards (*Neofelis diardi*, Matsuda et al. 2008; Morino 2011). However, with rare exceptions (e.g., Zhang et al. 1999; Matsuda et al. 2008), most accounts concerning predation on Asian primates rely on indirect evidence, such as contents of the stomach or feces of likely predators. Reports of primates' responses to encounters with any potential predators are therefore useful for improving our understanding of predator–prey relationships (see, e.g., Isbell 1991; Tutin et al. 1981).

The Sichuan snub-nosed monkey (Rhinopithecus roxellana, also called the golden snub-nosed monkey) is an Endangered colobine species endemic to China, with a declining population of fewer than 20,000 individuals (Li et al. 2001; Li and Zhao 2007; Yongcheng and Richardson 2021), mainly distributed in the montane forests at 1000-4100 m above sea level in Hubei, Shaanxi, Sichuan, and Gansu provinces (Qi et al. 2011). Our study population in the Qinling Mountains of Shaanxi Province has been studied since 2011 (Zhang et al. 2006; Qi et al. 2011; Yang et al. 2016a, b, c, 2022, 2023). These monkeys live in large groups of 100-400 members, in a multilevel society in which a group contains several one-male units (OMU) and one or more all-male units (AMU). Each OMU contains a single resident adult male and several adult females, juveniles, and infants; an AMU contains only adult and subadult males.

Here, we present four confirmed or suspected incidences of leopard predation, and we describe the reactions of members of the group to which the victims belonged.

Observations and results

Between 2011 and 2021, we recorded one confirmed and three highly likely instances of leopards preying on a wild group of Sichuan snub-nosed monkeys. In each case, while the monkeys were being followed or observed by members of our research team, a leopard suddenly attacked the monkeys; more specifically, one monkey. Predation targets were three adult males from the AMU of the study group, and an old female member of an OMU. The prey individual had sometimes either strayed out of the group or, in the case of the old female, lagged behind the group as it moved. In all four incidents, members of the group emitted alarm calls ("WU-GA," transcribed as "Wuka" by Li et al. 1993, who provide a sound spectrogram). This is a general warning call, usually given in response to a disturbance in the environment, or danger. The monkeys did not attempt to mob the leopard, but ran and climbed quickly into the tree canopy, where they engaged in frequent grooming and huddling,

appearing tense and anxious. Our study site is in a mixed forest with brush, bamboo, grass, and rocks, all of which provide good hiding places for a leopard to wait undiscovered by monkeys before suddenly attacking.

Observation 1. Capture of an AMU older male

On March 23, 2013, at about 16:50, the monkeys left their feeding site and climbed higher up the mountain, feeding as they moved toward a sleeping site. The AMU headed the group movement, and one OMU trailed behind the rest of the group. At 17:23, a scream came from the front of the group, which caused many group members to start "WU-GA" alarm calling. An adult male was the first to emit alarm calls, followed by other adult males, adult females, and juveniles. The group ran quickly back in the direction they had come from and climbed high into trees, from where they continued alarm calling while looking in the direction of the screams. Some minutes later, our field assistants discovered a leopard dragging a dead male snub-nosed monkey along the ground, about 200 m away from the group. The distance between the leopard and the closest field assistant was approximately 150 m. At this time, the group was still occasionally alarm calling from the trees, and some adult females, juveniles, and infants were huddling, vocalizing, and grooming. The monkeys remained in the trees, feeding and grooming, after the leopard left. At about 18:10, they began to move in another direction. We established that an older adult male (more than 17 years old) was missing from the AMU; this male usually fed and moved around the group alone, and moved relatively slowly. We found no corpse in the area, but we found some leopard footprints.

Observation 2. Capture of an OMU older female

On July 10, 2019, at approximately 08:40, as the group moved forward to feed, one older female (estimated to be more than 16 years of age) moved very slowly and lagged about 300 m behind the group. The field assistants heard an "Aaa" cry from the female's position, and then silence. The distance between the incident and the closest field assistant was about 200 m. The monkey group gave "WU-GA" alarm calls (an adult female first, followed by adult males, adult females, and juveniles), and all members ran to the trees and looked in the direction from which the female's cry had come. After about 10 min, the group calmed down and continued to move forward to forage. About 6 h later, we went to see if we could find the old female. We saw blood on the ground, but no corpse. We searched in an area of about 100 m² and found some leopard footprints. An infrared automatic



Primates (2023) 64:589–594 591

camera about 1000 m away had taken a photo of a leopard earlier that morning (at 07:17; Fig. 1A).

Observation 3. Capture of an AMU adult male

On April 23, 2020, at about 16:15, the monkeys were feeding below trees by the river. However, one AMU adult male was alone, more than 400 m away; he had been following the group at a distance as he had been attacked by group members several times when he got closer. At 16:21, from the direction of the lone monkey we heard a sudden crash of vegetation and an "Aaa" cry and screams from the monkey, and then silence. The closest field assistant was about 150 m away from the incident. The group emitted many "WU-GA" alarm calls (an adult female first, and then other members of the group), climbed high into the trees, and moved further away. After moving more than 500 m, they stopped and occasionally looked back toward the direction of the incident. After about another 10 min the monkeys became calm again, fed, and started to move towards a sleeping site farther away. The next day, we climbed to the place where the lone monkey had screamed and found some bloodstains, but no corpse. We searched in an area of about 200 m² and found some leopard footprints. An infrared automatic camera about 500 m away from here had taken a photo of a leopard at 19:55 the previous evening (Fig. 1B).

Observation 4. Capture of an AMU adult male

On January 9, 2021, at about 11:10, most members of the monkey group were feeding at the roadside of a ravine. Suddenly, shrieks were heard coming from about 300 m above

the group. The monkeys ran away while "WU-GA" alarm calling (an adult female first, and then other members of the group), and most of them quickly climbed high into trees. They continued to scream and alarm call intermittently in the trees, looking in the direction of the shrieks. After more than 10 min, the group moved quickly down into the ravine and down river until they were more than 1000 m away, when they stopped moving and started to feed and groom. About an hour later, author BY and several field assistants went to check the place where the original sound had come from. They carried shovels, machetes, and other objects for selfdefense in case of danger. From a distance, they saw a leopard walking up the mountain. After the leopard disappeared, the team moved to the side of the road near to where the shrieks had come from, and found the corpse of a Sichuan snub-nosed monkey, devoured except for one leg, tail, two forelimbs, and back skin; the head, internal organs, and other body parts were missing. The remains of the carcass were consistent with consumption by a leopard. The remains were of an adult male monkey, and we subsequently confirmed that the AMU was missing one member. In a search in an area of about 200 m² around where the remains were found, we found some leopard footprints. Within the next 2 days an infrared camera about 1 km away photographed a leopard.

Discussion

These observations, made in the context of a long-term study, confirm that leopards kill and eat wild Sichuan snub-nosed monkeys in the Qinling Mountains. Although clouded leopards also exist at this site, as yet we have no record of them preying on the monkeys. Our report also presents the first detailed descriptions of how Sichuan snub-nosed monkeys react to predatory attacks by leopards. When



Fig. 1 Photos related to predation events



592 Primates (2023) 64:589–594

such encounters occurred, the monkeys emitted alarm calls, grouped closer together, and fled into the tree canopy. We saw nothing resembling mobbing behavior, but clear signs of fear and nervousness, with grooming and hugging behaviors likely employed to relieve the tension.

Infrared automatic cameras installed in the field frequently photographed leopards, indicating their prominence in the study area and their role as a predator of these monkeys. In each of the recorded attacks, the leopard had probably detected the researchers but continued preparing its attack on the monkeys, which would suggest habituation to researcher presence. Also, in each attack the victim was an isolated or a peripheralized individual, which supports the hypothesis that predators maximize their chance of success by preferentially targeting the most vulnerable individuals in the group (Hamilton 1971; Quinn and Cresswell 2006; Josephs et al. 2016). However, we do not rule out the possibility that even individuals within the group, where vigilance may be relatively relaxed, may also be the target of predatory attacks.

As in several other primate species, adult male Sichuan snub-nosed monkeys may be particularly vulnerable to attacks by leopards. Male primates are often seen around the periphery of the group, foraging or moving (patas monkeys: Burnham and Riordan 2012; geladas: Snyder-Mackler et al. 2012), making them potentially more likely targets for ambush predators. In the cases reported here, AMU males, particularly those who were attacked, were almost always on the periphery of the larger group; elderly or sick females may also become separated from the group and thus more likely to be attacked. Furthermore, adult males may be more likely than other age-sex classes to directly confront predators, putting themselves at greater risk of being killed (van Schaik et al. 2022, and see Nautiyal et al. 2023).

Our observations suggest that predation risk for the study group of monkeys varied with the nature of the vegetation: long grass and shrubs afford concealment for ambush predators (Loarie et al. 2013). All attacks reported in this study occurred in low-visibility microhabitats, consistent with other reports of ambush attacks by felids on primates (e.g., baboons: Cowlishaw 1994; chimpanzees: Boesch 1991).

If they spot a potential predator either lurking or approaching, the monkeys typically emit alarm calls and flee. In the cases described here, however, the monkeys emitted alarm calls only after an attack occurred, which suggests that they were unaware of the leopard's presence before the attack. Post-attack, they showed high levels of arousal and fear. Alarm calling thus appears to be an important anti-predation response of Sichuan snubnosed monkeys. These reactions highlight the monkeys'

perception of leopards as a source of serious danger. We hypothesize that predation, particularly by large felids, has been a selective factor in the formation of Sichuan snubnosed monkeys' large groups and multilevel society, adaptations that address not only the pressures of predation but also intra-species competition and conflict. The study of the effects of predation pressure on primates requires more scientific evidence, which is one direction of our future research on Sichuan snub-nosed monkeys.

Acknowledgements We thank Huangguanshan Nature Reserve for permission to carry out this study. We greatly appreciate our field assistants for indispensable support, especially students from the Primate Research Center of Northwest University China. We thank two anonymous reviewers and an editor for constructive comments.

Author contributions BY conceived of the study; BY, JRA, NNG, BH, SYC, JL, YFC and KFW analyzed the data; BY, NNG, BH, SYC, JL, YFC, WWF, WFW, BJC, BGL and KFW collected the data; BY and JRA wrote the manuscript, and all authors revised and approved the final manuscript.

Funding The study was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31020302), the Natural Science Foundation of China (32271564, 31730104), "Western Young Scholars" Project of the Chinese Academy of Sciences (XAB2020YW02), Natural Science Foundation of Heilongjiang Province (LH2023C038), Key Research and Development Project of Shaanxi (2022NY-105), Technology Program of Shaanxi Academy of Sciences, China (2017 K-09, 2018 K-10), Leopard Resource Special Investigation Project of Shaanxi Province. The funding organizations had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Data availability All data are available upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing

References

Boesch C (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220–242

Boinski S, Treves A, Chapman CA (2000) A critical evaluation of the influence of predators on primates: effects on group travel. In: Boinski S, Garber PA (eds) On the move: how and why animals travel in groups. University of Chicago Press, Chicago, pp 43–72

Burnham D, Riordan P (2012) Avoidance of mammalian predators by patas monkeys (*Erythrocebus patas*) in a risk landscape. Folia Primatol 83:288–298

Busse C (1980) Leopard and lion predation upon chacma baboons living in the Moremi wildlife reserve. Botsw Notes Rec 12:15–21

Cheney DL, Wrangham RW (1987) Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 227–239

Cowlishaw G (1994) Vulnerability to predation in baboon populations. Behaviour 131:293–304

D'Amour DE, Hohmann G, Fruth B (2006) Evidence of leopard predation on bonobos (*Pan paniscus*). Folia Primatol 77:212–217



Primates (2023) 64:589–594 593

Hamilton WD (1971) Geometry for the selfsh herd. J Theor Biol 31:295-311

- Hart D (2007) Predation on primates: a biogeographical analysis.
 In: Gursky S, Nekaris K (eds) Primate anti-predator strategies.
 Springer, Boston, MA, pp 27–59
- Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behav Ecol 2:143–155
- Isbell LA, Bidner LR, Van Cleave EK, Matsumoto-Oda A, Crofoot MC (2018) GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. J Hum Evol 118:1–13
- Josephs N, Bonnell T, Dostie M, Barrett L, Henzi SP (2016) Working the crowd: sociable vervets benefit by reducing exposure to risk. Behav Ecol 27:988–994
- Karanth KU, Sundquist ME (1995) Prey selection by tiger, leopard, and dhole in tropical forests. J Anim Ecol 64:439–450
- Li BG, Zhao DP (2007) Copulation behavior within one-male groups of wild *Rhinopithecus roxellana* in the Qinling mountains of China. Primates 48:190–196
- Li B, Chen F, Luo S, Xie W (1993) Major categories of vocal behaviour in wild Sichuan golden monkey (*Rhinopithecus roxellana*). Acta Theriol Sinica 13:181–187
- Li BG, He PJ, Yang XZ, Wei WK, Ren BP, Yang JY, Si KC, Liu YP (2001) The present status of the Sichuan snub-nosed monkey in the Qinling mountains of China, and a proposed conservation strategy for the species. Biosphere Conserv 3:107–114
- Lin B, Foxfoot IR, Miller CM, Venkatamaran VV, Fashing PJ (2020) Leopard predation on gelada monkeys at Guassa, Ethiopia. Am J Primatol. https://doi.org/10.1002/ajp.23098
- Loarie SR, Tambling CJ, Asner GP (2013) Lion hunting behaviour and vegetation structure in an African savanna. Anim Behav 85:899–906
- Ludwig G, Aguiar LM, Miranda JMD, Teixeira GM, Svobada WK et al (2007) Cougar predation on black-and-gold howlers on Mutum Island, southern Brazil. Int J Primatol 28:39–46
- Lyngdoh S, Shrotriya S, Goyal SP, Clements H, Heyward MW et al (2014) Prey preferences of the snow leopard (*Panthera uncia*): regional diet specificity holds global significance for conservation. PLoS ONE 9(2):e88349. https://doi.org/10.1371/journal.pone.0088349
- Majolo B, de Bortoli VA, Schino G (2008) Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim Behav 76:1235–1247
- Matsuda I, Izawa K (2008) Predation of wild spider monkeys at La Macarena, Colombia. Primates 49:65–68
- Matsuda I, Tuuga A, Higashi S (2008) Clouded leopard (*Neofelis diardi*) predation on proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. Primates 49:227–231
- Matsumoto-Oda A (2015) How surviving baboons behaved after leopard predation: a case report. Anthropol Sci 123:13–17
- McLester E, Sweeney K, Stewart FA, Piel AK (2019) Leopard (*Panthera pardus*) predation on a red-tailed monkey (*Cercopithecus ascanius*) in the Issa Valley, western Tanzania. Primates 60:15–19
- Miller LE, Treves A (2011) Predation on primates. In: Campbell CJ, Fuentes A, Mackinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective. Oxford University Press, Oxford, pp 535–547
- Morino L (2011) Clouded leopard predation on a wild juvenile siamang. Folia Primatol 81:362–368
- Naha D, Sathyakumar S, Rawat GS (2018) Understanding drivers of human-leopard conflicts in the Indian Himalayan region: Spatio-temporal patterns of conflicts and perception of local communities towards conserving large carnivores. PLoS ONE 13(10):e0204528. https://doi.org/10.1371/journal.pone.0204528

- Nautiyal H, Tanaka H, Huffman MA (2023) Anti-predator strategies of adult male Central Himalayan langurs (*Semnopithecus schistaceus*) in response to domestic dogs in a human-dominated landscape. Primates 64:361–379
- O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139
- Peetz A, Norconk MA, Kinzey WG (1992) Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. Am J Primatol 28:223–228
- Qi XG, Yang B, Garber PA, Ji WH, Watanabe K, Li BG (2011) Sexual interference in the golden snub-nosed monkey (*Rhinopithecus roxellana*): a test of the sexual competition hypothesis in a polygynous species. Am J Primatol 73:366–377
- Quinn JL, Cresswell W (2006) Testing domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in focks. Proc R Soc B Biol Sci 273:2521–2526
- Santos JL, Paschoal AMO, Massara RL, Chiarello AG (2014) High consumption of primates by pumas and ocelots in a remnant of the Brazilian Atlantic forest. Braz J Biol 74:632–642
- Seidensticker J (1983) Predation by Panthera cats and measures of human influence in habitats of south Asian monkeys. Int J Primatol 4:323–326
- Shultz S, Opie C, Atkinson QD (2011) Stepwise evolution of stable sociality in primates. Nature 479:219–222
- Snyder-Mackler N, Beehner JC, Bergman TJ (2012) Defining higher levels in the multilevel societies of geladas (*Theropithecus gelada*). Int J Primatol 33:1054–1068
- StøenWegge O-GP (1996) Prey selection and prey removal by tiger (Panthera tigris) during the dry season in lowland Nepal. Mammalia 60:363–373
- Treves A (1999) Has predation shaped the social systems of arboreal primates? Int J Primatol 20:35–67
- Treves A (2000) Theory and method in studies of vigilance and aggregation. Anim Behav 60:711–722
- Tsukahara T (1993) Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. Am J Primatol 29:1-11
- Tutin CEG, McGrew WC, Baldwin PJ (1981) Responses of wild chimpanzees to potential predators. In: Chiarelli AB, Corruccini RS (eds) Primate behavior and sociobiology. Springer, Berlin, pp 136–141
- van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120-144
- van Schaik CP, Bshary R, Wagner G, Cunha F (2022) Male antipredation services in primates as costly signalling? A comparative analysis and review. Ethology 128:1–14
- Yang B, Anderson JR, Li BG (2016a) Tending a dying adult in a wild multi-level primate society. Curr Biol 26:R403–R404
- Yang B, Zhang P, Garber PA, Hedley R, Li BG (2016b) Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) consume cicadas in the Qinling mountains, China. Folia Primatol 87:11–16
- Yang B, Zhang P, Huang K, Garber PA, Li BG (2016c) Daytime birth and postbirth behavior of wild *Rhinopithecus roxellana* in the Qinling mountains of China. Primates 57:155–160
- Yang B, Anderson JR, Mao M, Wang K, Li BG (2022) Maternal caretaking behavior towards a dead juvenile in a wild, multilevel primate society. Sci Rep 12:4780. https://doi.org/10.1038/ s41598-022-08660-9
- Yang B, Hong B, Anderson JR, Fu WW, Ren Y et al (2023) Dead trees as an indicator in tourism risk monitoring at primate ecotourism sites. Curr Zool 69:103–105
- Yongcheng L, Richardson M (2021) Rhinopithecus roxellana (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2021: e.T19596A196491153. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T19596A196491153.en



594 Primates (2023) 64:589–594

Zhang S, Ren B, Li B (1999) A juvenile Sichuan golden monkey (*Rhinopithecus roxellana*) predated by a goshawk (*Accipiter gentilis*) in the Qinling mountains. Folia Primatol 70:175–176

Zhang P, Watanabe K, Li BG, Tan CL (2006) Social organization of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling mountains, Central China. Primates 47:374–382

Zuberbühler K, Jenny D (2002) Leopard predation and primate evolution. J Hum Evol 43:873-886

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

