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Coiling During Male-Male Combat in Snakes: Differences Between Vipers and Other Groups, and Between Constrictors and Non-Constrictors

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Abstract

During male-male combat (MMC) in snakes, combatants often coil around each other. To determine whether there are differences in this behavior between different snake groups, we examined video footage of 100 instances of MMC in 49 snake species from six families. Results show that in Viperidae, MMC involves smaller numbers of loops than in the other three clades considered here (Pythonidae+Loxocemidae, Elapidae+Pseudoxyrhophiidae, and Colubridae). In Viperidae, coiling also seems to be an accidental result of other movements and does not involve coil tightening, whereas in the other three clades it appears to be deliberate and is often enhanced by coil tightening. The duration of coiling is shorter in the clade Elapidae+Pseudoxyrhophiidae (most of which are non-constrictors) and Viperidae (non-constrictors) than it is in Colubridae (many of which are constrictors) and the clade Pythonidae+Loxocemidae (constrictors). It is also shorter in non-constricting colubrids than in constricting colubrids, although the number of loops does not differ between the two groups. We conclude that coiling is of lesser importance for MMC in Viperidae than in the other three clades, and that maintaining loops during MMC is of lesser importance in non-constricting groups than in constrictors. These results show that differences in the amount of coiling during MMC in snakes follow phylogenetic lines. The videos used in this study were collected from social media and demonstrate that social media can be useful in collecting data for scientific studies.

Keywords: Behavior; combat; constriction; social media; Viperidae.

Introduction

In snakes of the clade Afrophidia (the clade that is phylogenetically bracketed by the boa and python clade and the clade Caenophidia—see Vidal et al., 2007), males engage in a combat ritual that often involves combatants coiling around each other and raising their foreparts, with each combatant attempting to push the other's foreparts down (Carpenter, 1977; Senter et al., 2014; Abu Baker et al., 2021; Senter, 2022). Detailed descriptions of male-male combat (MMC) have been published for numerous snake species (reviewed in Carpenter, 1977; Shine, 1978, 1994; Senter et al., 2014; Abu Baker et al., 2021; Senter, 2022), but the number of loops in the coil is usually not reported.

In published illustrations of MMC in snakes, the number of loops is usually as few as one to three in members of Viperidae (Shaw, 1948; Carpenter et al., 1976; Carpenter, 1977; Nishimura et al., 1983; Andrén, 1986; Schuett and Gillingham, 1989), whereas it is often greater than three in members of other families (Fleay, 1951; Bogert and Roth, 1966; Turner, 1992; Almeida-Santos et al., 1998; Muniz-da-Silva et al., 2013; Guedes et al., 2019; Valencia et al., 2020; Abu Baker et al., 2021). If this difference is due to a tendency among vipers to use fewer loops during MMC, and not just an artifact of having been photographed at moments when fewer loops were used than is usual for vipers, then coiling may be a component of MMC that is of lesser importance in Viperidae than in other snake clades. If so, this would be a major behavioral difference in MMC between vipers and other snakes. Such a difference would be an aspect of the evolution of snake behavior that has not previously been reported. We therefore sought to determine whether vipers use fewer loops during

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MMC than is the case in other snake clades, by examining footage of MMC in vipers and other snakes.

Coiling is an integral part of constriction, and previous studies have recorded that at least some snakes that use constriction to dispatch prey also employ active constriction during MMC (Martin, 1976; Barker et al., 1979; Guedes et al., 2019). We therefore also sought to determine whether differences exist in the degree of coiling during MMC in constrictors versus non-constrictors.

Materials and Methods

Videos

Previous studies have demonstrated that social media can be useful in the collection of data for scientific study (Miranda et al., 2016; Liberatore et al., 2018; Paterson, 2018; Maritz and Maritz, 2020; Abu Baker et al., 2021). Applying this principle, we searched YouTube (www.youtube.com) for footage of MMC in snakes. Many YouTube videos of snakes have misleading titles in which the species is misidentified, courtship is mistaken for combat (or vice versa), or an interaction is misidentified as combat when one snake is merely treating the other as an inanimate obstacle during locomotion in a confined space. We were therefore careful to include a video in the study only if we could confirm (or correct) the species identification, and only if it recorded combat. Combat can be distinguished from courtship in afrophidian snakes in that it usually includes attempts by the combatants to push down each other's raised heads (in non-lampropeltine snakes) or to pin each other's heads to the ground (in lampropeltines) (Senter, 2022). In contrast, courtship usually lacks such elements and includes a different suite of behavioral elements that usually includes chin-rubs and jerking of the head or body, often with the male performing such behaviors while his head moves along the dorsum of the female toward her anterior (Senter, 2022). As shown in Table 1, the footage included in the study comprises 100 instances of MMC in snakes of 49 species in six families: 29 instances in the family Viperidae, one instance in the family Loxocemidae, 12 instances in the family Pythonidae, 18 instances in the family Elapidae, one instance in the family Pseudoxyrhophiidae, and 39 instances in the family Colubridae.

Analysis

We compared both the number of loops and the duration of coiling during MMC between Viperidae and three other clades: Pythonidae+Loxocemidae (henceforth, P+L for concision), Elapidae+Pseudoxyrhophiidae (henceforth, E+P for concision), and Colubridae. We considered Pythonidae and Loxocemidae together as a single clade, because the two are closely related (Reynolds et al., 2014). Likewise, we considered Elapidae and Pseudoxyrhophiidae together as a single clade, because the two are closely related (Zaher et al., 2019).

To count the number of loops in each instance of MMC, we considered a single loop to be a complete turn (360º, as viewed down the long axis) of one snake's body around the other snake's body (Fig. 1). During MMC, the number of loops continuously changes as the snakes roll about their long axes, generating new loops near the head while uncoiling near the tail, and it occasionally happens that coiled snakes suddenly decouple with a violent whipping motion, reducing the number of loops to zero. In our comparison of the number of loops, we therefore considered only the maximum number of loops in each video (Table 1). For each of the four clades, we calculated the mean and standard deviation of the maximum number of loops among the included instances of MMC (Table 2). To determine whether a significant difference exists in the maximum number of loops between clades, we ran a one-way ANOVA.

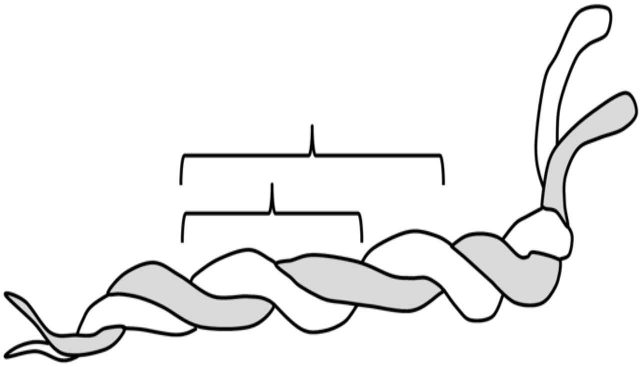

Figure 1. Method of counting loops. The white snake is coiled around the gray snake with four loops. The smaller bracket shows one loop of the white snake around the gray snake. The larger bracket shows 1.5 loops of the white snake around the gray snake.

To compare the duration of coiling between clades, we first calculated values that we called A, B, and C. For each clade, A is the total duration of all MMC footage in all the included videos of that clade, added together. For each clade, B is the total duration of MMC footage with coiling, in all the included videos of that clade, added together. For each clade, C is the total duration of MMC footage without coiling, in all the included videos of that clade, added together. For each clade, B / A × 100% = the percentage of MMC footage in which the combatants are coiled. We recorded that percentage for each clade in Table 2. To determine whether a significant difference exists in that percentage between clades, we used the Pearson chi-squared test to compare A and C between each pair of clades (Table 3).

To determine whether our data reveal a difference in the degree of coiling between colubrids that use constriction to dispatch prey (in our sample: *Dolichophis*, *Hierophis*, *Lampropeltis*, *Pantherophis*, *Pituophis*, *Spilotes*, *Zamenis*) and non-constricting colubrids (in our sample: *Dispholidus*, *Drymarchon*, *Masticophis*, *Philothamnus*, *Ptyas*), we repeated the analyses delineated above, comparing those two groups of colubrids.

We did not repeat the analyses to compare constricting vs.

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Table 1. Data on coiling during male-male combat in snakes, in the videos used in this study. DCoi = Duration of coiling in the footage. DCom = Duration of combat in the footage. MNC = maximum number of loops in the footage.

Family	Species	MNC	D Com	D Coi	Reference (author and year)
Xenopeltidae	*Xenopeltis unicolor*	2	18 s	18 s	Xtclueck, 2009
Pythonidae	*Aspidites melanocephalus*	5	123 s	123 s	NQ Dry Tropics NRM, 2016
	Morelia spilota	≥ 2	51 s	3 s	Afg Boii, 2018
	Morelia spilota	≥ 3	141 s	94 s	TomoNews US, 2016
	Morelia spilota	4	20 s	20 s	Browne Snake Removals, 2014
	Morelia spilota	≥ 3	105 s	30 s	Coldblooded Revolutions, 2015
	Morelia spilota	5	37 s	37 s	Andre, 2016
	Morelia spilota	4	146 s	146 s	Forgreenies, 2021
	Morelia spilota	6	118 s	118 s	Noosafifi, 2016
	Morelia spilota	7	639 s	639 s	Tisdall, 2017
	Morelia spilota	5	50 s	50 s	New York Post, 2018
	Morelia spilota	6	46 s	46 s	Linnett, 2014
	Morelia spilota	6	555 s	555 s	Majikfaerie, 2016
Viperidae	*Agkistrodon contrortrix* and *A. piscivorus*	1	200 s	30 s	Living Alongside Wildlife, 2016
	Agkistrodon contortrix	0	96 s	0 s	Louisiana Amphibian and Reptile Enthusiasts, 2018
	Agkistrodon piscivorus	1	136 s	4 s	Water Possum, 2015
	Agkistrodon piscivorus	0	104 s	0 s	Bruggemann, 2017
	Bitis arietans	0	93 s	0 s	Kruger Sightings, 2016
	Bitis arietans	≥ 2	226 s	10 s	Cape Snake Conservation, 2017
	Causus defilippi	0	12 s	0 s	Williams, 2016
	Daboia palaestinae	0	165 s	0 s	Reptiles, 2020
	Daboia russelii	≥ 2	83 s	4 s (very loose loops)	Searider1949, 2020
	Macrovipera lebetina	3	123 s	60 s	CityFreePress, 2019
	Montivipera xanthina	1	30 s	3 s	Gkousios, 2020
	Crotalus adamanteus	0	104 s	0 s	Browning, 2019
	Crotalus atrox	> 3	624 s	120 s	Ringo999999, 2009
	Crotalus atrox	2	54 s	3 s	Dana, 2010
	Crotalus atrox	0	83 s	0 s	FOX 5 Atlanta, 2016
	Crotalus atrox	3	254 s	10 s	Moser, 2018
	Crotalus atrox	2	65 s	2 s	SeanBlue622, 2011
	Crotalus durissus	2	88 s	76 s	Franco, 2015
	Crotalus horridus	3	75 s	68 s	Bauer, 2020
	Crotalus horridus	2	228 s	10 s	ThatAnimalGuy, 2018
	Crotalus mitchellii	0	24 s	0 s	Desert Museum, 2015
	Crotalus oreganus	3	57s	50s	Nature Picture Library, 2019
	Crotalus oreganus	0	28 s	0 s	San Jacinto Trail Report, 2017a
	Crotalus oreganus	2	33 s	6 s	San Jacinto Trail Report, 2017b
	Crotalus oreganus	2	69 s	62 s	Crabbe, 2018
	Crotalus ruber	1	35 s	1 s	Greg L, 2014
	Crotalus viridis	3	73 s	73 s	Paul Goins, 2014
	Crotalus viridis	2	51 s	30 s	Joshua Anderson, 2017
	Sistrurus miliarius	2	417 s	165 s	Crotalusco, 2008

Table 1. Continued.

Family	Species	MNC	DCom	DCoi	Reference (author and year)
Elapidae	*Demansia psammophis*	10	129 s	129 s	Still waters, 2012
	Demansia vestigiata	3	68 s	68	ParksAustralia, 2013
	Dendroaspis angusticeps	8	30 s	30 s	Best of Africa, 2017
	Dendroaspis angusticeps	9	880 s	540 s	Beach Bumz, 2016
	Dendroaspis polylepis	5	65 s	50 s	Kruger Sightings, 2015
	Dendroaspis polylepis	5	71 s	25 s	Kruger Sightings, 2017
	Micrurus frontalis	10	137 s	137 s	Peret, 2017
	Micrurus ibiboboca	6	47 s	47 s	Kemp, 2015
	Naja mossambica	3	185 s	50 s	Daily Mail, 2018
	Naja naja	≥ 7	530 s	180 s	Kumar, 2018
	Notechis scutatus	5	98 s	27 s	Snake Master, 2019
	Ophiophagus hannah	4	73 s	30 s	Madras Cr. Bank Trust, 2019
	Ophiophagus hannah	1	40 s	1 s	Felis Creations TV, 2014
	Ophiophagus hannah	≥ 7	757 s	60 s	Dinkelman, 2018
	Pseudechis guttatus	6	51 s	51 s	MH Outdoors, 2019
	Pseudechis porphyriacus	5	98 s	48 s	Maximus Marcus, 2017
	Pseudechis porphyriacus	≥ 15	183 s	80 s	Caters Clips, 2019
	Pseudonaja textilis	≥ 3	1384 s	300 s	Meek-and-wild, 2016
Pseudoxyrhophiidae	*Leioheterodon madagascariensis*	10	219 s	166 s	Trebbor Frog, 2015
Colubridae	*Dispholidus typus*	≥ 8	64 s	64 s	Nathan, 2020
	Dolichophis jugularis	≥ 5	158 s	158 s	Reptiles, 2021a
	Dolichophis jugularis	?	17 s	17 s	Reptiles, 2021b
	Dolichophis jugularis	4	20s	19 s	Reptiles, 2021c
	Dolichophis jugularis	5	?	?	Reptiles, 2021d
	Dolichophis jugularis	5	103 s	103 s	Reptiles, 2021e
	Dolichophis jugularis	5	14 s	14 s	Reptiles, 2021f
	Dolichophis jugularis	5	12 s	12 s	Reptiles, 2021g
	Dolichophis jugularis	4	23 s	23 s	Reptiles, 2021h
	Dolichophis jugularis	≥ 3	97 s	97 s	Reptiles, 2021i
	Dolichophis jugularis	4	36 s	36 s	Reptiles, 2021j
	Drymarchon corais	0	22 s	0 s	GeorgiaWildlife, 2014
	Drymarchon corais	0	48 s	0 s	Smith, 2011
	Hierophis viridiflavus	9	314 s	296 s	Bramham, 2008
	Hierophis viridiflavus	≥ 6	92 s	60 s	Gary and Rachel, 2015
	Hierophis viridiflavus	4	164 s	164 s	Canary Honey, 2014
	Lampropeltis californiae	0	118 s	0 s	Wetherbee, 2017
	Lampropeltis californiae	6	181 s	181 s	Douglas Collins, 2016
	Lampropeltis getula getula	11	48 s	48 s	Cimarronsc, 2008
	Lampropeltis holbrooki	5	184 s	152 s	Martin, 2016
	Lampropeltis triangulum	≥ 3	120 s	20 s	lukeovcrashcourse, 2017
	Lampropeltis triangulum	2	153 s	153 s	Vegged Out, 2020
	Masticophis flagellum	0	164 s	0 s	Favor, 2018
	Masticophis flagellum	7	196 s	182 s	Jacquiisaacson, 2008
	Pantherophis alleghanensis	≥ 5	247 s	40 s	Lewis, 2014
	Philothamnus semivariegatus	4	17 s	16 s	Marais, 2013
	Pituophis catenifer	≥ 5	60 s	25 s	Easter, 2016
	Pituophis catenifer	0	61 s	0 s	Webetubing, 2007
	Pituophis catenifer	3	91 s	91 s	Brennadl, 2019
	Pituophis catenifer	6	776 s	776 s	Robinson, 2014
	Ptyas mucosus	≥ 5	351 s	351 s	Nilaview, 2015
	Ptyas mucosus	≥ 4	143 s	20 s	Nat Geo Wild, 2018
	Ptyas mucosus	7	22 s	22 s	Randadath, 2012
	Ptyas mucosus	0	44 s	0 s	Krishnan, 2016
	Ptyas mucosus	7	124 s	124 s	Chavhan, 2015
	Ptyas mucosus	5	129 s	119 s	Dhinith S, 2018
	Ptyas mucosus	5	121 s	113 s	Reddy, 2020
	Spilotes pullatus	8	154 s	154 s	Mebert, 2017
	Zamenis longissima	5	618 s	420 s	Living Zoology, 2020

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Table 2. Data on coiling during MMC for each group.

Group	*A*: total duration (in seconds) of MMC footage	*B*: total duration (in seconds) of MMC footage with coiling	Percentage of *A* that consists of *B*	Mean maximum number of loops, and standard deviation
P+L	2049	1879	92	4.5 ± 1.61
Viperidae	3240	487	15	1.4 ± 1.15
E+P	5045	1853	37	6.4 ± 3.34
Colubridae	5306	4070	77	4.5 ± 2.61
Colubridae: non-constrictors[1]	1445	1011	70	4.0 ± 2.39
Colubridae: constrictors	3861	3059	79	4.72 ± 3.03

[1] *Dispholidus, Drymarchon, Masticophis, Philothamnus, Ptyas*

Table 3. Results of Pearson's chi-squared tests comparing A and C (see Materials and Methods) between pairs of clades.

	Viperidae	E+P	Colubridae
P+L	$X^2 = 2984.662$, $p < 0.0001$	$X^2 = 1766.3104$, $p < 0.0001$	$X^2 = 215.035$, $p < 0.0001$
Viperidae		$X^2 = 458.3458$, $p < 0.0001$	$X^2 = 3074.3047$, $p < 0.0001$
E+P			$X^2 = 1688.3559$, $p < 0.0001$

non-constricting members of E+P, due to a low sample size of constricting species in our sample of the clade. The E+P footage used here includes one instance apiece of MMC in two elapid species that are known to use constriction to dispatch prey: *Pseudonaja textilis* and *Demansia psammophis* (Shine and Schwaner, 1985). However, in the latter species, only juveniles are known to constrict prey (Shine and Schwaner, 1985), which reduces our sample size of videos of E+P species that constrict prey as adults, to only one video.

Results

During the collection of data from videos, it became evident that coiling in vipers is often an accidental result of the movements involved in the combat dance, that coil tightening is rare, and that active attempts to maintain a coil are also rare. In contrast, coiling in the other clades often appears to be deliberate, coil tightening is common, and the combatants often actively attempt to maintain large numbers of loops around each other, especially posteriorly.

As shown in Table 2 and Fig. 2, the maximum number of loops per instance of MMC tends to be lower in the Viperidae than in the other three clades ($\bar{x} = 1.4$ in Viperidae; $\bar{x} = 4.5$ in P+L; $\bar{x} = 6.4$ in E+P; $\bar{x} = 4.5$ in Colubridae) (Table 2).

One-way ANOVA revealed that a significant difference exists in the mean number of loops between at least two clades (F(3, 95) = 18.9407, p = 1.0389e-09). Tukey's HSD test for multiple comparisons found that the mean number of loops is significantly different between Viperidae and P+L ($p = 0.0011826 < 0.01$), between Viperidae and E+P ($p = 0.0010053 < 0.01$), between Viperidae and Colubridae (p 0.0010053 < 0.01), and between E+P and Colubridae ($p = 0.0199122 < 0.05$). It found no significant difference in the mean number of loops between P+L and E+P (p = 0.0994088) or between P+L and Colubridae (p = 0.8999947).

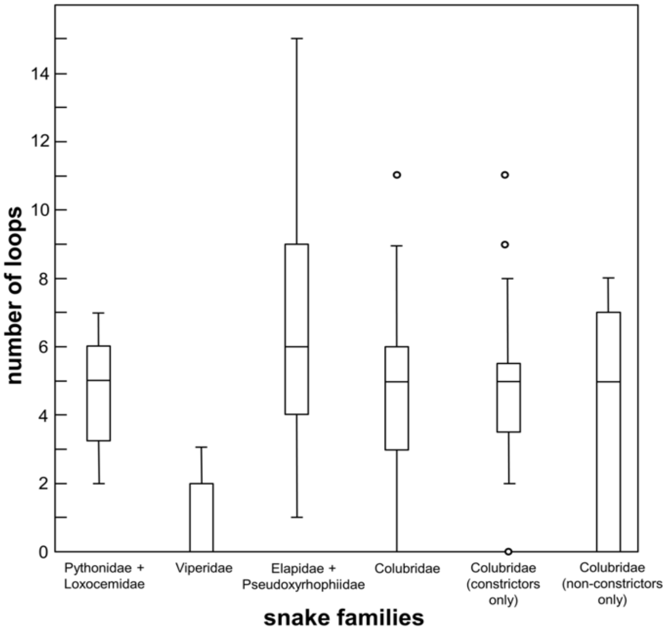

Figure 2. Box-and-whisker graph of maximum number of loops in each instance of MMC, for each clade. Outliers are represented by small circles beyond the box and whisker.

Pearson's chi-squared test found that between every pair of clades considered here, there is a significant difference in the duration of coiling during MMC (Table 3).

Our analysis uncovered no significant difference in the number of loops between constricting and non-constricting colubrids. For the maximum number of loops per instance of MMC, the mean is 4.0 in non-constricting colubrids and 4.72 in constricting colubrids (Table 2). One-way ANOVA found no significant difference between the maximum number of loops between the two groups ($F = 0.6461$, $p = 0.4268$). However, Pearson's chi-squared test found a significant difference in the duration of coiling between constricting and non-constricting colubrids ($X^2 = 50.4899$, $p < 0.0001$).

Discussion

Previous studies have shown that there are differences in MMC among different clades of snakes. For example, in the colubrid clade Lampropeltini, high head-raising (present in other afrophidian clades) is absent from the MMC repertoire, and dorsal bowing of the body (absent in other afrophidian clades) is present (Abu Baker et al., 2021; Senter, 2022). Biting during MMC is also more prevalent in Lampropeltini that it is in other snake clades (Abu Baker et al., 2021; Senter, 2022). Also, MMC is often absent in snake clades that subdue prey by means other than venom or constriction (Schuett et al., 2001). However, previous studies have not explored differences in the degree of coiling between snake clades. The results of this study therefore elucidate an aspect of snake MMC that has not previously been elucidated. As this study shows, the lesser importance of coiling in vipers is a real difference in MMC between Viperidae and other snake clades.

Furthermore, this study shows that the duration of coiling during MMC differs between snake groups, with the highest durations occurring in constrictors (Pythonidae+Loxocemidae and colubrid constrictors) and lower durations in E+P and non-constricting colubrids. This study is the first to document and quantify these differences. As such, it adds to current knowledge of variation in MMC across the clade Serpentes. It is interesting that in applying constriction to their opponents, constrictors incorporate their main prey-killing technique into MMC. In contrast, vipers usually do not incorporate their main prey-killing technique (a venomous bite) into MMC (Senter, 2022). It is also interesting that in colubrid MMC, constrictors remain coiled longer than non-constrictors but do not use a greater number of loops than non-constrictors. This suggests that if coiling during MMC has become reduced through evolution in non-constricting colubrids, the duration of coiling is more vulnerable to evolutionary reduction than is the number of loops in a typical coil. It further suggests that those two parameters may undergo separate evolutionary trajectories and are therefore not constrained to evolve in tandem.

Conclusions

Our results show that vipers tend to use fewer loops than do members of the other three clades considered here. Vipers also tend to spend less time coiled around opponents during MMC than do members of the other three clades considered here. In short, coiling is of less importance for MMC in vipers than in other snake clades. The predominantly accidental nature of the coiling in vipers and their apparent unconcern for maintaining or tightening the loops underscores the lack of importance of coiling as a component of combat in Viperidae.

Our results also indicate that the maximum number of loops per instance of MMC is not significantly different between P+L and Colubridae, nor between P+L and E+P. However, they also indicate that the duration of coiling during MMC differs between all three of these clades, with longer durations in clades in which constriction is common (P+L and Colubridae). Likewise, our results indicate a significant difference in the duration of coiling between constricting and non-constricting colubrids (the duration is longer in the constrictors), but not in the maximum number of loops per instance of MMC.

Further, this study demonstrates that social media can play an important role in the collection of data for scientific study. Previous studies that have incorporated data collection via social media have also confirmed that social media can be useful for that purpose (e.g. Miranda et al., 2016; Liberatore et al., 2018; Paterson, 2018; Maritz and Maritz, 2020; Abu Baker et al., 2021). This study provides another instance of it.

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