

1 RESEARCH ARTICLE

2 **Co-existence between Javan slow lorises (*Nycticebus javanicus*) and humans**  
3 **in a dynamic agroforestry landscape in West Java, Indonesia**

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14 ABSTRACT

15 In a world increasingly dominated by human demand for agricultural products, **we need to**  
16 understand wildlife's ability to survive in agricultural environments. We studied the  
17 interaction between humans and Javan slow lorises (*Nycticebus javanicus*) in Cipaganti, Java,  
18 Indonesia. After its introduction in 2013, **chayote (*Sechium edule*), a gourd grown on**  
19 **bamboo lattice frames**, became an important cash crop. **To evaluate people's use of this**  
20 **crop and to measure the effect of this increase on slow loris behaviour, home ranges, and**  
21 **sleep sites, we conducted interviews with local farmers and analysed the above variables in**  
22 **relation to chayote expansion between 2011-2015.** Interviews with farmers in 2011, 2013  
23 and 2015 confirm the importance of chayote and of bamboo and slow lorises in their  
24 agricultural practises. In 2015 chayote frames covered 12% of **land in Cipaganti**, occupying  
25 4% of slow loris home ranges, which marginally yet insignificantly increased in size with the  
26 increase in chayote. Slow lorises are arboreal and the bamboo frames increased  
27 connectivity within their ranges. Of **the** sleep sites we monitored from 2013-2016, 24 had  
28 disappeared, and 201 continued to be used by the slow lorises and processed by local  
29 people. The fast growth rate of bamboo, and the recognition of the value of bamboo by  
30 farmers, allow persistence of slow loris sleep sites. Overall introduction of chayote did not  
31 result in conflict between farmers and slow lorises, and once constructed the chayote  
32 bamboo frames proved to be beneficial for slow lorises.

33 KEY WORDS: agroforestry, conservation, ethnozoology, chayote, *Sechium edule*, sleep site,  
34 *Nycticebus javanicus*

## 35 INTRODUCTION

36 **Preservation of high quality forest habitats is vital for the conservation of** global biodiversity.  
37 Yet, in a world increasingly dominated by humans with their ever-growing demands for  
38 agricultural products, an understanding of wildlife's ability to survive and even thrive in  
39 agricultural environments is increasingly important (Bhagwat et al. 2008; Estrada et al. 2012;  
40 Stafford et al. 2016; **Estrada et al. 2017**). To meet this need, researchers have suggested  
41 new approaches to study biodiversity, integrating agricultural matrices into conservation  
42 planning for the preservation of rare species that also occur outside of pristine  
43 environments (Meijaard and Sheil 2008; Cassano et al. 2014). Farming systems that are  
44 intercropped by hedgerows or living fences of trees have often been regarded as vital  
45 contributors to alleviation of fragmentation (Michel et al. 2006). In Europe, where  
46 deforestation has been occurring for centuries, hedgerows are often the only habitat left for  
47 wildlife (Gelling et al. 2007), and have thus been well studied in the context of mammalian  
48 density, dispersal ability and behavioural ecology (Michel et al. 2007; Zhang and Usher  
49 1991). Even for forest specialists, hedgerows have been shown to be important habitats,  
50 making up parts of forest dwelling animals' home ranges and as dispersal vectors (Schlinkert  
51 et al. 2016). For tropical mammals, such studies have lagged behind, but are now necessary  
52 as **intact** habitats disappear at an alarming rate.

53         Researchers often study tropical mammals, including primates, in 'pristine' habitats,  
54 **rather than in disturbed, modified or anthropogenic habitats**, with an idea that evolutionary  
55 adaptations can only be studied in such contexts (Hockings et al. 2015). Increasingly,  
56 however, the importance of anthropogenic habitats to primate ecology, conservation and  
57 evolution are recognized (Asensio et al. 2009, Estrada et al. 2017). For some species,  
58 agricultural landscapes may be beneficial not only to primates, but also to humans when  
59 primates control pests, pollinate flowers, or simply live peaceably without damaging their  
60 crops (Estrada 2006, Williams-Guillén et al. 2006). Although such interactions are not always  
61 amicable, primates can show remarkable behavioural flexibility, including dietary and  
62 habitat switching, and changes in polyspecific interactions (Tisovec 2014; Moore et al. 2010;  
63 Morrogh-Bernard 2014; Nowak and Lee 2013), making the study of the long-term  
64 sustainability of such systems important for primate conservation.

65 Agroforestry systems, areas in which trees or shrubs are grown around or among  
66 crops or pastureland, are one type of landscape where humans and primates may come  
67 together (Estrada et al. 2012). Considering mainly diurnal primates, Estrada et al. (2012)  
68 defined a number of ways primates can be useful to these systems, benefits also offered by  
69 a number of nocturnal primates. Researchers have recorded the pollination of agricultural  
70 plants by nocturnal primates (Javan slow lorises *Nycticebus javanicus* in Java, greater slow  
71 loris *N. coucang* in Malaysia) (Nekaris 2014; Wiens et al. 2006). Insect consumption, which is  
72 also likely to include agricultural pests, has been observed in agroecosystems among Javan  
73 slow loris in Java (Rode-Margono et al. 2015), Mysore slender loris (*Loris lydekkerianus*  
74 *lydekkerianus*) in India (Nekaris and Rasmussen 2003; Kumara et al. 2016), Milne-Edward's  
75 potto (*Perodicticus edwardsi*) in Cameroon (Pimley et al. 2006), and by Dian's tarsier (*Tarsius*  
76 *dianae*) in Sulawesi (Merker et al. 2005).

77 Being able to survive in human-modified landscapes is not enough; a tolerance  
78 between humans and primates must exist, in that humans do not trap primates for food or  
79 pets, or harm them over conflicts for food resources (Lee 2010). Mantled howler monkeys  
80 (*Alouatta palliata*) can feed and persist well in shade coffee plantations if left undisturbed  
81 by humans, including capturing them for the pet trade (Williams-Guillén et al., 2006).  
82 Additional management by humans may also be required, such as increasing connectivity  
83 between planted trees to aid in travel or predator avoidance, such as was observed in  
84 Brazil's cacao (*Theobroma cacao*) agroforests for Wied's marmosets (*Callithrix kuhlii*) and  
85 golden-headed lion tamarins (*Leontopithecus chrysomelas*) (Tisovec et al. 2014). Several  
86 macaque (*Macaca* spp) populations also can persist alongside humans, where being caught  
87 for pets or for the biomedical industry is a looming threat (e.g. Shepherd 2010).

88 The island of Java, Indonesia, is one of the most densely populated areas on earth.  
89 Java is largely deforested and most of the remaining 10% forest covers (parts of) the  
90 numerous volcanoes on the island (Whitten et al. 1996). Forest has been replaced by a  
91 mosaic of cities and villages, agricultural land, cash-crop plantations, and forest plantations  
92 (e.g., teak *Tectona grandis*, Sumatran pine *Pinus merkusii*, rubber *Hevea brasiliensis*)  
93 (Nijman 2013). About 17% of the agricultural land on Java consists of home gardens and  
94 agroforest, whose forest-like structure more or less mimic natural forest (Whitten et al.  
95 1996), thus greatly increasing connectivity for many species.

96 Javan slow lorises, nocturnal primates endemic to Java, are characterized by fully  
97 arboreal slow climbing locomotion (Nekaris 2014). As such, one would expect them to be  
98 particularly vulnerable to habitat fragmentation where movement on the ground is often a  
99 requirement (c.f. Mortelliti et al. 2013; Vaughan et al. 2007). Slow lorises in general,  
100 however, are adapted to life at forest edges where increased sunlight creates a dense  
101 network of branches (Chivers 1980). Studies in the village of Cipaganti, Java, an agroforest  
102 ecosystem with a particularly high density of this Critically Endangered primate, show that  
103 slow lorises enter a sleep site at dawn, where they remain until dusk. As with most other  
104 primates (Anderson 1998), slow lorises do not use nests but instead sleep on a branch or  
105 tangle of branches, curled in a ball or huddled against group mates, within their chosen  
106 sleeping tree (Nekaris 2003). Such sleep sites are generally dense and have been  
107 hypothesised to protect them from extreme temperatures and predators (Nekaris 2014).  
108 Being territorial, the sleep sites of a slow loris group (male-female pair and offspring) fall  
109 exclusively within their own home range. Bamboo stands comprise 96% of sleep sites for  
110 Javan slow lorises in Cipaganti, as well as substrates for feeding and avoiding ground  
111 movement (Nekaris 2014). Bamboo stands are used (and re-used) as sleep sites daily by  
112 slow lorises. Typically, 20 to 40 bamboo sleep sites are present in each slow loris' home  
113 range (first author, unpubl. data).

114 Cipaganti is characterized by shifts in agriculture, with the types of crops grown  
115 depending on local economic trends. For example in 2012, when tomatoes (*Solanum*  
116 *lycopersicum*) were economically valuable, farmers heavily planted this crop. Similarly, in  
117 2013, farmers began growing a gourd, chayote (*Sechium edule*), and by 2015 it became the  
118 crop of choice. Chayote, locally known as *labu*, relies on a network of bamboo frames in  
119 order to grow (Fig. 1). These frames are erected at ~1.6 m in height and can be up to 1 ha in  
120 size, and cover what would have been open ground with a network of chayote vines  
121 growing on the frames. **Due to** the increasing interest by farmers in planting chayote, we  
122 noted an accelerated rate of cutting of bamboo, possibly impeding on the survival of the  
123 Javan slow lorises. Here, we examine the impact of this new agricultural development on  
124 the behaviour of slow lorises by addressing five questions. (1) Did farmers' perceptions of  
125 slow lorises, **slow lorises** perceived roles as consumer of agricultural pests and the  
126 importance of chayote to farmers change over the study period? **We assessed** this through

127 informal interviews with farmers over the period 2011-2015. (2) Did the amount of land  
128 planted with chayote change, and did chayote frames make up a significant proportion of  
129 slow loris home ranges? **We assessed** this by measuring the proportion of land allocated to  
130 growing chayote in 2014 and 2015, as well as measuring the proportion of the slow loris  
131 home range comprised of chayote, also for 2014 and 2015. (3) Did slow loris home range  
132 sizes change or move position? **We assessed this** for 2014 and 2015 through direct  
133 observations. (4) How did slow lorises behave in and around chayote frames? **We assessed**  
134 **this** through behavioural observations in 2012 through 2016. (5) Did cutting bamboo for  
135 chayote affect availability of slow loris bamboo sleep sites? **We assessed this** in 2016 by  
136 measuring the presence and intactness of bamboo sleep sites at differing altitudes that had  
137 been used in the period 2013 to 2015.

138

## 139 METHODS

### 140 *Ethical Note*

141 We conducted all animal research in adherence with RISTEK (Indonesian Ministry of Science  
142 and Technology), as well as ethical guidelines provided by the Association for the Study of  
143 Animal Behaviour; Oxford Brookes University Animal Ethics Sub-committee **granted our**  
144 **research approval**. For the interviews we followed the ethical guidelines proposed by the  
145 Association of Social Anthropologists of the UK and Commonwealth and that the University  
146 Research Ethics Committee of Oxford Brookes University **approved**.

### 147 *Study site and its changing farming practices*

148 This study forms part of a long-term community conservation project to protect Asia's slow  
149 lorises and other imperilled nocturnal animals via ecology, education, and empowerment  
150 (Nekaris 2016). We conducted the study in an area of ~60 ha at the outskirts of the village of  
151 Cipaganti, Cisurupan, Garut Regency, West Java, Indonesia (7°16'44.30 "S, 107°46'7.80 "E,  
152 1200 m asl) (Fig. 2). Cipaganti is home to about 3,000 people, living at a density of 135  
153 people km<sup>-2</sup> (Nekaris 2016). The village is located at 1,345 m asl on Gunung Puntang, a  
154 mountain that is a part of the Java-Bali Montane Rain Forests ecoregion. The climate is  
155 everwet with a mean annual precipitation exceeding 2,500 mm. The habitat around

156 Cipaganti is a mosaic of traditional gardens, where local farmers practice an annual  
157 perennial rotating crop system. This system consists of a variety of crop formations, with tall  
158 trees planted in rows along farm property boundaries, or interspersed between crop types  
159 (Reinhardt et al., 2016). In our study site, **slow lorises heavily** use certain plants including  
160 string bamboo (*Gigantochloa atter*), clumping bamboo (*G. pseudoarundinacea*), giant  
161 bamboo (*Dendrocalamus asper*), cajeput tree (*Malaleuca leucadendra*), red fairy duster  
162 (*Calliandra calothyrsus*), green wattle (*Acacia decurrens*), avocado (*Persea americana*) and  
163 Indonesian mahogany (*Toona sureni*) (Rode-Margono et al. 2014). Within the village of  
164 Cipaganti, agricultural production provides the main source of household income, yielding  
165 crops such as tea (*Camellia sinensis*), coffee (*Coffea robusta*), chayote (*Sechium edule*),  
166 carrot (*Daucus carota*), white cabbage (*Pieris brassicae*), tomato (*Solanum lycopersicum*),  
167 cassava (*Manihot esculenta*) and potato (*Solanum tuberosum*).

168  
169 Chayote is a medium- to high-altitude crop (300 to 2,000 m asl) that requires a high relative  
170 humidity of around 80 to 85%, high annual precipitation of at least 1,500 without a marked  
171 dry season, and 12 hours of daylight to initiate flowering. The temperature should be  
172 between 13 and 21°C; temperatures below 13°C damage small and unripe fruits whereas  
173 temperature above 28°C leads to excessive growth, loss of flowers and unripe fruit, and  
174 ultimately reduced production (Saade 1996). **Cipaganti matches these conditions** extremely  
175 well. The Garut Regency in which Cipaganti is situated is an important grower of chayote,  
176 both in absolute and relative terms, and the area set aside for growing the crop in Garut has  
177 increased from 188 ha in 2012 (22% of the provincial total) to 360 ha in 2015 (33% of the  
178 provincial total). Production in 2015 was 14,499 t a year (c.f. Morton 1981). If both the  
179 official government figures and the estimates from the farmers in Cipaganti are correct then  
180 the wider Cipaganti area (which stretches beyond our study area) is responsible for some  
181 60% of the regency's chayote production, suggesting that this crop will at least be around  
182 for the foreseeable future with a continuing impact on slow lorises.

183

184 *Interviews with Informants*

185 In June 2011, June 2013, December 2015 and June 2016 we held informal interviews  
186 (Newing 2011) with opportunistically selected key informants **with farms** situated within the  
187 home ranges of collared slow lorises (six informants in 2011, 16 in 2013, and 17 in 2015).  
188 Most informants lived in the village and were long-time residents (and typically born here or  
189 had moved into the area during childhood); in addition **we interviewed** five informants from  
190 neighbouring villages. In 2011 and 2013 the conversations focussed on the importance of  
191 slow lorises to the village, both from a cultural, natural and economic perspective. Given  
192 that chayote was not of particular importance at that time, **farmers did not single** out this  
193 crop but discussed it in the context of general agricultural crops. In 2015 the topic of  
194 discussion was similar to that in 2011 and 2013 but now much of it centred on chayote;  
195 given the dominant role of chayote in the agricultural landscape and the village economy,  
196 **informants initiated discussions on this topic.**

197 **We held** informal interviews in Bahasa Indonesia, the national language that is very  
198 widely spoken on Java (Sneddon 2004), **repeating** key concepts in Bahasa Sunda, the  
199 regional language spoken in this part of the island. Informal interviews were open, allowing  
200 informants to talk freely about slow lorises, their significance in culture or the beliefs  
201 surrounding them, and their role in the agricultural system. To ensure independence of  
202 data, we interviewed informants individually; other members of the community sometimes  
203 were present, but we used only the responses of the informant in analysis. At the end of  
204 each interview, we repeated key points to ascertain whether we captured the essence of  
205 the informant's opinions/expressions correctly. Informants did not receive gifts or money  
206 for their participation.

207 We asked informants to share any knowledge they had of slow lorises, touching  
208 upon any topic they felt to be relevant, without any constraint placed upon them by us  
209 (Bernard 2011; Puri 2011). We converted these conversations into freelists, from which we  
210 extracted the frequency of occurrence for each item (i.e. what proportion of informants  
211 mentioned topics such as 'slow lorises are useful for pest control', 'bamboo', or 'chayote')  
212 and the rank for each item (i.e. were they mentioned early on or at the very end of the  
213 interview, on a scale from 1 to 4) (Puri 2011). This procedure allowed us to check whether  
214 these topics were locally salient or meaningful. Salience was quantified by calculating  
215 Smith's S ( $S = ((L - R_j + 1)/L)/N$ , where L is the number of distinct items listed by the



216 informants,  $R_j$  is the rank of item J in the list, and N is the number of lists / informants in the  
217 sample). Smith's S ranges from 0 to 1, with topics having values close to 1 being the ones  
218 that were mentioned by most informants early on in the conversation, and topics having  
219 values close to 0 being the ones that **few informants** mentioned, and if so often late in the  
220 conversation (Puri 2011).

### 221 *Slow loris behavioural observations*

222 To examine the presence of chayote in slow loris home ranges, we surveyed the study site  
223 to locate each chayote frame, measuring their perimeters and monitoring change in their  
224 presence from January 2014 to May 2015. To examine the behaviour of slow lorises in  
225 relation to chayote frames, we analysed behavioural data collected on collared slow lorises  
226 from the first time **we saw them** enter a chayote frame in June 2014 until June 2016.  
227 Because Javan slow lorises live in stable uni-male uni-female pairs with almost 100% range  
228 overlap and share sleep sites (Nekaris 2014), we examined the impact of chayote frames on  
229 social groups rather than individuals. We focus on adult individuals belonging to eight focal  
230 uni-male uni-female social pairs (Table 1). After catching the slow lorises by hand, we  
231 equipped them with 19 g VHF collars (PIP3, Biotrack, Wareham, United Kingdom). With the  
232 assistance of local field trackers, we located collared individuals using an antenna (Lintec  
233 flexible, Biotrack, Wareham, United Kingdom) and a receiver (Sika receiver, Biotrack,  
234 Wareham, United Kingdom), and recorded their location every 15 minutes using a handheld  
235 GPS unit (GPS62s, Garmin International, Olathe, USA). For direct observations we used head  
236 torches (HL17 super spot, Clulite, Petersfield, UK) fitted with a red filter. To observe the  
237 behaviour of slow lorises in chayote, we followed slow lorises for 3199 hours **between**  
238 17:00-05:00 hrs, **from** January 2014 to December 2015 **(a mean of  $13 \pm 7$  nights per month)**.  
239 We used all occurrences sampling to record each instance one of the 16 focal lorises  
240 entered chayote using a modified version of the Rode-Margono et al. (2014) behavioural  
241 ethogram. Chayote frames are very dense and often when slow lorises enter these frames  
242 they are out of sight until they re-emerge into a tree or bamboo. To see if slow lorises  
243 altered their home range use between 2014-2015, we computed the home ranges of the  
244 eight focal pairs based on 5851 locations using the 95% minimum convex polygon (MCP).  
245 We performed all GIS work using R (R 3.0.2, adehabitatHR package) (R Core Team 2013).

246 *Sleep sites*

247 We defined a bamboo sleep site as the stand of bamboo in which a slow loris social group  
248 slept. A single stand can contain over 100 stems or culms of bamboo. **During** one sleeping  
249 period, slow lorises sometimes move from one stem to another, making the stand the unit  
250 of analysis. We recorded location of bamboo sleep sites of the eight focal pairs of slow  
251 lorises once per week from **January** 2013 (before the appearance of intensive chayote) to  
252 **December** 2015, georeferencing each site using a handheld GPS unit. To measure sleep site  
253 reuse we plotted the points collected during 2013, 2014, and 2015 in ArcGIS version 10.3.  
254 We created a 5 m buffer around each point to account for standard GPS error in the area,  
255 and then counted each point within overlapping buffers as a single reused sleep site. In  
256 June 2016, we returned to the locations of 225 unique bamboo sleep sites; each site  
257 revisited fell only in the range of one social pair. In particular, we examined: if the bamboo  
258 sleep site still stood in 2016; if yes, had it been cut, including number of whole and cut  
259 stems remaining and the number of newly sprouting stems; if no, we recorded what was  
260 there instead of the bamboo.

261 *Statistical analysis*

262 **Behavioural, sleep site and ranging data** did not deviate significantly from a normal  
263 distribution. To investigate the influence of the chayote production on slow loris, we tested  
264 whether the percentage of chayote frame could explain observed variation in individual  
265 home range size. We fitted a **multiple linear regression** to the data, with the percentage of  
266 chayote frame within a home range and the year as **the explanatory** variables. We  
267 conducted the analyses in R. We present descriptive statistics of the characteristics of  
268 bamboo sleep sites, reporting the mean and  $\pm 1$  standard deviation, with P set at the 0.05  
269 level.

270 RESULTS

271 *Farmers' perceptions of slow lorises, pests and crops*

272 In 2011 one out of six informants indicated that slow lorises were allies to farmers as they  
273 consumed pest insects, but **they** mentioned **this concept** only late in the conversation. In  
274 2013 many more informants (13/16) were aware that slow lorises consumed agricultural

275 pests and they brought up this topic earlier on in the conversation. The situation was similar  
276 in 2015 when 15/17 informants mentioned it. Quantitatively, salience, as measured by  
277 Smith's *S* of 'slow lorises and pest control' started at a low 0.04 in 2011, and then increased  
278 to 0.69 in 2013 and 0.72 in 2015.

279         The knowledge of the importance of bamboo for slow lorises was high in 2011, with  
280 five out of six informants mentioning it. This knowledge remained high in 2013 (14/16) and  
281 2015 (13/17), with some informants mentioning it early on in the conversation and others  
282 later on. Quantitatively, Smith's *S* of 'slow lorises and bamboo' was 0.54 in 2011, 0.49 in  
283 2013 and 0.53 in 2015. Chayote as a crop was not significant enough for the informants to  
284 mention it in 2011 and 2013. In 2015, all informants mentioned chayote as a crop, two-  
285 thirds early on. As such salience of chayote was zero in 2011 and 2013 but Smith's *S*  
286 equalled 0.83 in 2015, surpassing that of all the other topics they discussed.

287         The importance of chayote as a crop led farmers we interviewed to claim that  
288 chayote was probably the most important cash crop in the area by December 2015. It then  
289 had a market value of Rp 5000-6000 (US\$0.35-0.42) per kg. On average five trucks of  
290 differing sizes collected chayote daily, with a capacity to carry four to seven metric tonnes  
291 per truck. Informants estimated that some 25 t of chayote was produced a day in the wider  
292 Cipaganti area, which is larger than the area where we study the slow lorises. While initially  
293 chayote farmers organised their business independently, by early 2016 a chayote-growing  
294 cooperation was started where 50 of the largest chayote farmers joined forces to share  
295 costs, logistics, knowledge and profits.

296         To create a chayote frame, which in our study area on measures a mean of 1500 m<sup>2</sup>,  
297 or 0.15 ha, 150 bamboo stems of approximately 2 m tall are required for the main vertical  
298 supports and 120 lengths of bamboo measuring 6 m each are needed for the main  
299 horizontal supports. Farmers we interviewed reported that up to 30% of the poles need to  
300 be replaced every six months, a cost that must be considered when investing in chayote.  
301 Three species of bamboo occur frequently in Java, but differ in price according to our  
302 interviews, including string bamboo at Rp 5000 (US\$0.35) per stem; giant bamboo at Rp  
303 9000 (US\$0.64) per stem; and clumping bamboo at Rp 20,000 (US\$1.41) per stem. At the  
304 beginning of the chayote boom our interviewees reported that they sourced most, if not all,

305 this bamboo locally but by 2015 farmers ordered truckloads of bamboo from the north  
306 coast of Central Java (i.e., some 250 km to the east) to meet their demands. Some farmers  
307 in our area used more durable concrete poles instead of bamboo ones as a longer-term  
308 option, but these are far more costly at Rp 30,000 (US\$2.12) for a 2 m length of pole. Using  
309 mean figures, the initial investment for a bamboo chayote frame, with labour costs, and  
310 plants amounts to some US\$500. After four months farmers can harvest the first fruits, and  
311 from then on production is more or less continuous. With an annual yield of ~40 t per ha  
312 (Morton 1981) the break-even point in terms of financial investment is reached well within  
313 the first year.

#### 314 *Chayote in the slow loris landscape*

315 Planting of chayote began in the study area in early 2014 with just a few small frames. By  
316 July 2014, many farmers had planted chayote; we recorded 34 chayote frames  
317 encompassing an area of 1.6 ha. The numbers increased, with an additional 58 frames  
318 encompassing 2.5 ha planted by November 2014. By April 2015 we recorded 145 chayote  
319 frames representing a total of 7.2 ha (i.e. 12% of the study area). This represents 2.7%  
320 (range 0 -5.6 %) of the social pairs home ranges in 2014 and and 3.9 % (range 0 – 13.0%) in  
321 2015 (Fig. 3).

322 In 2014, the mean slow loris home range size was 7.1 ha  $\pm$  2.0. In 2015, the mean  
323 was 6.6 ha  $\pm$  1.2 (Table 1, Fig. 3). Over both years the mean was 7.5 ha  $\pm$  1.1. Home range  
324 size was not affected by the year or percentage of chayote frame ( $F_{2,13} = 1.75, P = 0.21, n =$   
325 16).

326

#### 327 *Behaviour of slow lorises in chayote*

328 We first recorded use of chayote frames by two social pairs of slow lorises (LU, SI) in June  
329 2014. By October 2014, we had also observed pairs SH and OE using the frames. By June  
330 2015, we had recorded all social pairs regularly using chayote frames; the last pair to use the  
331 frames was MA with the first record dating to January 2016. Slow lorises used the frames as  
332 if they were a normal bamboo substrate, moving fluidly across the bamboo poles to reach

333 rows of trees on opposite ends of farmers' fields. Chayote frames are very dense and  
334 difficult for a human observer to move under, and thus we could only record 211 all  
335 occurrences sample points of slow loris behaviour in the chayote. Slow lorises used chayote  
336 most frequently for travelling (68%), followed by foraging for or feeding on insects (22%),  
337 allogrooming (6%), resting (2%), and other (2%). We could not identify insects to the species  
338 level, but noted that slow lorises consumed flying insects that they caught with their hands  
339 as well as those that they orally removed from the chayote frames.

#### 340 *Slow loris sleep sites*

341 We recorded the social pairs in a bamboo sleep site a total of 1350 times, comprising 514  
342 unique locations, 211 of which had been reused (2013, n=340 with 95 reused; 2014, n=444  
343 with 53 reused; 2015, n=566 with 89 reused). Slow lorises used three species of bamboo,  
344 with 8 sleep sites comprised of clumping bamboo, 52 comprised of giant bamboo, and 454  
345 comprised of string bamboo (Fig. 4). In 2016, we revisited 225 bamboo sleep sites used in  
346 the period 2013-2015 comprising a mean of  $28 \pm 21$  bamboo sleep sites unique to each pair  
347 (Table 2) and found that 89.3% of sleep sites (n=201) remained and were still being used by  
348 slow lorises. 11 sleep sites had been replaced by chayote, 11 were replaced by bare ground,  
349 and two had disappeared as a result of landslides. The remaining 201 sleep sites ranged in  
350 size from 1 to 101 stems, with a mean of  $35.5 \pm 24.5$  stems per bamboo stand. Only three of  
351 these stands remained fully intact, with 198 containing cut stems. The mean number of cut  
352 stems per bamboo stand was  $19.9 \pm 15.8$ , with the mean number of newly sprouting stems  
353 being  $7.57 \pm 10.9$ . Social pairs differed in the number of sites destroyed, cut stems, and new  
354 sprouting stems (Table 2).

355

#### 356 DISCUSSION

357 Farmers in Cipaganti increasingly recognised the importance of slow lorises in the control of  
358 agricultural pests, and chayote became more important over time. In 2015 some 12% of the  
359 study area was used to grow chayote and on average 4% of the slow lorises' home range  
360 comprised chayote frames. Range size of slow lorises only marginally increased over time  
361 and remained stable in terms of their geographic position (i.e. no home range size shifts

362 were recorded). Over time Javan slow lorises started using the chayote frames, mostly for  
363 travelling but also for feeding and social interactions. Although cutting for chayote disturbed  
364 sleep sites, the fast growing bamboo meant that animals still had more than adequate  
365 places to sleep.

366 Researchers have heralded agroforestry as a positive step towards achieving co-existence  
367 between wildlife and farmers. Chayote is as a useful vine in such forests, providing shade for  
368 lower strata plants (Clerck and Negreros-Castillo 2000). Humans domesticated chayote  
369 centuries ago and worldwide have used it for its economic and cultural value (Lira et al.  
370 2002). Chayote has replaced other more traditional agroforestry practices no longer viable  
371 on Java (Iskandar et al. 2016). In Cipaganti, it provides excellent economic services, and  
372 requires less intensive farming practices compared to root vegetables, being easy to harvest  
373 and not requiring the use of pesticides (Morton, 1981). People introduced chayote into the  
374 “traditional bamboo garden” (*kebun tatangkalan*) landscape of Cipaganti, where the crop  
375 has partially persisted on the basis of deep cultural affinities to this ancient farming practice  
376 (Abdoellah et al. 2015). Together with bamboo and other planted trees, chayote frames and  
377 the associated climbers provide a form of living fence or canopy corridor for slow lorises and  
378 other wildlife, including rare species such as Javan leopard (*Panthera pardus melas*), Javan  
379 ferret badger (*Melogale orientalis*), banded linsang (*Prionodon linsang*), and binturong  
380 (*Arctictis binturong*). Such a system, as opposed to monoculture plantation, seems to allow  
381 this mammalian diversity to persist in Cipaganti while providing an excellent economic  
382 commodity to local people.

383 Despite the increase in growth of chayote, farmers we interviewed showed  
384 sensitivity towards slow lorises, and did so increasingly over the study. In particular, more  
385 farmers recognised the role of slow lorises as pest controls and realised that bamboo  
386 species are important plants for slow lorises. Since 2012, we have disseminated information  
387 about slow lorises and other native species to farmers through newsletters and other events  
388 and by providing classes to their children (Nekaris 2016). We also distributed materials such  
389 as leaflets, umbrellas and t-shirts emphasising the role of slow lorises in the ecosystem.  
390 Such modes of outreach have proven successful in conservation education and community  
391 outreach programmes (Evans et al. 1996, Vaughan et al. 2003, Walter 2009). Indeed,  
392 Waylen et al. (2010) suggest that integrating the community into conservation programmes

393 is a key way to change attitudes and allow a conservation project to succeed. **Human**  
394 **attitudes towards Javan slow lorises** differ in adjacent areas, including an unsustainable pet  
395 trade in the species, thus any conservation of them in human-modified landscapes must  
396 include a human outreach component (Nijman and Nekaris 2015).

397         Although chayote frames comprised more than 3% of slow lorises' home ranges,  
398 home range sizes of the social pairs remained stable and completely within the agroforest  
399 matrix. Chayote frames provided a substrate to move across open fields that had been  
400 previously planted with low growing plants treated with pesticides, such as carrots and  
401 cassava. Chayote frames appeared to offer the slow lorises a network of substrates that  
402 shielded them from predators and contained an abundance of insects. **Researchers have**  
403 **previously reported** the ability to maintain home ranges completely within for wood mice  
404 (*Apodemus sylvaticus*), golden-headed lion tamarins (*Leontopithecus chrysomelas*) and  
405 three-toed sloths (*Bradypus variegatus*) (Vaughan et al. 2007, Oliviera et al. 2011, Rosalino  
406 et al. 2011). Wood mice can exploit planted olive groves, and also showed a preference for  
407 areas with understory; these preferences were interpreted as improving female fitness and  
408 avoiding predators (Rosalino, et al., 2011). Golden-headed lion tamarins and three-toed  
409 sloths could survive with their home ranges completely in agroforests (**Vaughan et al. 2007,**  
410 **Oliviera et al. 2011**). Although tamarin home ranges were smaller than in primary forest,  
411 animals were heavier in size and reproduced well. Tamarins relied largely on planted  
412 jackfruit (*Artocarpus heterophyllus*). In the case of three-toed sloths, **they integrated**  
413 **human-planted** living fences into their home ranges. A similar scenario can be observed in  
414 Javan slow lorises, whose plant consumption of exudates and nectar is completely from  
415 human-introduced species, and whose movements rely heavily on human-planted  
416 substrates (Rode-Margono, et al., 2014). Unlike these taxa, however, slow lorises eat mainly  
417 gum, insects, and nectar, meaning that resources they consume do not put them in  
418 competition with humans, and even have the capacity to help humans.

419         The chayote bamboo frames **provided** a new substrate network that slow lorises  
420 used for both foraging and moving across their fragmented landscape. Indeed, the full range  
421 of behaviours exhibited by slow lorises in chayote in this study mirror the general  
422 behavioural ethogram reported Rode-Margono et al., (2014) for the same population  
423 (foraging and feeding – 22.4% in this study vs 31% in Rode-Margono, et al., 2014; resting 2%



424 vs 33%; travelling 68% vs 14%; grooming 6% vs 7%, other 2% vs 13%). The connectivity  
425 provided by chayote frames and the high number of insects available due to lack of  
426 pesticides can help explain the higher proportion of feeding and travelling. The rapid  
427 incorporation of the frames into **the slow loris** behavioural repertoire is an example of their  
428 flexibility and ability to survive in human-modified landscapes, at least for the period of our  
429 study. Indeed, slow lorises conform to Nowak and Lee's (2013) statement that the ability to  
430 expand niche breadth via resource switching, including substrate choice and modification of  
431 diet, is key to withstanding the risks of anthropogenic habitat modification.

432         The harvesting of the fast-growing bamboo led to the disappearance of some 10% of  
433 bamboo sleep sites. Most (98%) of the remaining bamboo sleep sites were affected by the  
434 harvesting practises for chayote but enough bamboo stems remained for the slow lorises to  
435 keep using bamboo stands as sleep sites. Bamboo is by far the most important sleep site for  
436 slow lorises in Cipaganti comprising 96% of all sites observed since 2012 (1<sup>st</sup> author,  
437 unpublished data). Throughout their range, slow lorises never use tree holes and rely on  
438 forms of closed substrates for sleeping including dense shrubs, palms, lianas and bamboo  
439 stands (Kenyon et al. 2014, Wiens 2002). Pygmy lorises (*N. pygmaeus*) sleep on high clumps  
440 of terminal tree branches with a preference for very dense edge forests (**Streicher and**  
441 **Nadler 2003**). **Slow** lorises have been never been observed to sleep on the ground and are  
442 typically found at 1.8-35.0 m height (Wiens 2002). The maintenance of bamboo shrubs in  
443 Cipaganti is clearly vital for their perseverance in this human-dominated landscape, and the  
444 current human practice of only cutting parts of bamboo stands is for the time being allowing  
445 this persistence.

446         We agree with Sheil and Meijaard (2010) who describe the 'tainted nature delusion',  
447 whereby conservationists neglect the value of human-modified habitats. Researchers in  
448 temperate regions have long recognised the value of these ecosystems (Cassano et al. 2014)  
449 and it would be prudent for those working in tropical and subtropical regions to follow suit.  
450 Studying a difficult to observe, cryptic nocturnal primate like the Javan slow loris in a  
451 human-modified landscape has several advantages. While experiencing the effects of rapid  
452 environmental change, the Javan slow loris has created an opportunity for researchers to  
453 understand their ecological, behavioural, physiological and cognitive capacities (Hockings, et  
454 al. 2015). Studying flexibility in these situations may shed light on the evolution and



455 adaptability of extant strepsirrhine and extinct early primates. Species level evolutionary  
456 history plays an important role in the response to novel environments (Hendry et al. 2001).  
457 An organism's response to human disturbance can be categorized as addressing novel  
458 predators, using novel resources, avoiding novel abiotic threats, and acclimating to  
459 fluctuating spatiotemporal conditions (Sih et al. 2011). In the case of the Javan slow loris,  
460 our findings highlight their behavioural **flexibility in a human-modified landscape**. Recent  
461 IUCN Red List assessments have determined that over 50% of primates face extinction  
462 (Estrada, et al. 2017). With the rapid change in habitat transformation for agricultural  
463 practices sweeping the tropics, we feel it is urgent to understand the behaviour of primates  
464 in such landscapes, and to find ways they can continue to share these spaces with humans.

465

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483

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651

652

653 Figure Legends

654 Figure 1. Photographs of chayote frame structure in the Cipaganti area; a.) View from below  
655 a fully covered chayote frame; b.) View from above a chayote frame, built as cover, over a  
656 farmer's coffee plantation. Photos by Kathleen Reinhardt.

657

658 Figure 2. Location of Cipaganti in West Java, Indonesia.

659

660 Figure 3. Chayote frames and 95% MCP of Javan slow lorises social pairs (n=8) over the study  
661 area in Cipaganti, Java, Indonesia in 2014 and 2015. The names of the social pairs are  
662 indicated at the top.

663

664 Figure 4. **Images of Javan slow lorises in Cipaganti and their bamboo habitats.** (A) stand of  
665 string bamboo; (B) a close up of a Javan slow loris in string bamboo; and (C) a typical image  
666 of a slow loris from a distance in string bamboo as indicated by the arrow.

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669