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36 **Abstract:**

37 Smooth-coated otters (*Lutrogale perspicillata*) are inhabitants of the waterways of India and  
38 Singapore. Otter families typically consist of a single mating pair with mature, nonbreeding  
39 siblings living in family groups, or “romps”. We note here the presence of multiple  
40 reproductive female otters within some romps, as well as the possible existence of simultaneous  
41 litters by different mothers. This phenomenon has not been recorded among *L. perspicillata*  
42 before. Here we address possible influences leading to multiple reproductive females within  
43 romps of smooth-coated otters, including inclusive fitness, incomplete suppression of  
44 reproduction, and existing in an urban environment. The numerous, recurring observations of  
45 multiple reproductive females warrant further investigation; while uncommon, this  
46 phenomenon is not as rare as once thought.

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48

49

50 **Introduction:**

51 The evolution of communal and cooperative breeding systems are long-studied topics in animal  
52 behavior (e.g., Hayes 2000; Gilchrist 2006; Clutton-Brock 2009; Lukas and Clutton-Brock  
53 2012a, 2012b; Federico et al. 2020), with various species relying on such systems to raise  
54 young and maintain their territories. Cooperative breeding systems are uncommon in  
55 mammals, present in about 5% of mammalian species (Lukas and Clutton-Brock 2012b). In  
56 these species, a group typically includes a single mating pair, while other members provide  
57 alloparental care for the offspring of the mating pair (Lukas and Clutton-Brock 2012b).  
58 Nonbreeding adults can be prevented from reproducing via suppressive means, such as  
59 infanticide or hormonal cues (Clutton-Brock 2009). The nonbreeders remain with the family  
60 into adulthood, often until either one or both of the breeding pair dies, are ousted, or the  
61 offspring disperse and form their own groups (Lukas and Clutton-Brock 2012b). In some  
62 species, such as giant otters (*Pteronura brasiliensis*), aging females are known to cease  
63 reproduction and become “grandmothers”, with younger females taking over the role of  
64 reproduction while the former matriarch provides parental care (Davenport 2010).

65

66 In contrast, communal breeding entails systems where multiple females in a group breed and  
67 share resources in raising young (e.g., Hayes 2000; Lukas and Clutton-Brock 2012b; Federico  
68 et al. 2020). Here reproductive suppression does not occur, and individuals can reproduce once  
69 sexually mature. Banded mongooses (Gilbert 2006) and numerous rodent species (Hayes 2000)  
70 are examples of communal breeders. Females in some rodent species may even share milk with  
71 non-offspring, i.e., allonurse them, which can be extremely costly (Hayes 2000). Benefits of  
72 communal breeding include improved thermoregulation (huddling), defense, and foraging  
73 (Hayes 2000).

74

75 While allonursing is common in communally breeding species (MacLeod et al. 2013), in  
76 cooperative systems where non-dominant females are generally not sexually active (Lukas and  
77 Clutton-Brock 2012b), allonursing can be especially costly to the nonbreeding individuals.  
78 Most potential benefits of allonursing among cooperative breeders seem to be kin-based, where  
79 dispersal is heavily delayed, and where groups consist mostly of close relatives (Lukas and  
80 Clutton-Brock 2012b, Federico et al. 2020). Among meerkats, allonursing females are often  
81 subordinate females who have recently been pregnant and return after having been evicted from  
82 the group (MacLeod et al. 2013).

83

#### 84 **Multiple reproductive females in smooth-coated otters:**

85 Smooth-coated otters (*Lutrogale perspicillata*) are medium-sized predators (up to 10 kg) that  
86 are largely socially monogamous, living in family groups, or “romps”, that may include a  
87 dominant breeding pair (the “matriarch” and “patriarch”) and as many as 22 individuals from  
88 successive broods of offspring (personal observations). They perform several group-level  
89 behaviors, including group territorial defense, group defense against potential predators, and  
90 group foraging (personal observations). They can be the apex predator in many ecosystems.  
91 Smooth-coated otters live in Asia, especially South and Southeast Asia, often inhabiting  
92 mangroves, coastal rivers, and other waterways, including ones in Western India and  
93 Singapore.

94

95 Here we collate observations of romps of smooth-coated otters with what appear to be multiple  
96 reproductive females (**MRF**). We include data from camera traps, from our own personal  
97 observations, from interviews with other otter watchers, and gleaned from social media.  
98 Although social media is comprised of largely *ad libitum* observations (Altmann 1974), it is  
99 useful for recording uncommon events (Nelson and Fijn 2013). We include observations from

100 rural sites in Goa, India, and from Singapore, one of the most densely populated countries in  
101 the world. Smooth-coated otters returned to Singapore after decades of absence (Khoo and Lee  
102 2020). Singapore now has at least eleven distinct romps living in the city's highly canalized  
103 waterways (Khoo and Sivasothi 2018). Some families are extremely habituated to humans, and  
104 a loose network of photographers, naturalists, students, and other scholars watch some romps  
105 almost daily. Territories are fairly stable, week to week, and observers can distinguish most  
106 families based on their locations, the number of animals in a group, and individual markings  
107 on some otters. We also include evidence from a necropsy of a dead otter pup found in  
108 Singapore.

109

110 We consider any of the following criteria to indicate multiple females exhibiting some  
111 reproductive activity within a romp: 1) pups of substantially different sizes and stages of  
112 development, indicating they are not from the same litter; 2) more than one female in a romp  
113 with enlarged nipples; 3) more than one female in a romp actively nursing pups. We consider  
114 the presence of females with enlarged nipples as likely evidence of recent birth or lactation.

115

116 Although smooth-coated otters primarily practice cooperative breeding (Hussain 1996; Hwang  
117 and Larivière 2005; Sivasothi and Khoo 2018b), we note eight instances of romps with MRF  
118 between 2015 and 2021: two in Goa and six in Singapore, with one Singaporean romp having  
119 had three MRF events over four years (**Table 1**).

120

121 **Table 1.** Observations of romps with multiple reproductive female smooth-coated otters in Goa,  
122 India, and Singapore.

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Location	Approx. coordinates	Family	Approx. date	Observation
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Amona, Goa, India	15.53°, 73.97°	NA	Dec. 2015 – Jan. 2016	4-9 otters, 2 lactating females
Britona, Goa, India	15.52°, 73.86°	NA	Feb. 2015	9 otters, 2 lactating females
Kallang River Basin, Singapore	1.30°, 103.87°	Bishan	Dec. 2017	12 otters, 2 lactating females. Temporary eviction of matriarch in early 2019.
Ulu Pandan River, Singapore	1.32°, 103.77°	Pandan	Jun. 2019	22 otters, 9 pups, 2 lactating females
Singapore River, Singapore	1.29°, 103.84°	Singapore Botanic Gardens (SBG)	Nov. 2019	7 otters, 4 pups, 2 lactating females
Kallang River Basin, Singapore	1.30°, 103.87°	Bishan	Nov. 2020	18 otters, 7 pups, 2 lactating females
Singapore Botanic Gardens	1.30°, 103.82°	Zouk	Dec. 2020	13 otters, 7 pups, 2 lactating females
Kallang River Basin, Singapore	1.30°, 103.87°	Bishan	May 2021	22 otters, 5 pups, 3 lactating females

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123 **Note:** Singapore romps are named for the first location where the families were observed. Notice the  
124 Bishan family has had three observed cases of MRF over four years, including a case with 3 lactating  
125 females.

126

127 Members of the research organization Wild Otters placed video camera traps at several otter  
128 latrine (“spraint”) sites, including in Amona and at an otter holt in Britona (**Table 1**). Both  
129 locations include mangrove habitats with abundant prey for smooth-coated otters. Both  
130 observations of MRF in India entailed short videos from these camera traps. In each case a  
131 romp of otters included two different females that had substantially enlarged nipples (e.g., Fig  
132 1E).

133

134 The earliest observation of MRF in Singapore occurred about two weeks after the Bishan  
135 matriarch’s 4th litter emerged in late 2017 (Khoo and Sivasothi 2018). Otter watchers spotted  
136 a subordinate female (“Crazy Sis”) of the Bishan family carrying a small pup. The emerging  
137 pups were much larger and probably weeks older; smooth-coated otter pups typically emerge  
138 from their holts around six weeks after birth and start to swim about a week later (Khoo and  
139 Sivasothi 2018). Days later, a small pup was found dead near the Bishan holt. A necropsy  
140 concluded the cause of death was multiple bite wounds from conspecifics (Fig 1D). Although  
141 the necropsy suggests territorial conflict as the cause (Supp. Fig 1), and the Bishan family had  
142 been involved in a series of intense and lethal territorial disputes months prior (personal  
143 observations), we know of no territorial conflict between Bishan and other romps at the time  
144 of the pup’s death. A possible cause of death is wounds inflicted by adults in the Bishan romp.  
145 If so, this is the only recorded instance of infanticide in smooth-coated otters by family  
146 members.

147



148 In May 2019, the Pandan romp consisted of nine adults and nine pups, an unusually large  
149 number of pups, given a previously recorded mean litter size of 4.86 (Khoo and Sivasothi  
150 2018); these pups likely belonged to litters from two females. June 2019 photographs  
151 confirmed the existence of two MRF (Table 1; Supp. Table 1), although there was no indication  
152 of which female each pup belonged to.

153

154 The Singapore Botanic Garden (SBG) family originally consisted of two same-aged sisters  
155 from the Marina family and a male of unknown origins. In November 2019, one sister gave  
156 birth to one pup, then the second sister (“Lightbulb”) gave birth to three more (Table 1; Supp.  
157 Table 1). This romp has since suffered several mortalities, and Lightbulb disappeared in 2020.  
158 The matriarch now has a new partner, giving birth to four pups in April 2021.

159

160 In late 2020, the Bishan matriarch had her seventh litter. Weeks after her pups emerged, a much  
161 smaller pup was spotted with one of the subordinate adult females in the romp (Table 1). The  
162 family abandoned the pup, which had yet to open its eyes when it was euthanized by the  
163 authorities. There is no evidence of infanticide (Supp. Table 1). The mother of this pup gave  
164 birth to two pups later in March 2021, along with 3 from another subordinate female at the  
165 same time (Table 1). The matriarch and both subordinate females have been observed nursing  
166 these 5 new pups, (e.g., Fig1A-C; File S1) and in May 2021 the romp had 22 members (Supp.  
167 Table 1).

168

169 In December 2020, the Zouk romp displayed MRF, with the matriarch and a daughter  
170 (“Flowerhead”) each having enlarged nipples (Table 1). Although it is uncertain whether the  
171 group of seven Zouk pups were from one or two mothers, pups were observed nursing from  
172 both females (Supp. Table 1)

173

## 174 **Discussion**

175 The repeated occurrence of MRF in India and Singapore suggests that these events are  
176 uncommon but not especially rare. We review several hypotheses, including ones related to  
177 incomplete suppression of reproduction, inclusive fitness, and urban environments (**Table 2**).

178

179 **Table 2.** Hypotheses for the cause of multiple reproductive otter females

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<b>Hypothesis</b>	<b>Rationale</b>
<i>Incomplete suppression</i>	
Large group size	Dominant females are unable to effectively suppress reproduction among subordinate females (Hackländer et al. 2003).
Synchronized birthing	Subordinates avoid suppression by synchronizing the timing of their births with the dominant female (Cant et al. 2014).
Old or injured breeding adults	Dominant females become incapable of effectively suppressing reproduction due to age or injury.
<i>Inclusive fitness</i>	
Relatedness	Dominant females are less likely to suppress subordinates they are related to (Hackländer et al. 2003).

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Low cost

Allonursing may evolve in cooperative breeding systems when the cost is sufficiently low (MacLeod and Lukas 2014).

### *Urban environments*

Resource abundance

Subordinate females can reproduce with little fitness consequence to the dominant female, due to abundant resources.

Urban ecosystem benefits

The urban environment facilitates delayed dispersal and reduces suppression efforts.

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180

181

### 182 **Hypotheses for multiple reproductive females**

183 The first evolutionary step towards communal or cooperative breeding may be delayed  
184 dispersal, and the distinction separating the two breeding systems is reproductive suppression  
185 (Federico et al. 2020). When successful, suppression enables the dominant mating pair to  
186 monopolize breeding and to recruit other individuals to provide various levels of care for the  
187 offspring. Suppression can occur via several means, such as hormonal cues, aggression and  
188 physical violence towards subordinates, and infanticide (Spiering et al. 2010; Lukas and  
189 Huchard 2019). Suppression is present in giant (*Pteronura brasiliensis*) and small-clawed  
190 (*Aonyx cinereus*) otters (Groenendijk et al. 2014; Perdue et al. 2013), which are also  
191 cooperative breeders. Notably, MRF has been recorded in giant otters, although this is limited  
192 to one observation (Leuchtenberger and Mourao 2009).

193

194 In marmots, the frequency and severity of agonistic suppression varies depending on the  
195 relatedness of the matriarch to other females in the group (Hackländer et al. 2003).  
196 Furthermore, as group size increases, dominant females are less fertile, suggesting there is a  
197 cost associated with policing behavior (Hackländer et al. 2003). Dominant female banded  
198 mongooses also police subordinate female reproduction. Subordinate females appear to  
199 synchronize births to increase pup survival rates; dominant females are less likely or less  
200 capable of committing infanticide, leading to higher survivorship, while subordinate females'  
201 pups born before the dominant female's pups are more often killed (Cant et al. 2014). This  
202 pattern suggests that dominant females are not able to effectively distinguish their own  
203 offspring from others when they are of similar age.

204

205 We report evidence of what may be policing by the Bishan dominant female of a subordinate  
206 female's pup (Fig 1D). Smooth-coated otters sometimes violently evict other otters from  
207 romps. After several other social changes to the Bishan family, including the death of the  
208 Bishan patriarch and the subsequent takeover of the romp by another adult male ("Scarface"),  
209 a Bishan daughter ("Crazy Sister") evicted the Bishan matriarch from the romp, before  
210 apparently being evicted herself by another subordinate ("White Tip"). These conflicts, which  
211 occurred between April and July 2019, ended with all three females rejoining the romp at  
212 different times, remaining until present (Supp. Table 1). Such conflict suggests a dynamic like  
213 that of mongooses (MacLeod et al. 2013), where allonursing may follow pregnancy, eviction,  
214 and return, of subordinate females. We suspect policing may also have occurred with the birth  
215 of the small Bishan pup, although there was no actual physical injury, and the subordinate  
216 female abandoned the pup without any known conflict.

217

218 Large smooth-coated otter romps may consist of two, three, or more, successive broods of  
219 offspring, and the dominant pair may be several years old. Therefore, one possibility for MRF  
220 is that the matriarch is simply too old or the romp too large to effectively suppress reproduction.  
221 Two of the Singapore otter families (Bishan, Pandan) were among the largest, each with 22  
222 members at their peaks. However, small, young romps such as SBG have been observed with  
223 MRF, and the Indian romps experiencing MRF were not especially large, suggesting aging  
224 matriarchs or overly large romps are unlikely to be the only cause of MRF. In SBG's case, the  
225 subordinate female even had more pups (three) than the presumed dominant female (one).  
226 Other factors may contribute to MRF, perhaps including stress and injury associated with  
227 violent group territorial conflict between rival romps. However, while such "otter wars" do  
228 occur between romps of Singapore's otters, these territorial disputes have not been observed in  
229 all cases of MRF. Violent territorial defense may contribute to MRF but it too is unlikely to be  
230 an only cause.

231

232 Allonursing between mothers and daughters does have potential inclusive fitness benefits, and  
233 smooth-coated otter romps typically consist of a breeding pair and their offspring, which are  
234 likely to be full siblings. Therefore, these inclusive fitness benefits may be substantial, and they  
235 contribute to allonursing in other systems (e.g., Hackländer et al. 2003). In free-ranging dogs,  
236 pups have even been observed to steal milk from other mothers (Paul and Bhadra 2017). The  
237 cost of allolactation may not be especially high depending on the conditions (MacLeod and  
238 Lukas 2014), which could favor allolactation in smooth-coated otters. However, the evidence  
239 of policing and the observations of females' eviction suggest potential within-group conflict  
240 related to reproduction. How these individual and inclusive fitness benefits interact is not clear.

241

242 Cooperative breeding has been intensely scrutinized, and while the traditional explanation is  
243 that kinship plays a large role in obtaining these indirect fitness benefits, another body of  
244 evidence suggests that group dynamics among non-kin could also contribute to the  
245 development of this breeding system (Lukas and Clutton-Brock 2012b). Groups of cooperative  
246 breeding giant otters include unrelated individuals, for example (Ribas et al. 2015), suggesting  
247 that members of different giant otter families sometimes merge to form romps. At least some  
248 of Singapore's smooth-coated otter romps are closely enough watched that merging of  
249 unrelated families into one romp seems unlikely; otter watchers can trace the growth of romps  
250 brood by brood. But without a more detailed analysis we cannot know how kinship and other  
251 group dynamics contribute to the development of MRF within smooth-coated otters.

252

253 Another factor influencing MRF may be smooth-coated otters' existence in urban Singapore.  
254 In other animals that returned to Singapore recently, some notable behaviors have been  
255 attributed to the urban environment. For example, pied hornbills have returned to Singapore in  
256 the last two decades, and they are frequently observed eating nestlings and fledglings of other  
257 birds, perhaps because those nestlings are easy to find in an urban environment (Loong et al.  
258 2021). Conditions unique to an urban environment may also favor otter romps with multiple  
259 reproductive females.

260

261 The overall population density of smooth-coated otters in Singapore seems to be high. This  
262 high density suggests that they may enjoy unnaturally favorable conditions. Indeed, many of  
263 Singapore's waterways are full of introduced fish. By one estimate, Singapore's otters prey on  
264 large, introduced species of cichlids more than 90% of time while in Singapore's freshwater  
265 reservoirs (Theng et al. 2016). Conditions with ample prey and few predators could potentially  
266 favor delayed dispersal and impose few fitness costs on the dominant female if subordinate

267 females reproduce. Alternatively, abundant resources could lead to fewer ecological constraints  
268 and greater fitness gains if subordinate animals disperse early and establish their own  
269 territories. This latter hypothesis could lead to smaller territories among otter clans than in less  
270 abundant environments. The interplay between ecological constraints, demographics of a long-  
271 lived carnivore, and inclusive fitness is complex (e.g., Emlen 1982, Hatchwell and Komdeur  
272 2000, Pen and Weissing 2000, Frederico et al. 2020); our aim is not to disentangle those factors  
273 here. However, we observed MRF in both urban Singaporean environments and rural Indian  
274 environments. Therefore, we posit that it is unlikely MRF is solely a consequence of urban  
275 ecological factors, such as abundant forage, or absence of predators.

276

## 277 **Conclusion**

278 We note several occurrences of multiple reproductive females within smooth-coated otter  
279 romps, eviction of subordinate females, and what may be infanticide by romp members. The  
280 growing pool of observations suggest that MRF in smooth-coated otter romps is not  
281 especially rare. Its occurrence in several families in Singapore, including repeated instances  
282 in one romp, suggests that this largely cooperatively breeding mammal has a social system  
283 more complex than originally thought. We consider hypotheses that may contribute to MRF  
284 but find that none by itself adequately explains MRF in smooth-coated otters.

285

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296

297

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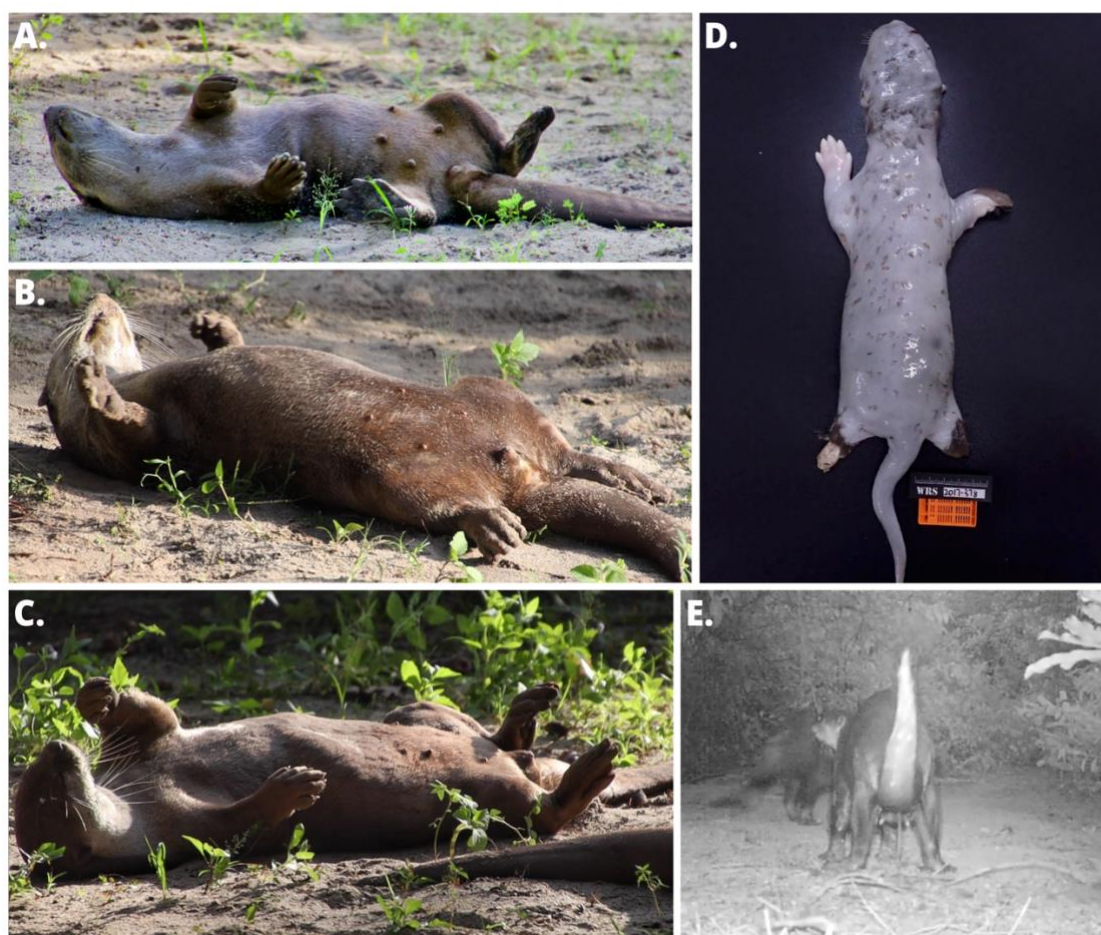
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396 **Figures**

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399 **Figure 1.** Examples of confirmed multiple-lactating-females from the Bishan  
400 family, June 2021. A-C were taken on the same day, showing the three mothers  
401 within the romp; C is the matriarch, identified by her 5<sup>th</sup> nipple. D was taken from  
402 the necropsy of the dead pup from 2017, a suspected infanticide (see text). E was  
403 taken in Amona, India, in early 2016; two females were lactating in the romp.

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406 **Supplementary materials**

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408 **Table S1.** Links to relevant photographs, videos, and chronicles, from public otter-watching

409 groups on Facebook.

URL	Source	Description/Remarks
<a href="https://www.facebook.com/Myottermelon/posts/160263052300211">https://www.facebook.com/Myottermelon/posts/160263052300211</a>	Myottermelon	Taken June 2019, depicting the two lactating females of the Pandan family at that time
<a href="https://www.facebook.com/otterscene/photos/p.1461416984063439/1461416984063439/?type=3">https://www.facebook.com/otterscene/photos/p.1461416984063439/1461416984063439/?type=3</a>	Omnichannel	From November 2020, showing one of the subordinate females of Bishan, shortly after the matriarch had her 7 <sup>th</sup> litter.
<a href="https://www.facebook.com/ottercity/posts/527917597983138">https://www.facebook.com/ottercity/posts/527917597983138</a>	Ottercity	From December 2017, depicting the earliest known instance of a romp with multiple mothers. The small pup was killed in a suspected case of infanticide, per the necropsy report.
<a href="https://www.facebook.com/ottercity/posts/530834741024757">https://www.facebook.com/ottercity/posts/530834741024757</a>	Ottercity	Story describing the Bishan matriarch's temporary expulsion in 2019. It is unknown whether the daughter who evicted the matriarch was lactating at the time, but the 6 pups present were the matriarch's.
<a href="https://www.facebook.com/ottercity/posts/567144877393743">https://www.facebook.com/ottercity/posts/567144877393743</a>	Ottercity	The subsequent evictions and return of the three females of Bishan, April-July 2019.

<a href="https://www.facebook.com/ottercity/posts/818899978884897">https://www.facebook.com/ottercity/posts/818899978884897</a>	Ottercity	Description of the SBG family's two mothers and 4 pups
<a href="https://www.facebook.com/otterscene/posts/1472227652982372">https://www.facebook.com/otterscene/posts/1472227652982372</a>	Omnichannel	"Flowerhead" of the Zouk family with enlarged nipples, December 2020.
<a href="https://www.facebook.com/ottercity/posts/969184930523067">https://www.facebook.com/ottercity/posts/969184930523067</a>	Ottercity	Links and video describing the small Bishan pup found in late 2020, which was later euthanized after abandonment.
<a href="https://www.facebook.com/ottercity/posts/971386860302874">https://www.facebook.com/ottercity/posts/971386860302874</a>	Omnichannel	
<a href="https://www.facebook.com/otterscene/posts/1535971979941272">https://www.facebook.com/otterscene/posts/1535971979941272</a>		
<a href="https://www.facebook.com/watch/?v=788003621806664">https://www.facebook.com/watch/?v=788003621806664</a>	Omnichannel	The latest round of 5 pups from two subordinate Bishan females.

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412 **File S1.** Video of Bishan romp "grooming" in which the matriarch and two subordinate

413 females with enlarged nipples are visible.



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## NECROPSY REPORT CASE # N

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DATE OF DEATH : 24/12/2017	DATE OF REPORT : 24/12/2017	TIME BETWEEN DEATH AND NECROPSY <8hrs
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419

SPECIES : <i>Lutrogale perspicillata</i> / Smooth-coated otter		ORIGIN : wild
ID	HOUSE NAME	AGE : pup
GENDER: M <input type="checkbox"/> F <input checked="" type="checkbox"/> U <input type="checkbox"/>		VETERINARIAN : Chia-Da Hsu
CONDITION OF CARCASS : FRESH <input type="checkbox"/> REFRIGERATED <input type="checkbox"/> FROZEN <input type="checkbox"/> AUTOLYSIS <input checked="" type="checkbox"/>		
BODY SCORE : 1 <input type="checkbox"/> 2 <input checked="" type="checkbox"/> 3 <input type="checkbox"/> 4 <input type="checkbox"/> 5 <input type="checkbox"/>		EUTHANISED: YES <input type="checkbox"/> NO <input checked="" type="checkbox"/>
METHOD:		

420

421

<b>ANAMNESIS :</b>
Wild smooth-coated otter pup

422

423

<b>MAJOR MACROSCOPICAL FINDINGS :</b>
The body was wet and covered with gravels. The fur of the animal could be easily peeled off. Both hindlegs were amputated. The whole right hindleg was completely gone and the left one was found amputated from the distal femur. The skull was found with multiple fractured by palpation and x-ray examination. There were numerous bite marks all over the body and two lacerations were noted at the left inguinal region. The subcutaneous tissues presented edematous and hyperemic/hemorrhagic. The intestine was ruptured and the gastrointestinal content was found in the abdominal cavity. Some of the bites were noticed penetrated into the chest.

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<b>CAUSE OF DEATH</b>
Trauma

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<b>COMMENT</b>
From the bite marks, the animal was suspected to be attacked by multiple individuals. The animal was killed but not eaten. Hence, the attack was more for territorial conflict instead of predation. The critical blow was the bite that crashed the skull.

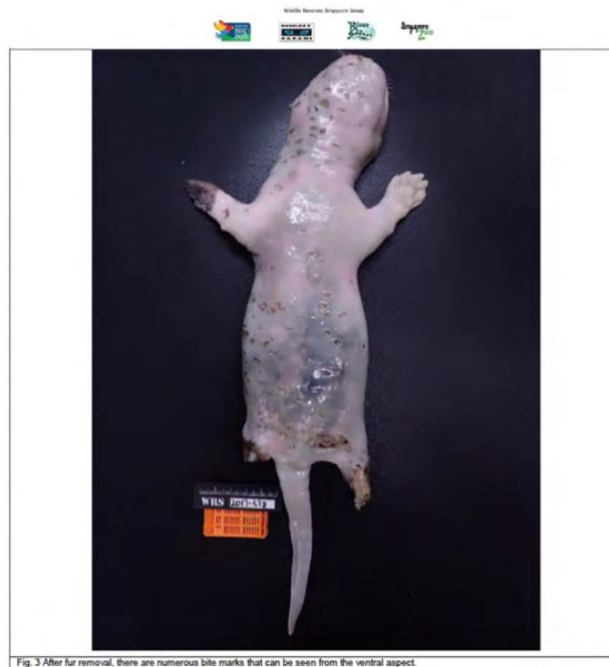


Fig. 3 After fur removal, there are numerous bite marks that can be seen from the ventral aspect.

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427 **Figure S1.** Necropsy report of dead otter pup found near Bishan holt.

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