

1 **TITLE**

2 Dispersal of a human-cultivated crop by wild chimpanzees (*Pan troglodytes verus*) in a
3 forest-farm matrix

4

5 **SHORT RUNNING TITLE**

6 Chimpanzee crop dispersal

7

8 **ABSTRACT**

9 With the conversion of natural habitats to farmland, nonhuman primates (hereafter
10 primates) are increasingly exposed to agricultural crops. Although frugivorous primates are
11 important seed dispersers which sometimes feed on agricultural fruits, evidence for
12 dispersal of crops by primates is lacking. Here, we examine flexible feeding on cacao
13 (*Theobroma cacao*) fruit and seed dispersal patterns by chimpanzees (*Pan troglodytes*
14 *verus*) at Bossou in Guinea, and consequent cacao germination and survival. From direct
15 observations we confirm that cacao fruit is not an important food to chimpanzees,
16 representing 0.23% of focal feeding time. Chimpanzees ingest cacao pulp and either spit
17 the large seeds intact from unripe cacao fruit, or swallow the seeds from ripe cacao fruit
18 which are consequently deposited in faeces. From ecological surveys we show that
19 chimpanzees distributed cacao extensively throughout their home range, at a mean distance
20 of $407 \pm \text{SE } 0.6$ m (N=90 clusters, range: 4-1130 m) from cacao plantations. As distance
21 from the cacao plantation increased, cacao plants were more likely to survive. Other factors
22 including number of cacao plants in a cluster, plant height, and openness of the understory
23 did not predict short-term cacao survival. Cacao plants within the forest did not produce

24 fruit. By contrast, when chimpanzees deposited seeds in a plantation, cacao plants produced
25 fruits due to farmer's maintenance of the area. Our local-scale findings emphasize the
26 complex behavioural and ecological interconnections between coexisting humans and
27 primates in agricultural landscapes, and generate interesting questions regarding primate
28 niche construction and crop 'ownership' related to who 'plants' the crop.

29

30 Keywords: human-wildlife interactions, anthropogenic habitat, seed dispersal, cultivated
31 foods, cacao (*Theobroma cacao*), niche construction

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47 INTRODUCTION

48 We are in a new epoch, the Anthropocene, with most wildlife species exposed in one way
49 or another to the effects of humans and their activities (Woodroffe *et al.* 2005; Candolin
50 and Wong 2012). Understanding wildlife interactions with rapid human-induced
51 environmental changes and their impact on populations, communities, and ecosystems
52 presents a burgeoning horizon for behavioural and ecological science (Sih *et al.* 2011;
53 Wong and Candolin 2015). There have been decades of research into the ways in which
54 natural ecosystems function (i.e. the biological, geochemical and physical processes and
55 components that occur within an ecosystem), but less is known about the mechanisms and
56 processes that contribute to the development of human-impacted habitats, and the role of
57 wildlife in shaping such changes. For example, humans are dominant niche constructors,
58 but niche construction (i.e. the process in which an organism changes its own or other
59 species' environment) by nonhuman species might also impact ecosystem dynamics at local
60 scales through influencing available resources (Laland and Boogert 2008; Fuentes 2012).
61 Anthropogenic habitats will involve new components of human-plant-primate interactions
62 and hence new levels of complexity (Fuentes and Wolfe 2002; Sengupta *et al.* 2015).

63 There is growing evidence that anthropogenic disturbance – forest fragmentation,
64 hunting, selective logging, introduction of exotic species – affects ecosystem services such
65 as seed dispersal (i.e. the movement of seeds away from their parent plant) through altering
66 animal-plant interactions (Dennis *et al.* 2007; Wright 2007; Jordano *et al.* 2011). Such
67 processes can consequently influence animal-mediated dispersal impacting the number of
68 seeds dispersed and the local species richness of seedlings (especially for large-seeded
69 species which are less likely to be dispersed by smaller animals), as well as the dispersal

70 distances of fleshy-fruited tree species (Webb and Peart 2001; Cramer *et al.* 2007; Stoner *et*
71 *al.* 2007; Wang *et al.* 2007; Markl *et al.* 2012). In particular, the loss of large-bodied
72 frugivorous vertebrates, which are often disproportionately impacted by anthropogenic
73 pressure (Linder and Oates 2011; Wright 2003), will result in reduced frugivory and seed
74 dispersal activities within an ecosystem (Chapman and Chapman 1995; Babweteera and
75 Brown 2009).

76 Many primate species and populations live in environments that have been affected
77 by human activities including agriculture (Paterson and Wallis 2005; Fuentes and Hockings
78 2010; Estrada *et al.* 2012; Hockings and McLennan 2012; Hockings *et al.* 2015). For the
79 maintenance of habitat fragments and to understand the effects of seed dispersal on plant
80 populations and communities, it is important to identify frugivores that can persist in
81 degraded human-impacted habitats and those which are capable of dispersing larger seeds
82 within these habitats (Russo and Chapman 2011; Albert *et al.* 2014). There has been recent
83 interest in the importance of seed dispersal roles of more disturbance-tolerant and
84 ecologically flexible species, and their capacities to disperse numerous large seeds across
85 large distances (Albert *et al.* 2014; Arroyo-Rodríguez *et al.* 2015). If primates are not
86 persecuted directly through hunting and can respond flexibly to human-induced
87 environmental changes, there is the possibility to examine longer-term human-animal-plant
88 interactions.

89 Human settlement and cultivation introduces new plant species to areas where they
90 were previously absent (Hockings and McLennan 2012). These can become integrated into
91 a primate's diet resulting in changes to their behaviour, including activity budgets,
92 foraging, ranging and grouping patterns, and potentially their survival, including reduced

93 inter-birth intervals (for example, macaques (*Macaca tonkeana*): Riley 2008; baboons
94 (*Papio anubis*): Strum 2010; capuchins (*Cebus capucinus*): McKinney 2011; orangutans
95 (*Pongo abelii*): Campbell-Smith *et al.* 2011; chimpanzees (*Pan troglodytes*): Hockings *et*
96 *al.* 2012, McLennan 2013; gorillas (*Gorilla beringei beringei*): Seiler and Robbins 2016).
97 Studies on the impact of animal-mediated dispersal of exotic species show complex plant-
98 human-animal interactions. For example, the landscape-spread of *Opuntia stricta*, a highly
99 invasive cactus that was introduced by people to the Laikipia Plateau in Kenya, is a
100 response to recent changes in land use, primarily the sedentarization of pastoralists and
101 subsequent livestock grazing, as well as the feeding and ranging behaviour of its numerous
102 mammalian consumers (Strum *et al.* 2015). The ecological impacts of primates in
103 agricultural landscapes, for example, on nutrient cycles and seed dispersal, are for the large-
104 part unknown (Estrada *et al.* 2012). Equally, there are no empirical data on the dispersal of
105 cultivated foods by primates. This is despite many species inhabiting forest-farm matrices
106 and a huge literature on primate seed dispersal including some species that inhabit
107 plantations (such as black howler monkeys, *Alouatta pigra*, inhabiting cacao plantations:
108 Zárate *et al.* 2014).

109 Studies of animal disperser–plant interactions often examine behavioural patterns
110 (including foraging activity, movement patterns, and gut passage time) to explain overall
111 seed distance distributions and differential seed dispersal by microsite (Nathan and Muller-
112 Landau 2000). Seed dispersal effectiveness is determined by dispersal quantity (i.e. the
113 number of seeds that are dispersed) and quality (i.e. the likelihood that a dispersed seed
114 germinates and survives until reproductive maturity) (Schupp 1993). Examination of seed
115 shadows (i.e. the number of seeds at varying distances from the parent plant) or seed

116 dispersal kernels (i.e. the probability distribution of dispersed seeds in relation to distance)
117 are the most common methods to assess the spatial distribution of dispersed seeds
118 (Chapman and Russo 2007; Nathan and Muller-Landau 2000). The spatial distribution of
119 seeds can be influenced by various factors including seed handling (Lambert 1999) and
120 secondary dispersal and predation (Chapman 1989). Moreover, seed and seedling mortality
121 should be higher in proximity to the parent plant due to higher densities/numbers of
122 predators or pathogens (Janzen 1970; Connell 1971; Balcomb and Chapman 2003).
123 However, incorporating animal behaviour into estimates of seed dispersal shadows remains
124 a challenge (Garber 1986; Russo and Augspurger 2004). The mechanisms that impact the
125 spatial distribution of trees within a habitat are complex (Levine and Murrell 2003). Some
126 research shows that adult tree distributions and primary dispersal patterns by primates are
127 spatially aggregated (e.g. near to or under sleeping sites and feeding trees: spider monkeys,
128 *Ateles paniscus*, Russo and Augspurger 2004; capuchin monkeys, *Cebus capucinus*:
129 Valenta *et al.* 2015), even though mortality should be higher when seeds are deposited in
130 such high density clumps.

131 Large bodied primate frugivores, such as nonhuman great apes, are considered
132 important seed dispersers because of their dietary diversity, their capacity to feed on large
133 fruits and ingest large seeds as well as their ability to break into fruits with hard-husks, the
134 large quantities of seeds they disperse, and long dispersal distances which might improve
135 seed survivorship (Lambert 1997; Lambert and Chapman 2005; Vidal *et al.* 2013; Beaune
136 *et al.* 2013, 2015; Haurez *et al.* 2015). Chimpanzees provide an appropriate model species
137 to examine seed dispersal of crops in anthropogenic habitats as they (1) occur in proximity
138 to agriculture throughout their geographic range (Hockings *et al.* 2015; Hockings and

139 McLennan 2012) and exhibit the ecological flexibility to exploit such human-influenced
140 habitats (Hockings *et al.* 2009; McLennan 2013; McLennan and Hockings 2014; Krief *et*
141 *al.* 2014; Bessa *et al.* 2015), and (2) are large-bodied frugivores that have been identified as
142 important seed dispersers (Wrangham *et al.* 1994; Lambert 1997). The diet of wild
143 chimpanzees is dominated by ripe fruit, irrespective of the environment (Goodall 1986;
144 Tutin *et al.* 1997; Pruetz 2006; Hockings *et al.* 2009; Watts *et al.* 2012).

145 Hockings and McLennan (2012) conducted a systematic review of crop feeding in
146 wild chimpanzees and found that chimpanzees consume 36 different crops from 27 sites
147 across tropical Africa with fleshy fruit crops targeted preferentially. The fruit pulp of cacao
148 (*Theobroma cacao*), a cultivated fruit species also known as cocoa, was among the most
149 commonly eaten crops across the chimpanzees' range and is predictably eaten wherever
150 chimpanzees have access to it. Crop consumption by chimpanzees, including cacao which
151 is typically grown as a commercial crop, is often not tolerated by local people.

152 Understanding any potential benefits to crop feeding by primates (such as the dispersal of
153 crops that might be used by humans) can promote the sustainability of human-primate
154 interactions through increasing human tolerance towards problematic behaviours.

155 Here we present data on chimpanzee use and dispersal of cacao across the core of
156 the chimpanzees' home range at Bossou. We examine factors that impact whether or not
157 cacao plants survive short-term. We hypothesised that chimpanzee flexible feeding
158 behaviour and processing of cacao, including whether seeds are ingested or not, will impact
159 cacao dispersal and survival. We predicted that chimpanzee dispersed cacao plants that
160 survived did so because they (1) were located further from the cacao plantation area
161 because plants are more likely to survive at increasing distance from the plantation area, (2)

162 were part of a cluster with fewer cacao plants because plants are more likely to survive with
163 fewer competing plants within the same cluster (3) were taller as more established plants
164 are more likely to survive than smaller plants, and (4) were in a location with a more open
165 understory because reduced competition with understory plants favours cacao growth.

166

167 **MATERIALS AND METHODS**

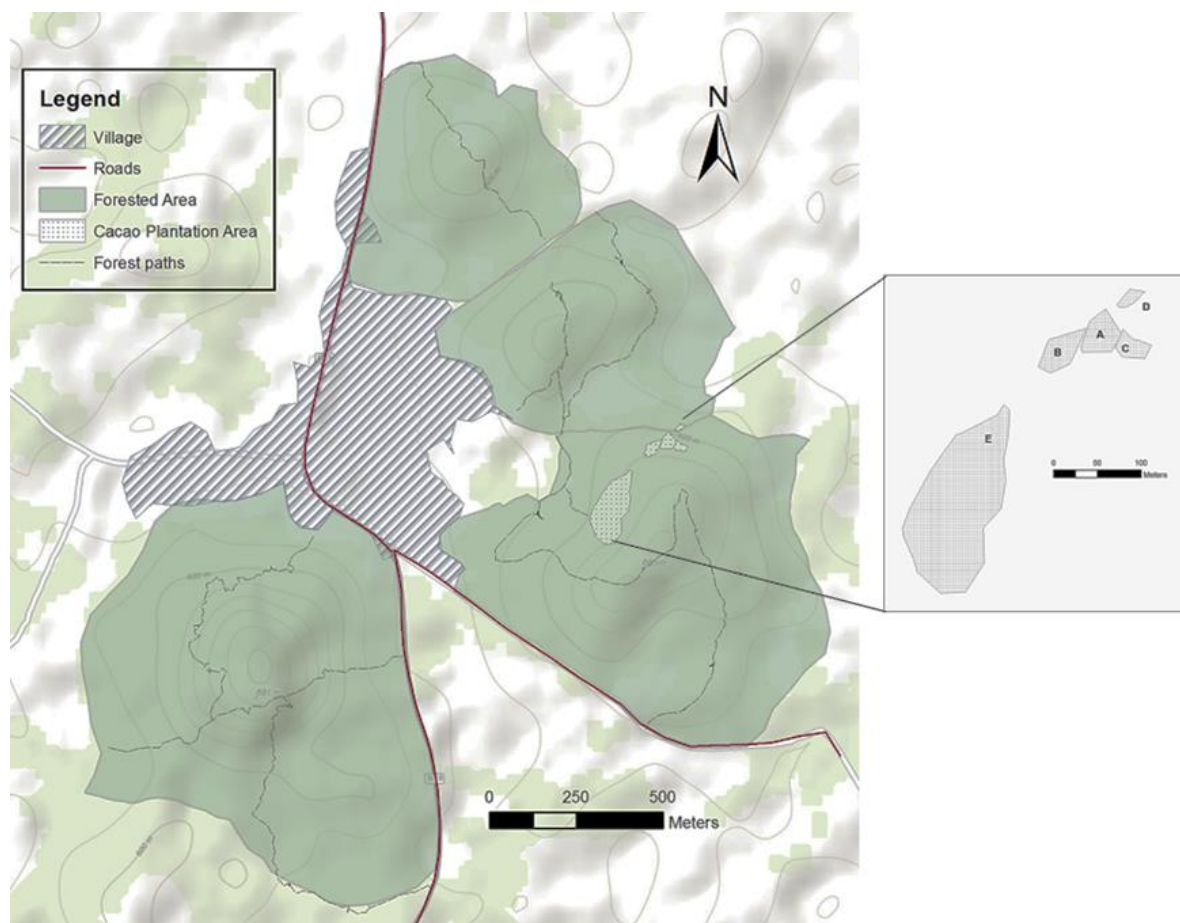
168 **Study site and subjects**

169 The village of Bossou is situated in the forest region in south-eastern Republic of Guinea,
170 West Africa (latitude 7° 38'71.7" N; and longitude 8° 29'38.9" W), approximately 6 km
171 from the Nimba Mountain range (Matsuzawa *et al.* 2011). The village is mainly inhabited
172 by the Manon ethnic group. The Manon family that founded Bossou remains one of its
173 most influential families and holds the sympatric chimpanzees as a sacred totem
174 (Yamakoshi 2011). Due to these local cultural beliefs humans and chimpanzees have
175 coexisted over many generations. Parts of the remaining forest at Bossou are also sacred in
176 local mythology. However, in recent years, aspects of development, various socioeconomic
177 factors, such as reliance on a cash income from crop sales, and fear of attack by
178 chimpanzees on local persons (Hockings *et al.* 2010; McLennan and Hockings 2016), have
179 altered human-chimpanzee relationship dynamics at Bossou. This has contributed to people
180 becoming less tolerant of chimpanzee crop feeding, despite chimpanzees at Bossou having
181 exploited agricultural foods for generations (Yamakoshi 2011).

182 The hills that constitute the 7 km² core of the chimpanzees' home range are split by
183 roads (Fig. 1; Hockings *et al.* 2006) and are mostly covered in secondary or regenerating
184 forest with small areas of primary forest. There are numerous paths/trails within the forest

185 that were created by humans and chimpanzees. Swidden (or ‘slash-and-burn’) agricultural
186 practices have resulted in a mosaic of thicket, cultivated fields and orchards within and
187 bordering the reserve. Chimpanzees at Bossou consume 17 crop species, including cacao,
188 and numerous parts, including fruit, leaf, pith, nut, tuber (Hockings *et al.* 2009). Crops were
189 consumed year-round and comprised 14% of feeding time, with variation across months
190 (monthly range: 3.6-26.3 %, \pm SD 76.9). The climate at Bossou is classified as tropical wet
191 seasonal; there is a clear wet season from March to October and a dry season from
192 November to February (Hockings *et al.* 2009; Takemoto 2004). There has been no previous
193 research on seed dispersal by chimpanzees at Bossou.

194



195

196 **Fig. 1.** Map of Bossou village and roads, the surrounding forested hills (including relief),
197 and the paths walked during ecological surveys. The plantation area is enlarged to show the
198 five areas A to E (see Table 2 for additional details).
199

200 Cacao is a small evergreen tree in the family Malvaceae. Cacao is cultivated as an
201 understory plant and was introduced from South America to West Africa in the 19th
202 Century by the Portuguese (Howes 1946). Both the young and mature leaves are distinctive
203 and easily identifiable; leaves are alternate, entire, and unlobed. The fruit, called a cacao
204 pod, is ovoid, and contains seeds, often called ‘beans’, embedded in a sweet white
205 mucilaginous pulp that chimpanzees feed on (Hockings and McLennan 2012). Mature
206 cacao pods of standard size at Bossou were 24.3 cm in circumference (\pm SE 0.5, N=10) and
207 14.9 cm in length (\pm 0.3). Each pod (hereafter called fruit) contained a mean of 45.5 ± 0.8
208 seeds (range: 41-49). Seeds are large, averaging $2.4 \text{ cm} \pm 0.3$ length and $1.4 \text{ cm} \pm 0.1$ width
209 (N=162 seeds measured from four pods at Bossou) and whole seeds are visible in
210 chimpanzee faeces. Riley *et al.* (2013) measured the nutritional content of cacao pulp and
211 compared it to forest fruits commonly ingested by Tonkean macaques in Sulawesi. Cacao
212 pulp contained significantly lower levels of protein, lipids and fibre, yet higher levels of
213 digestible carbohydrate, indicating greater digestibility and energy content than the forest
214 fruits sampled.

215

216 **Other species and cacao dispersal**

217 A methodological challenge in understanding seed dispersal by vertebrates is the
218 identification of the frugivore species disseminating the seeds (Gonzalez-Varo *et al.* 2014).
219 Aside from chimpanzees, no other large-bodied wildlife ingest whole cacao seeds at

220 Bossou. Although hornbills are present, hornbills generally feed at significantly higher
221 strata in the forest canopy i.e. greater than 20 m (Poulsen *et al.* 2002) and were never
222 observed (during long-term chimpanzee observations) feeding on cacao fruit or seeds.
223 Janson (1983) emphasizes that small bats and avian frugivores are less able to open fruits
224 protected in hard-husks than primates and other mammals. The large number of cacao seeds
225 that are found in clusters (see results) precludes that other smaller-bodied animals are
226 responsible for the cacao dispersed outside the plantation area at Bossou. Local people at
227 Bossou do not consume cacao fruit as part of their local feeding traditions; hence cacao
228 dispersal is not a result of local people feeding. Cacao is a small-scale commercial crop at
229 Bossou and people are not permitted to take it from plantations – which would be classified
230 as stealing – due to its high economic value. Furthermore, the original cacao plantation
231 (plantation zone A) is positioned at the bottom of a steep hill (Fig. 1); hence abiotic factors
232 such as wind and rain (i.e. during tropical storms) could not be responsible for the dispersal
233 patterns of large cacao seeds observed outside of the plantation area. Although it is unlikely
234 that dispersal from the original plantation to neighbouring plantation zones B and C (Fig. 1)
235 is a result of abiotic factors or secondary seed dispersal (e.g. by dung beetles moving
236 chimpanzee faeces), due to their immediate proximity to the original plantation this cannot
237 be completely ruled out. However, it was possible to confirm cacao dispersal by
238 chimpanzees to the furthest plantation in zone E through speaking directly with the
239 plantation owner who explained the origin of each cacao plant.

240

241 **Behavioural Observations**

242 Chimpanzee community size at Bossou varied over the complete study period (2004 to
243 2013) from 8 to 14 individuals (Matsuzawa *et al.* 2011). In 2004 to 2005, we collected
244 behavioural data to record cacao fruit feeding by chimpanzees across 12 months.
245 Community size varied over this period from 12 to 14 individuals, with five to six adult
246 females and the same three adult males present throughout. We randomly selected a focal
247 adult (we excluded all immatures) from a predetermined list each day and when possible
248 followed that individual from 0630h to nesting, that was usually between 17h00 and
249 19h00 (approx. 2500 hrs, \bar{x} = 8.95 hrs per day; Hockings *et al.* 2012). Every 5 min we
250 employed instantaneous sampling to record the ongoing activity of the focal individual, and
251 we noted the food species and part when feeding (Hockings *et al.* 2009, 2012). While
252 following the focal individual, we used all occurrence sampling to record cacao fruit
253 feeding by all individuals excluding infants. A cacao feeding event is defined as any
254 successful foray by an individual to obtain cacao fruit (Hockings *et al.* 2009).

255 In October and November 2011, we selected and followed an adult focal (based on
256 individuals who were considered most likely to feed on cacao fruit) to maximize the
257 likelihood of observing cacao feeding and cacao dispersal (N = 22 days, approx. 149 hrs,
258 mean = 6.8 hrs per day). If we observed a chimpanzee consuming cacao fruit who was
259 known not to have consumed cacao in the previous three days, that individual was selected
260 as a focal and followed continuously until the faeces contained no more cacao seeds (total
261 N = 4 follows, including 3 individuals). This was possible as we knew exactly how many
262 fruits had been consumed and the approximate number of seeds in each fruit. We recorded
263 the locations of seeds that were spat out and those deposited in faeces after being ingested
264 to monitor if germination occurred or not (see below for details). We obtained data on the

265 approximate gut passage time of cacao seeds from nest to nest focal follows of adult
266 individuals that we observed feeding on cacao fruit and ingesting the seeds. We ensured the
267 focal had not fed on cacao fruit in the preceding three days, and were continuously
268 followed without being lost until their faeces no longer contained cacao seeds; hence we
269 accounted for all cacao seeds. Based on chimpanzee behavioural observations, we define
270 cacao clusters as ‘spatial aggregations of seeds or plants that were deposited in the same
271 faeces or in the same feeding spot by an individual’. In 2013, we did not employ systematic
272 ethological data collection methods throughout the entire two month data collection period
273 as new Bossou site regulations restricted chimpanzee follows. However, during this period
274 we followed an adult male for one week and we observed one cacao fruit feeding event and
275 we confirmed the gut passage time of cacao (see results).

276 On the two occasions when we observed consumption of unripe fruit (i.e. pod green
277 in colour but full-sized and with mature seeds) they were transported short distances by the
278 chimpanzee resulting in two clusters (see Fig. 2 for an example of a cluster) of dropped
279 cacao seeds per occasion (total N=4 clusters). When the seeds from ripe fruits (yellow in
280 colour) were ingested on two occasions, five faeces (hence five clusters) were deposited on
281 both occasions (total N=10 clusters). If we did not directly observe a cacao feeding event
282 but fresh chimpanzee traces were found directly after the feeding event, then we monitored
283 the seeds (N=4 clusters, only unripe fruits). We monitored a total of 18 clusters of cacao
284 seeds (N=245 seeds) for germination success. Beyond looking for evidence of crushed or
285 damaged seeds, and whether the seeds germinated or not, we did not assess the survival of
286 the seedlings (over the 2 month study period in 2013) and efficacy of different seed
287 handling techniques due to the limited observations.

288

289 **Cacao plantations**

290 When we first collected behavioural data on chimpanzee crop feeding in 2004, cacao was
291 grown in one small orchard, hereafter the ‘original plantation’ (Fig. 1, area A). The owner
292 started planting cacao at this location in 1986 and abandoned it in 2004 (but remained the
293 recognised owner). When we collected data on cacao dispersal in 2011 and 2013, three
294 newer plantations had been established that contained cacao and that were in proximity to
295 the original plantation (areas C, D, E). There was also one cultivated area that had been
296 abandoned in 1992 that contained banana plants, mango and avocado trees on the slope
297 leading down to the original plantation (area B). In this abandoned plantation, chimpanzees
298 often rested in a large *Ficus anomanii* tree after feeding on cacao and sometimes defecated
299 cacao seeds from the tree canopy. These five plantations are hereafter named the ‘plantation
300 area’. These were the only sources of cacao from which the chimpanzees could feed from
301 during the study period; this avoids one of the main methodological challenges in
302 understanding vertebrate-mediated dispersal (Gonzalez-Varo *et al.* 2014).

303 Each plantation was mapped using GPS. For each cacao plant (excluding those in
304 the fruit-fall zone of mature plants) within each plantation, we collected data in 2013 on (1)
305 the GPS location of the plant, (2) cacao plant height, (3) whether the plant had previously
306 produced fruit or not, and (4) whether there was evidence that chimpanzees had consumed
307 cacao fruit from that plant, either from direct observations (from long-term direct
308 observations of chimpanzee behaviour) or from distinguishing between the methods used
309 by humans and chimpanzees to detach the pods. At Bossou, farmers cut the pods from the
310 plants with large knives attached to poles, leaving different traces to chimpanzees that tear

311 the pods from the trunk or branch. We asked the owners of plantations A,C,D,E which
312 cacao they had planted (the previous owner of plantation B could not be located) along with
313 their planting techniques and cacao requirements. Humans did not plant cacao outside of
314 the plantations.

315

316 **Cacao surveys**

317 From October to November in 2011 we made an initial assessment of cacao distribution by
318 chimpanzees across the core of their home range, to which the Bossou chimpanzees mostly
319 confine daily activities (Humble 2011). Then in the same period in 2013 we monitored the
320 same plants to assess short-term cacao survival (i.e. over the two years). We conducted
321 surveys (methods replicated in 2011 and 2013) through systematically walking the main
322 paths (Fig. 1, total= 8.7 km) used by chimpanzees on four hills that constitute the core of
323 their home range: Gban (3.5 km of paths), Guein (2.7 km), Gboton (1.7 km), and Ueyaton
324 (0.8 km). The distribution of paths was originally designed to be evenly distributed across
325 the chimpanzees' habitat, and chimpanzees habitually use the paths for travel. This method
326 was chosen over more random sampling (e.g. random plots) which is impractical in this
327 human-impacted habitat as many areas are private and/or sacred and hence cannot be
328 modified (e.g. through cutting vegetation or through use of tagging tape). We counted all
329 cacao plants within a 5 m perpendicular distance from the centre of the path (total survey
330 area 8.7 ha). During chimpanzee follows we opportunistically recorded cacao plants that
331 had been dispersed by chimpanzees but which we did not encounter during surveys on the
332 main paths.

333 When we located single cacao plants or clusters, we gave the plant or cluster a code
334 to enable later identification. For each plant or cluster of plants we collected the following
335 data: (1) GPS location; (2) number of plants; (3) furthest distance between plants within a
336 cluster; (4) the height of each plant; (5) the openness of the understory (horizontal visibility
337 beyond 10m was classified as open, and less than 10m was classified as closed). Cacao
338 plants require appropriately spaced canopy trees for optimal growth. Certain conditions are
339 also favoured, including specific trees to provide shade for the cacao and fertilize the soil
340 especially during the dry season, as well as trees that do not serve as alternative hosts to
341 disease and pests which can affect the cocoa underneath it (Asare 2006). It was beyond the
342 scope of this research to determine the complex yet specific combination of shade tree
343 species and characteristics required for maintaining optimal cacao growth in a forested
344 habitat. As a measure for the amount of light reaching the cacao on the forest floor, we
345 rated the horizontal openness of the understory in proximity to cacao, with an open rather
346 than closed understory resulting in reduced competition with other plants (Asare 2006).

347 We classified seedlings as <50 cm high, saplings as 50-200 cm high, poles as 201-
348 400 cm high, and mature plants as >400 cm based on the ability of plants of that size to
349 produce fruit in plantations (adapted from Beaune *et al.* 2015). We employ the term ‘plant’
350 to cover all size classifications. For mature cacao plants, we recorded whether a plant had
351 conjoined trunks (i.e. formed from the growth of multiple closely deposited seeds) or
352 whether it had a single trunk (i.e. came from a single seed). We took care to distinguish
353 between cacao plants from a single seed that had split and had multiple branches to those
354 that had separate trunks to ensure we accurately counted the number of plants.

355

356 **Data analysis**

357 We analysed data statistically using SPSS version 22 (SPSS Inc., Chicago, IL, U.S.A.). We
358 conducted parametric analyses only when data were normally distributed with homogeneity
359 of variance (Sokal and Rohlf 1995), and we checked data for multicollinearity. We
360 considered all the hypotheses as two tailed and tested at $P < 0.05$. We present averages as
361 means with standard errors (SE).

362 We calculated % focal feeding time on cacao fruit and other species by dividing the
363 time spent feeding on cacao fruit by all adults across the 12 months by the total feeding
364 time on all wild and cultivated species and food parts across the same period.

365 We calculated the straight-line dispersal distance between georeferenced cacao
366 plants (outside the cacao plantation area) and the closest part of the plantation area using
367 ArcGIS version 10.2.1.

368 To examine whether the cacao clusters varied greatly in their spread (defined as the
369 furthest distance between cacao plants within a cluster) according to the number of cacao
370 seeds in the cluster we ran a Spearman's rank test on all clusters with greater than one seed
371 ($N=59$; cacao plants identified in 2011 or 2013).

372 From direct observations in 2011 we examined if seeds spat out or deposited in
373 faeces by chimpanzees germinated or not (265 seeds deposited in 18 separate clusters by at
374 least three individuals). We calculated the short-term survival of all cacao identified in
375 2011 (through ecological surveys or whilst following the chimpanzees) by examining
376 whether at least one plant in a cluster survived for two years or not. To examine the factors
377 impacting plant survival or not in the two year period, we ran a Logistic Regression with
378 plant survival in each cluster (total clusters, $N=59$) as the binary response dependent

379 variable. As independent variables we included (1) distance to plantation (m), (2) number
380 of cacao plants per cluster, (3) average height of cacao plants (cm) in 2011, and (4)
381 horizontal openness of habitat.

382 Our non-random methods to examine the distribution of cacao across the habitat
383 precluded randomized estimates of cacao density in relation to distance from the plantation
384 area. However, to gain an approximation of how distance from the plantation area impacts
385 cacao densities, we examined the number of cacao clusters corresponding to the total area
386 of path surveyed and the total area within each 100 m distance category. Using ArcGIS we
387 created multiple ring buffers at 100 m intervals from the plantation area polygon. Using the
388 tabulate intersection function in ArcGIS, for each distance category we calculated (1) how
389 many cacao clusters were present, (2) the total forested area in the chimpanzees core range
390 area, and (3) the total path distance surveyed. We divided the number of cacao clusters by
391 the total path area (i.e. path length multiplied by 10 m) and total area within 100 m distance
392 categories from the plantation area.

393

394 **Ethical note**

395 All research involving wild chimpanzees was non-invasive and strictly adhered to ethics
396 guidelines detailed by the Association for the Study of Animal Behaviour (UK), and the
397 ethical committee of the Bossou and Nimba International Research Group at Kyoto
398 University. Permission to carry out this fieldwork was granted by the Direction Nationale
399 de la Recherche Scientifique et de l'Innovation Technologique (DNRSIT) and Institut de
400 Recherche Environnementale de Bossou (IREB), and adheres to the legal requirements of
401 the Republic of Guinea in which the research was conducted.

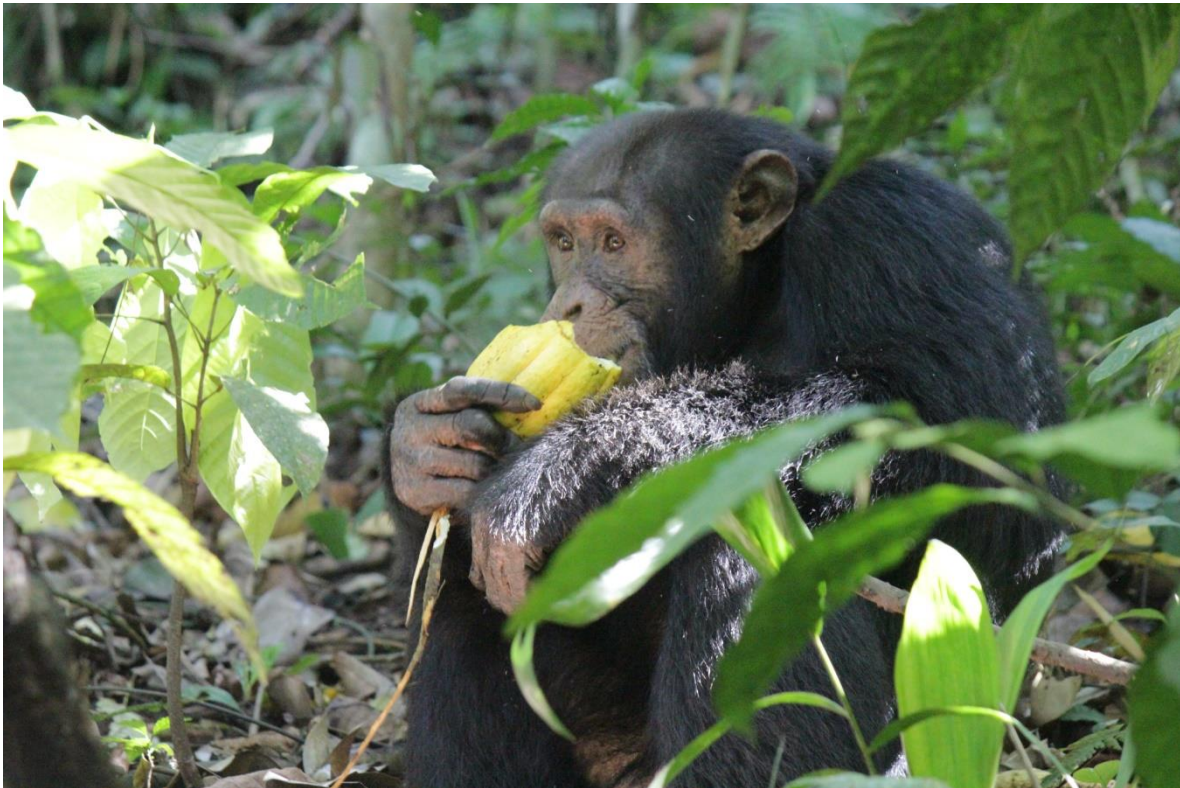
402

403 **RESULTS**

404 **Chimpanzee cacao feeding behaviour and gut passage times**

405 Chimpanzees at Bossou consumed cacao fruit in 13 of 187 focal observation days, with a
406 total of 34 cacao feeding events. Cacao was eaten in five months of the year but mostly in
407 October (21 of 34 events). Although we observed most chimpanzees ingesting cacao (10 of
408 12 individuals excluding infants present for all-occurrence sampling during 2004-2005
409 cacao season), cacao was not an important food in this community, constituting only 0.23
410 % of total focal feeding time (N=9 focal adult individuals, range: 0-15 mins, mean=5.56 ±
411 1.76). Chimpanzees spent between 1.17 to 13.93 % of their feeding time on their 25 most
412 consumed food species and parts, and cacao was ranked in 55th in its importance in their
413 diet (Supplementary Table 3). The chimpanzees consumed pulp from both ripe and unripe
414 cacao fruits, although mostly selected ripe fruits (28 of 34 events; Fig. 2). Chimpanzees
415 dropped or spat out the seeds from unripe cacao, whereas they swallowed the seeds and
416 pulp from ripe cacao in all cases (Supplementary video 1). The chimpanzees subsequently
417 deposited the ingested cacao seeds in faeces and dispersed a mean of 14.72 ±SE 2.84 cacao
418 seeds per cluster (defecated clusters: mean=10.80 ± 3.35, range: 1-34 seeds: N=10; spat out
419 clusters: mean=19.63 ± 4.44, 1-39 seeds, N=8). The gut passage times for cacao ranged
420 from 6.9 h to 25.8 h (see Supplementary results for descriptions of events). We did not
421 observe any instances of cacao seed destruction by chimpanzees and did not find chewed or
422 damaged seeds in faeces.

423



424
425
426
427
428
429

Fig. 2. Adult male chimpanzee at Bossou feeding on ripe cacao fruit. The ripped branch, from where the chimpanzee tore the fruit from the cacao tree, is attached to the pod in his hand (photo taken by N. Bryson-Morrison).

430 **Cacao dispersal and short-term survival**

431 The seeds from 17 of 18 monitored cacao clusters germinated within one week of
432 deposition by chimpanzees, with an average 92.9 % germination success per cluster (range:
433 50-100 %, N=17 clusters including a total of 249 seeds). Cacao seeds can germinate in
434 faeces or when spat out by chimpanzees whilst feeding on the pulp. The seeds that did not
435 survive were either found rotten or had disappeared and were likely preyed upon by other
436 animals.

437 Across the survey periods in 2011 and 2013, we recorded 436 cacao plants in 90
438 clusters that had been deposited by chimpanzees outside of the plantation area (Fig. 3 for

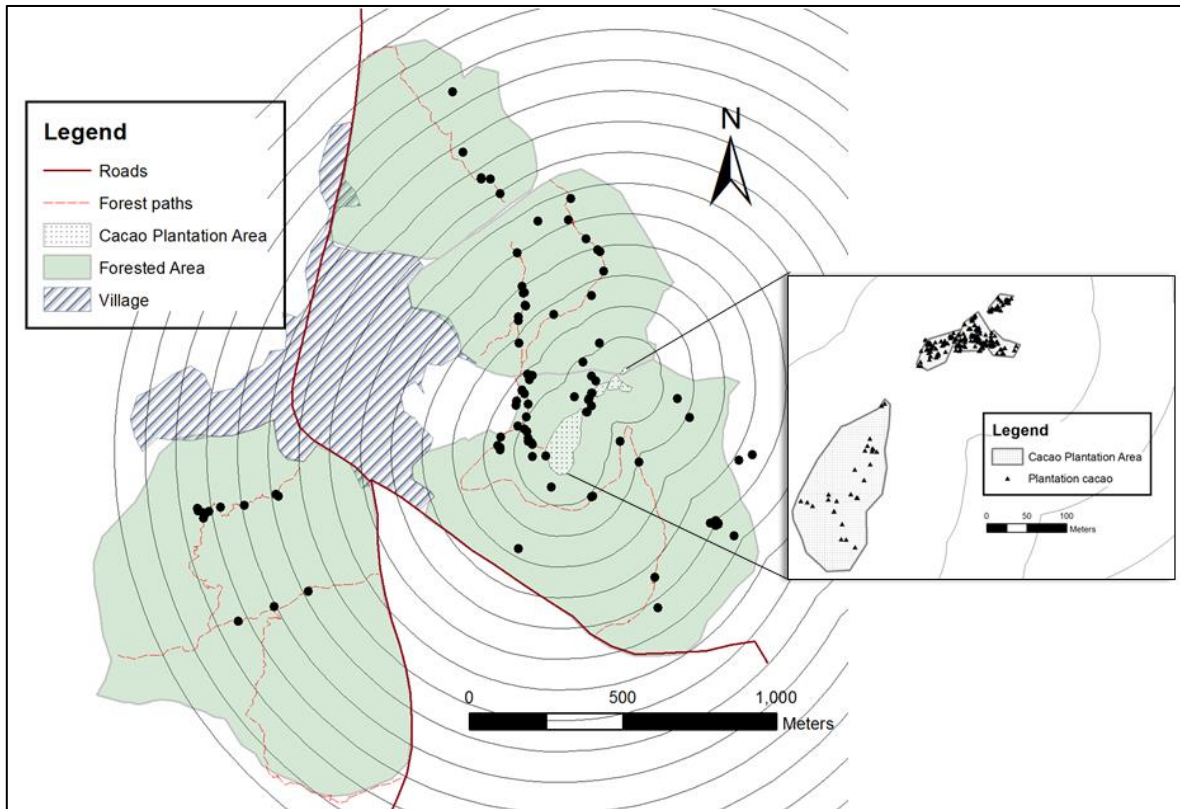
439 examples of cacao plants and clusters). 59 clusters were identified in 2011 and an
440 additional 31 clusters were identified in 2013, taking the total number of clusters identified
441 during the research period to 90. Of the 90 clusters, 60 were located through surveys along
442 paths and 30 through chimpanzee follows. Chimpanzees dispersed cacao from 4 m up to
443 1130 m outside of the plantation area, with a mean distance of $406.82 \pm SE 0.56m$ (N=90
444 clusters). Cacao plants were distributed across the four main hills within the core of the
445 chimpanzees' home range (Fig. 4).

446



447

448 **Fig. 3.** (a) ripe cacao pod with seeds surrounded by white pulp, (b) cluster of cacao
 449 seedlings from the same faeces, (c) young cacao sapling with distinctive bright green
 450 leaves, (d) cluster of saplings on the edge of a main chimpanzee path, (e) mature cacao tree
 451 with a conjoined trunk, a result of more than one seed from the same chimpanzee faeces
 452 growing and reaching maturity.
 453
 454

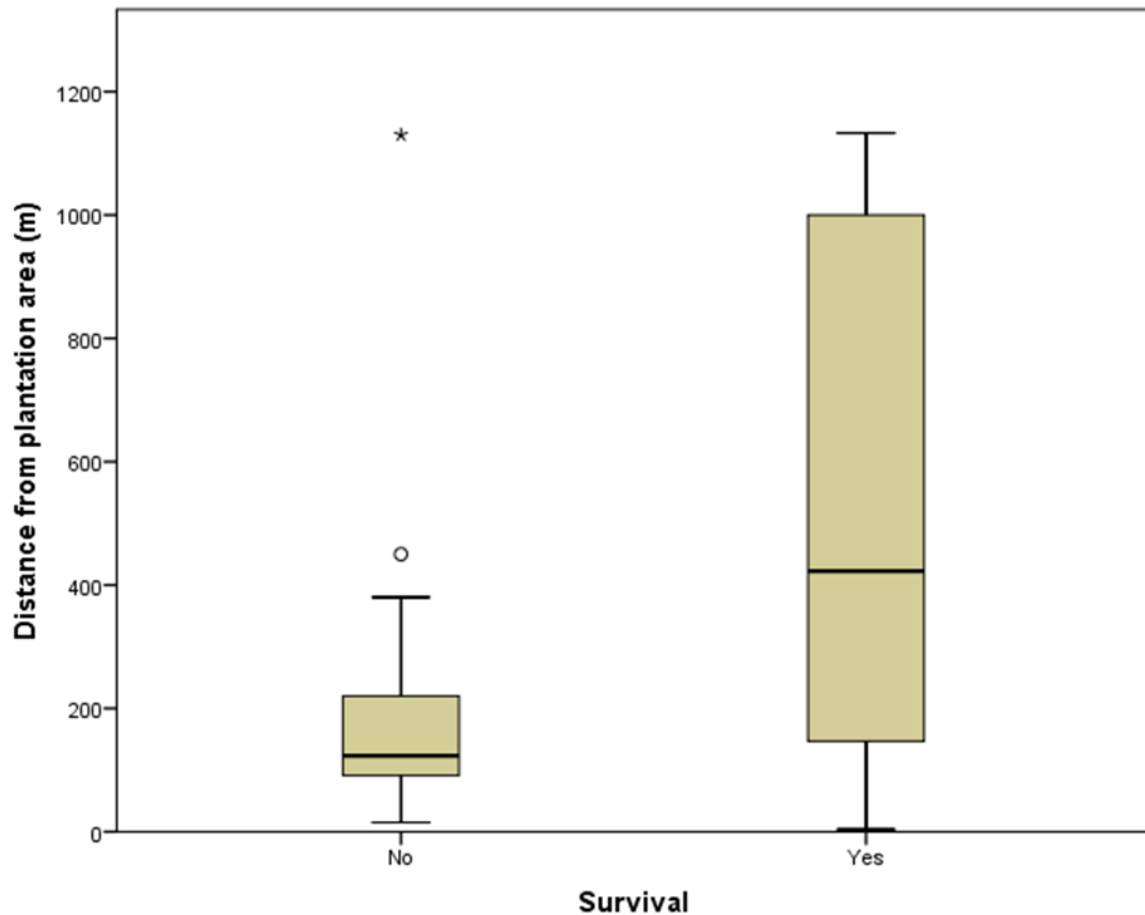


455
 456 **Fig. 4.** Cacao distribution (cacao plants/clusters are shown by black dots) across the core of
 457 the Bossou chimpanzees' home range with 100 m distance rings from the plantation area
 458 (also shown enlarged).
 459

460 The mean number of plants per cluster was $4.84 \pm SE 0.61$ (range: 1-27) and clusters
 461 with more cacao plants had a significantly wider spread (i.e. the furthest distance between
 462 plants within a cluster) than those with fewer plants (Spearman's rank: $r_s=0.503$, $N=59$,
 463 $P=0<0.001$). The mean height of plants per cluster was $98.3 \text{ cm} \pm SE 13.22$, although

464 maximum plant height was 700 cm. 51.1 % of clusters were seedlings (N=46), 35.6 % were
465 saplings (N=32), 10 % were poles (N=9), and 3.3 % mature plants (N=3).

466 Cacao survival in the forest was predicted by distance from plantation area (Table
467 1): cacao closer to the plantation area was less likely to survive the two year period than
468 those further away, but there was high variation in the distances from which plants survived
469 (Fig. 5). Other factors did not predict short-term cacao survival (Table 1).
470



471 **Fig. 5.** Box plot (showing maximum and minimum values as whiskers above and below the
472 central rectangle which spans the first quartile to the third quartile; the horizontal line inside
473 the rectangle shows the median, and outliers are shown as an open circle and asterisk) of
474 cacao survival from 2011 to 2013 (total N=59; died N=21, survived n=38) at different
475 distances (m) from the plantation area.
476

477
 478
 479
 480
 481

Table 1. Factors included in the logistic regression model and their significance in predicting cacao survival.

	β	s.e.	wald	df	exp(β)	95 % C.I.		Sig.
						Lower	Upper	
Understory	.093	.652	.020	1	1.097	.306	3.938	.887
Distance to Plantation	.003	.001	4.607	1	1.003	1.000	1.005	.032*
Number of cacao plants	.090	.117	.587	1	1.094	.869	1.377	.443
Plant height	.012	.007	2.555	1	1.012	.997	1.026	.110
Constant	-1.524	.872	3.056	1	.218			.080

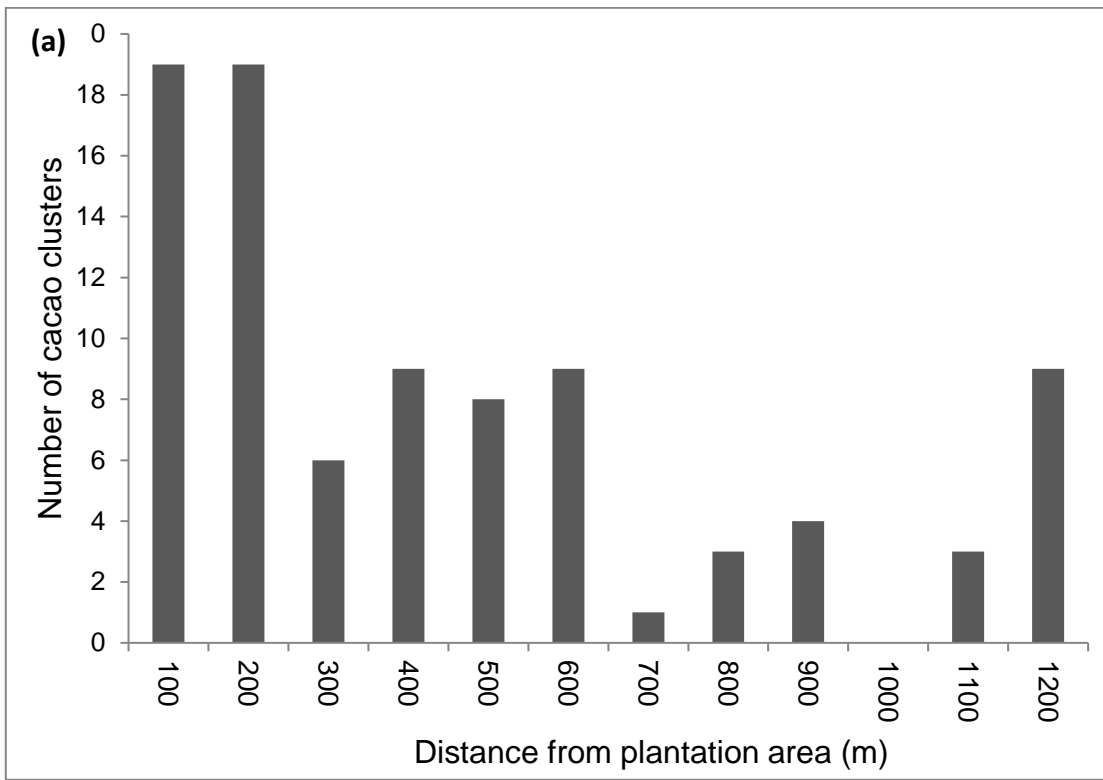
482 Logistic Regression where overall model $X^2 = 16.50$, $df=4$, $P<0.01$, $N=59$, $R^2 = .24$ (Cox and Snell). For each
 483 factor the following model parameters are shown: unstandardised b-coefficients (β) with associated standard
 484 error (s.e.) and 95% confidence intervals (CI), odds ratio (exp (β)), and the tests significance.

485

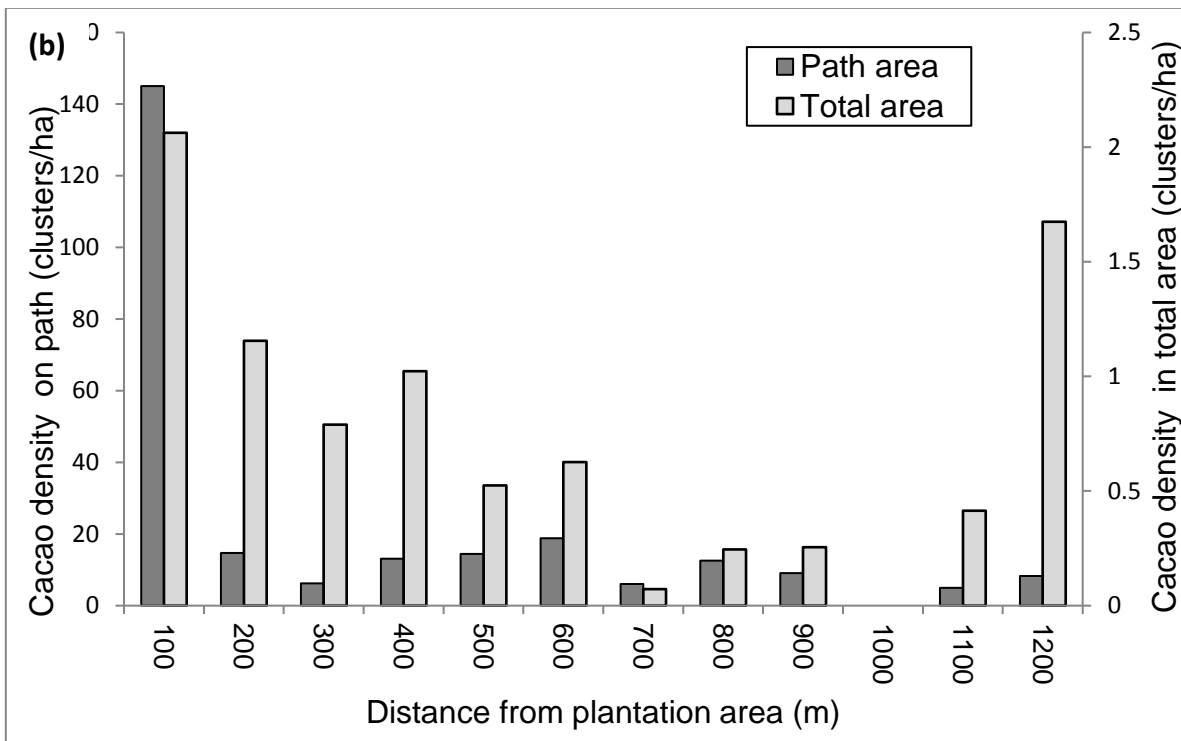
486 The number of cacao clusters decreased with increasing distance from the plantation
 487 area, but increased again at distances of 1100 to 1200m (Fig. 6a). A similar pattern
 488 occurred when we calculated cacao density from total area of forest within each distance
 489 ring (Fig. 6b). When we calculated densities using path area surveyed within each distance
 490 category, the density of cacao was high up to 100m from the plantation area but then low at
 491 all other distance categories (Fig. 6b).

492

493



494



495

496 **Fig. 6.** (a) Frequency distribution of cacao clusters from the cacao plantation area across
497 different distance classes (0-100m, 101-200m, and so on), and (b) Densities of cacao
498 clusters (number per ha) calculated from path area and total area across different distance
499 classes.
500

501 **Cacao maturity and fruit production**

502 The height of fruit-producing cacao in plantations was greater than that of cacao unable to
503 produce fruit, and ranged from 357 to 1100 cm, averaging 578 cm (\pm SE 19.6). Despite
504 some cacao plants in the forest attaining maturity (i.e. >400 cm height), they were unable to
505 produce fruit. In contrast, cacao dispersed by chimpanzees into a guarded mixed-crop
506 plantation (plantation area E) was able to mature and to produce fruit (Table 2). The owner
507 said that chimpanzees frequently crossed his banana (*Musa spp.*) plantation and deposited
508 the cacao seeds in their faeces, and that he subsequently tended to the cacao seedlings to
509 ensure their survival. Four of the mature cacao plants in that location had multiple
510 conjoined trunks and had been formed from a cluster of cacao seeds within one chimpanzee
511 faeces (Fig. 3e; Table 2).

512

513

514

515

516

517

518

519

520 **Table 2.** Forest and plantation areas at Bossou containing cacao.

Guard level	Area size (ha)	No. cacao plants (clusters)	% (N) cacao planted by humans	No. mature cacao clusters	% (N) fruit-producing mature cacao	% (N) mature cacao conjoined	
Forest	230	436 (90)	0	3	0 (0)	33.3 (1)	
Plantation							
A. Original	Abandoned	0.15	86 (74)	51.4 (38)	48	87.5 (42)	4.2 (2)
B.	Abandoned	0.11	119 (48)	0	9	11.1 (1)	11.1 (1)
C.	Guarded	0.08	36 (25)	0	11	63.6 (7)	18.2 (2)
D.	Guarded	0.04	24 (24)	100 (24)	0	-	-
E.	Guarded	1.53	47 (27)	7.4 (2)	15	86.7 (13)	26.7 (4)

521

522 In the original plantation (plantation A), the cacao planted by the owner in 1986
 523 accounted for over half the total cacao present in that zone during surveys (Table 2). From
 524 2004 to 2005, we recorded that chimpanzees solely consumed cacao from this plantation
 525 and frequently spat out the seeds of unripe fruits. The remaining cacao that the owner had
 526 not planted himself was either a result of chimpanzee feeding (or feeding in-situ by other
 527 small-bodied animals) or natural fruit-fall under the canopy. To optimize cacao growth, the
 528 owner of plantation A employed a 3m x 3m spacing pattern between cacao seedlings,
 529 planting one seed per spacing and hence none of these mature cacao plants had conjoined
 530 trunks. In contrast, between 4.2 and 26.7 % of mature cacao trees across plantations were
 531 created by multiple cacao seeds in the same cluster (which physically differs from cacao
 532 trees from one seed with multiple stems; Table 2, Fig. 2F)

533

534 **DISCUSSION**

535 This paper provides empirical data on the dispersal of a crop by a large-bodied mammal in
536 a tropical agricultural landscape, demonstrating interactions between flexible foraging
537 behaviour by chimpanzees (i.e. feeding on cultivated foods and crop handling), human
538 behaviour, and plant survival. Even though cacao was only available seasonally at Bossou
539 and was not an important food to this community (based on the amount of time spent
540 feeding and not on the absolute quantity ingested and/or nutritional value), it was dispersed
541 by chimpanzees across the core part of their home range. As predicted, the way in which
542 chimpanzees handled cacao impacted its subsequent dispersal. When fruits were ripe the
543 seeds were swallowed with the pulp, whereas when the fruits were unripe chimpanzees spat
544 out the seeds. At Bulindi in Uganda the chewed cacao pulp was detected in 12.3 % of
545 chimpanzee faeces and was consumed in 12 of 13 survey months (McLennan 2013).
546 Despite long-term monitoring of chimpanzee diet at this site through faecal sampling,
547 mature cacao seeds were rarely observed in chimpanzee faeces. Chimpanzees at Bulindi
548 often consume immature pods that lack fully formed seeds, and when ripe pods are eaten,
549 the chimpanzees appear not to ingest the seeds and instead spit them out (McLennan pers
550 comm). Chimpanzees show inter-community differences in the crops that they target even
551 if the same crops are available (McLennan and Hockings 2014). Our results indicate that
552 chimpanzees might also exhibit different food processing techniques, in this case for
553 cultivated foods, impacting the likelihood and potential patterns of crop dispersal. Given
554 that primates will be increasingly exposed to novel food resources in anthropogenic
555 habitats, examining variations in the techniques employed to process novel resources by
556 different primate species and/or groups of primates is an interesting line of future enquiry.

557 The number of dispersed seeds depends on the number of visits to the plant by an
558 animal disperser and the number of seeds swallowed per visit. The quality of seed dispersal
559 depends on the quality of the treatment given to the seed in the animal's mouth and gut, and
560 the quality of seed deposition which can be directly associated to animal behaviour and
561 physiology (e.g. their diet, ranging, gut size, food passage rates and defecation patterns, i.e.
562 whether they deposit seeds singularly or in clumps) (Schupp 1993). Both cacao seeds
563 swallowed (and passed in faeces) and spat out by the chimpanzees germinated. This
564 research did not investigate the effect of seed predators and secondary dispersers on the
565 post-dispersal fate of cacao seeds, but are likely important in plant-primate interactions
566 (Arroyo-Rodríguez *et al.* 2015). The cacao plants identified during the surveys (many of
567 which were already saplings, poles or mature plants when surveys started) show that cacao
568 dispersed by chimpanzees in the forest can survive for multiple years but does not produce
569 fruit. However, contrary to predictions, cacao plant size and the number of cacao plants per
570 cluster did not significantly impact likelihood of survival. To understand why the density of
571 the understory vegetation did not impact cacao survival, more fine-tuned data on specific
572 characteristics of the surrounding vegetation down to the species level and the requirements
573 of cacao in forested habitats are required. Distance from the plantation area was the only
574 measured factor that significantly influenced whether cacao survived or not, which is
575 consistent with ecological seed dispersal theory whereby mortality should be higher in
576 proximity to the parent plant due to higher densities/numbers of predators or pathogens
577 (Janzen 1970; Connell 1971). Some cacao did survive in proximity to the cacao plantations,
578 likely due to large numbers of cacao seeds being deposited in the area: chimpanzees
579 transported cacao short distances before feeding and spitting the seeds, or sometimes rested

580 in nearby trees after feeding on cacao and subsequently defecated the seeds (which were
581 shown to have low gut passage times) in large quantities. This is consistent with other
582 studies that demonstrate clumped patterns of seed deposition in areas where primates
583 repeatedly defecate, irrespective of low per capita seed survival under nesting sites or
584 parent trees (Russo and Augspurger 2004).

585 Chimpanzees at Kibale dispersed seeds a greater distance from either the parent tree
586 or any other tree of that species compared to sympatric primates due to long digestive
587 passage times (mean passage time = 31.5 h) and daily travel distances of up to several
588 kilometers (Lambert 1997). Bonobos at Salonga National Park in the Democratic Republic
589 of Congo, ingested *Dialium* fruits with seeds that are disseminated in their faeces at
590 considerable distances (average: 1.25 km after 24 hr of average passage time) and after gut
591 passage, seeds are better able to germinate (Beaune *et al.* 2013). Our estimates for gut
592 passage times were shorter than these previous estimates in wild chimpanzees. This might
593 be due to the large seed sizes of cacao and the large number of seeds ingested which
594 encourage them to pass rapidly through the gut. However, cacao was generally dispersed
595 over relatively large distances of up to 1100 m from the cacao plantation area. As seeds
596 were often swallowed whole by chimpanzees at Bossou, dispersal characteristics were
597 inherently related to chimpanzee ranging behaviour. Our data are consistent with what we
598 know about chimpanzee ranging behaviour in this community whereby individuals can
599 travel between the four main hills over the course of one day. Future research should link
600 spatial data on chimpanzee daily movements with seed dispersal patterns over time (Zárate
601 *et al.* 2014). Seed shadows of dispersal patterns of cacao were similar when calculated
602 using numbers and densities per total area of forest in each distance category, with cacao

603 decreasing at increasing distance from plantation area, albeit with a slight increase between
604 1100-1200 m. However, cacao densities calculated from total path area surveyed within
605 each distance category showed a different distribution pattern with high densities up to 100
606 m from the plantation, then consistently low densities at all other distance categories. An
607 increased likelihood of encountering cacao whilst following chimpanzees in the forested
608 areas in proximity to the cacao plantations during cacao season might account for this
609 discrepancy.

610 Cacao located in the forest was never observed to produce fruit – if monitored
611 plants had produced fruit outside the research periods (which coincided with the main
612 cacao season within the plantation area at Bossou), distinctive traces would have been
613 found on the cacao plant itself. The dense upper canopy within the forest restricts cacao
614 maturation, especially fruit production, as it restricts light to the understory and young
615 cacao plants are forced to compete with other vegetation (Asare 2006). In contrast, cacao
616 that had been deposited by chimpanzees into plantations did survive until maturity and
617 were able to produce fruit. We have observed chimpanzees feeding on cacao from mature
618 cacao plants in plantation E that they had originally dispersed to that location. The owner
619 described how he identified the cacao seedlings deposited by chimpanzees within his
620 plantation and in the neighbouring forest that he subsequently cleared to expand his
621 plantation. Due to the high economic value of cacao, he frequently cleared any understory
622 vegetation and removed most large canopy trees, leaving a few remaining shade trees,
623 which provided optimal growing requirements for the cacao. Due to these maintenance
624 activities, he emphasized his ownership of the cacao, despite acknowledging the cacao had
625 been ‘planted’ by the chimpanzees. Although the farmer tolerated some cacao feeding by

626 chimpanzees, he said he was forced to harvest cacao quickly otherwise chimpanzees would
627 take it all, and expressed annoyance that chimpanzees frequently consumed other crops
628 including bananas in his plantation.

629 Cacao dispersal by chimpanzees outside of plantations does not result in the
630 production of additional fruit and hence does not enrich the Bossou chimpanzees' diet. The
631 dispersal of this crop is unlikely to have long-term implications for chimpanzee persistence
632 at this site especially in light of an ageing and declining chimpanzee community (Sugiyama
633 2004; Matsuzawa *et al.* 2011). However, this research has highlighted the possibility that
634 animal-mediated dispersal of crops at other sites has the potential to positively impact the
635 ability of wildlife to persist in human-impacted habitats, especially if farmers obtain
636 economic benefits through wildlife crop dispersal. To examine this requires an
637 understanding of the local crop assemblages and their growing requirements, and the crops
638 targeted by primates at that location. A more complete understanding is required of
639 frugivorous primates as niche constructors and how the dispersal of wild and crop foods at
640 human-impacted sites by primates determines the abundance, diversity and distribution of
641 tropical plants and other animal species, and how this potentially benefits local human
642 populations (Sengupta *et al.* 2015). Like other large-bodied frugivores inhabiting disturbed
643 habitats (e.g. western lowland gorillas, *Gorilla gorilla gorilla*; Haurez *et al.* 2013), the
644 local extirpation of chimpanzees at Bossou will potentially result in changed and
645 impoverished tree regeneration of a whole forest ecosystem (e.g. for brown lemurs,
646 *Eulemur fulvus*; Ganzhorn *et al.* 1999).

647 We agree with Sih *et al.* (2015) that new behavioural ecology theory should be
648 incorporated into population/community models to predict both adaptive and maladaptive
649 (e.g. if they incite human retaliation) behavioural responses to rapid human-induced
650 environmental changes. We suggest that this new theory must take account of human
651 behaviour (for example through quantifying the degree of risk humans pose to wildlife) at a
652 local-scale and the degree to which this determines if an animal's behaviour is adaptive or
653 not. Effective long-term strategies to conserve wildlife that utilise agricultural areas require
654 a combination of approaches that protect habitat, target wildlife behaviour, and increase
655 local people's tolerance towards wildlife, and secure their livelihoods (Treves *et al.* 2006).
656 To predict the threshold beyond which wildlife populations are unable to accommodate
657 human presence and activities, and local people will no longer tolerate wildlife presence,
658 further research on the numerous ways that animals modify their behaviour and the
659 ecological consequences of these behaviours, both positive and negative, is needed.

660

661 **Conflict of Interest:** The authors declare that they have no conflict of interest.

662 **Supporting Information:** Supplemental results (Appendix S1) and Supplemental movie
663 (Appendix S2) are available online.

664

665 **REFERENCES**

666 Albert, A., McConkey, K., Savini, T., & Huynen, M. C. (2014). The value of disturbance-
667 tolerant cercopithecine monkeys as seed dispersers in degraded habitats. *Biological*
668 *Conservation*, 170, 300–310.

669 Arroyo-Rodríguez, V., Andresen, E., Bravo, S. P., & Stevenson, P. R. (2015). Seed
670 dispersal by howler monkeys: current knowledge, conservation implications, and future
671 directions. In M. M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D.
672 Youlatos D (Eds.). *Howler Monkeys* (pp. 111–139). New York, USA: Springer.

673 Asare, R. (2006). Learning about neighbour trees in cocoa growing systems - a manual for
674 farmer trainers. Forest and Landscape Development and Environment Series 4.
675 Horsholm, Denmark: The Danish Centre for Forest, Landscape and Planning.

676 Babweteera, F., & Brown, N. (2009). Can remnant frugivore species effectively disperse
677 tree seeds in secondary tropical rain forests? *Biodiversity and Conservation*, *18*, 1611–
678 1627.

679 Balcomb, S. R., & Chapman, C. A. (2003). Bridging the gap: influence of seed deposition
680 on seedling recruitment in a primate-tree interaction. *Ecological Monographs*, *73*, 625–
681 642.

682 Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M., Bourson, C., &
683 Fruth, B. (2013). The bonobo–dialium positive interactions: seed dispersal mutualism.
684 *American Journal of Primatology*, *75*, 394–403.

685 Beaune, D. (2015). What would happen to the trees and lianas if apes disappeared? *Oryx*,
686 *49*, 442–446.

687 Bessa, J., Sousa, C., & Hockings, K. J. (2015). Feeding ecology of chimpanzees (*Pan*
688 *troglodytes verus*) inhabiting a forest-mangrove-savanna-agricultural matrix at
689 Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau. *American Journal of*
690 *Primatology*, *77*, 651–665.

691 Campbell-Smith, G., Campbell-Smith, M., Singleton, I., & Linkie, M. (2011). Raiders of
692 the lost bark: Orangutan foraging strategies in a degraded landscape. *PLoS ONE*, *6*,
693 e20962.

694 Candolin, U., & Wong, B. B. M. (2012). *Behavioural responses to a changing world:
695 mechanisms and consequences*. Oxford, UK: Oxford University Press.

696 Chapman, C. A. (1989). Primate seed dispersal: the fate of dispersed seeds. *Biotropica*, *21*,
697 148–154.

698 Chapman, C. A., & Chapman, L. J. (1995). Survival without dispersers: seedling
699 recruitment under parents. *Conservation Biology*, *9*, 675–678.

700 Chapman, C. A., & Russo, S. E. (2007). Primate seed dispersal: Linking behavioural
701 ecology and forest community structure. In C. J. Campbell, A. F. Fuentes, K. C.
702 MacKinnon, M. Panger, & S. Bearder (Eds.), *Primates in Perspective* (pp.510–525).
703 Oxford, UK: Oxford University Press.

704 Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in
705 some marine animals and rain forest trees. In P. J. de Boer, & P. R. Gradwell (Eds.),
706 *Dynamics of populations* (pp.289–312). Wageningen: The Netherlands: Centre for
707 Agricultural Publishing and Documentation.

708 Cramer, J. M., Mesquita, R. C. G., & Williamson, G. B. (2007). Forest fragmentation
709 differentially affects seed dispersal of large and small-seeded tropical trees. *Biological
710 Conservation*, *137*, 415–423.

711 Dennis, A. J., Schupp, E. W., Green, R. J., & Westcott, D. A. (2007). *Seed dispersal:
712 theory and its application in a changing world*. Wallingford, UK: CAB International.

713 Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and primate
714 conservation in the tropics: a review. *American Journal of Primatology*, *74*, 696–711.

715 Fuentes, A. (2012). Ethnoprimateology and the anthropology of the human-primate
716 interface. *Annual Review of Anthropology*, *41*, 101–117

717 Fuentes, A., & Wolfe, L. D. (2002). *Primates face to face: the conservation implications of*
718 *human-nonhuman primate interconnections*. Cambridge: Cambridge University Press.

719 Fuentes, A., & Hockings, K. J. (2010). The ethnoprimateological approach in primatology.
720 *American Journal of Primatology*, *72*, 841–847.

721 Ganzhorn, J. U., Fietz, J., Rakotavao, E., Schwab, D., & Zinner, D. (1999). Lemurs and the
722 regeneration of dry deciduous forest in Madagascar. *Conservation Biology*, *13*, 794–804.

723 Garber, P. A. (1986). The ecology of seed dispersal in two species of callitrichid primates
724 (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology*, *10*, 155–
725 170.

726 Gonzalez-Varo, J. P., Arroyo, J. M., & Jordano, P. (2014). Who dispersed the seeds? The
727 use of DNA barcoding in frugivory and seed dispersal studies. *Methods in Ecology and*
728 *Evolution*, *5*, 806–814.

729 Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge,
730 Massachusetts: Harvard University Press.

731 Haurez, B., Petre, C., & Doucet, J. (2013). Impacts of logging and hunting on western
732 lowland gorilla (*Gorilla gorilla gorilla*) populations and consequences for forest
733 regeneration. A review. *Biotechnology, Agronomy, Society and Environment*, *17*, 364–
734 372.

735 Haurez, B., Dainou, K., Tagg, N., Petre, C., & Doucet, J. (2015). The role of great apes in
736 seed dispersal of the tropical forest tree species *Dacryodes normandii* (Burseraceae) in
737 Gabon. *Journal of Tropical Ecology*, *31*, 395–402.

738 Hockings, K. J., McLennan, M. R. (2012). From forest to farm: systematic review of
739 cultivar feeding by chimpanzees – management implications for wildlife in
740 anthropogenic landscapes. *PLoS ONE*, *7*, e33391.

741 Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road-crossing in chimpanzees:
742 a risky business. *Current Biology*, *16*, 668–670.

743 Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2009). Use of wild and cultivated foods
744 by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-
745 influenced environment. *American Journal of Primatology*, *71*, 636–646.

746 Hockings, K. J., Yamakoshi, G., Kabasawa, A., & Matsuzawa, T. (2010). Attacks on local
747 persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives.
748 *American Journal of Primatology*, *72*, 887–896.

749 Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socio-ecological adaptations by
750 chimpanzees (*Pan troglodytes verus*) inhabiting an anthropogenically impacted habitat.
751 *Animal Behaviour*, *83*, 801–810.

752 Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R.,
753 Dunbar, R. I. M., Matsuzawa, T., McGrew, W. C., Williamson, E. A., Wilson, M.,
754 Wood, B., Wrangham, R., Hill, C. M. (2015). Apes in the Anthropocene: flexibility and
755 survival. *Trends in Ecology and Evolution*, *30*, 215–222.

756 Howes, F. N. (1946). The early introduction of cocoa to West Africa. *African Affairs*, *45*,
757 152–153.

758 Humle, T. (2011). Location and ecology. In T. Matsuzawa, T. Humle, Y. Sugiyama (Eds.),
759 *Chimpanzees of Bossou and Nimba* (pp.13–21). Tokyo, Japan: Springer Verlag.

760 Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical
761 forest. *Science*, *219*, 187–189.

762 Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The*
763 *American Naturalist*, *104*, 501-528.

764 Jordano, P., Forget, P-M., Lambert, J. E., Bohning-Gaese, K., Traveset, A., & Wright, S. J.
765 (2011). Frugivores and seed dispersal: mechanisms and consequences for biodiversity of
766 a key ecological interaction. *Biology Letters*, *7*, 321–323.

767 Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J-M., & Masi, S. (2014). Wild
768 chimpanzees on the edge: nocturnal activities in croplands. *PLoS ONE*, *9*, e109925.

769 Laland, K., & Booget, N. (2008). Niche construction, co-evolution and biodiversity.
770 *Ecological Economics*, *69*, 731–736.

771 Lambert, J. E. (1997). Digestive strategies, fruit processing, and seed dispersal in the
772 chimpanzees (*Pan troglodytes*) and redbtail monkeys (*Cercopithecus ascanius*) of Kibale
773 National Park, Uganda. PhD thesis. University of Illinois, USA.

774 Lambert, J. E. (1999). Seed handling in chimpanzees (*Pan troglodytes*) and redbtail monkeys
775 (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine
776 fruit-processing strategies and seed dispersal. *American Journal of Physical*
777 *Anthropology*, *109*, 365–386.

778 Lambert, J. E., & Chapman, C. A. (2005). The fate of primate dispersed seeds: deposition
779 pattern, dispersal distance, and implications for conservation. In P-M Forget, J. E.

780 Lambert, P. Hulme, & S. Vander Wall (Eds.), *Seed Fate: Predation, Dispersal and*
781 *Seedling Establishment* (pp.137–150). Wallingford, UK: CAB International.

782 Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed
783 dispersal patterns. *Annual Review of Ecology and Systematics*, 34, 549–574.

784 Linder, J. M., & Oates, J. F. (2011). Differential impact of bushmeat hunting on monkey
785 species and implications for primate conservation in Korup National Park, Cameroon.
786 *Biological Conservation*, 144, 738–745.

787 Markl, J., Schleuning, M., Forget, P-M., Jordano, P., Lambert, J. E., Travaset, A., &
788 Wright, J. (2012). Impact of human disturbance on seed dispersal by animals: A meta-
789 analysis. *Conservation Biology*, 26, 1072–1081.

790 Matsuzawa, T., Humle, T., & Sugiyama, Y. (2011). *The Chimpanzees of Bossou and*
791 *Nimba*. Tokyo, Japan: Springer.

792 McKinney, T. (2011). The effects of provisioning and crop-raiding on the diet and foraging
793 activities of human-commensal white-faced capuchins (*Cebus capucinus*). *American*
794 *Journal of Primatology*, 73, 439–448.

795 McLennan, M. R. (2013). Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in
796 Bulindi, Uganda: foraging strategies at the forest–farm interface. *International Journal*
797 *of Primatology*, 34, 585–614.

798 McLennan, M. R., & Hockings, K. J. (2014). Wild chimpanzees show group differences in
799 selection of agricultural crops. *Scientific Reports*, 4, 5956.

800 McLennan, M. R., & Hockings, K. J. (2016). The Aggressive apes? Causes and contexts of
801 great ape attacks on humans. In F. M. Angelici (Ed.), *Problematic wildlife: A Cross-*
802 *Disciplinary Approach* (pp. 373-394). Switzerland: Springer.

803 Nathan, R., & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their
804 determinants and consequences for recruitment. *Trends in Ecology and Evolution*, *15*,
805 278–285.

806 Paterson, J. D., & Wallis, J. (2005). *Commensalism and conflict: The human-primate*
807 *interface*. Norman, USA: American Society of Primatologists.

808 Poulsen, J. R., Clark, C. J., Connor, E. F., & Smith, T. B. (2002). Differential resource use
809 by primates and hornbills: implications for seed dispersal. *Ecology*, *83*, 228–240.

810 Pruetz, J. D. (2006). Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at
811 Fongoli, Senegal. In G. Hohmann, M. Robbins, & C. Boesch (Eds.), *Feeding ecology in*
812 *apes and other primates* (pp.326–364). Cambridge, UK: Cambridge University Press.

813 Riley, E. P. (2008). Ranging patterns and habitat use of Sulawesi Tonkean macaques
814 (*Macaca tonkeana*) in a human-modified habitat. *American Journal of Primatology*, *70*,
815 670–679.

816 Riley, E. P., Tolbert, B., Farida, W. R. (2013). Nutritional content explains the
817 attractiveness of cacao to crop raiding Tonkean macaques. *Current Zoology*, *59*, 160–
818 169.

819 Russo, S. E., & Augspurger, C. K. (2004). Aggregated seed dispersal by spider monkeys
820 limits recruitment to clumped patterns in *Viola calophylla*. *Ecology Letters*, *7*, 1058–
821 1067.

822 Russo, S. E., & Chapman, C. A. (2011). Primate seed dispersal: Linking behavioural
823 ecology and forest community structure. In C. J. Campbell, A. F. Fuentes, K. C.
824 MacKinnon, M. Panger, & S. Bearder (Eds.), *Primates in Perspective* (pp.523–534).
825 Oxford, UK: Oxford University Press.

826 Schupp, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals.
827 *Vegetatio*, 108, 15–29.

828 Seiler, N., & Robbins, M. (2016). Factors influencing ranging on community land and crop
829 raiding by Mountain Gorillas. *Animal Conservation*, 19, 176–188.

830 Sengupta, A., McConkey, K. R., & Radhakrishna, S. (2015). Primates, Provisioning and
831 Plants: Impacts of Human Cultural Behaviours on Primate Ecological Functions. *PLoS*
832 *ONE*, 10, e0140961.

833 Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to
834 human-induced rapid environmental change. *Evolutionary Applications*, 4, 367–387.

835 Sih, A., Ehlman, S., & Halpin, R. (2015). On connecting behavioural responses to HIREC
836 to ecological outcomes: a comment on Wong and Candolin. *Behavioral Ecology*, 26,
837 676–677.

838 Sokal, R. R., & Rohlf, F. J. (1995). *The Principles and Practice of Statistics in Biological*
839 *Research*, 3rd edition. New York, USA: W.H. Freeman.

840 Stoner, K. E., Vulinec, K., Wright, S. J., & Peres, C. A. (2007). Hunting and plant
841 community dynamics in tropical forests: a synthesis and future directions. *Biotropica*,
842 39, 385–392.

843 Strum, S. C. (2010). The development of primate raiding: implications for management and
844 conservation. *International Journal of Primatology*, 31, 133–156.

845 Strum, S. C., Stirling, G., & Kalusi Mutunga, S. (2015). The perfect storm: Land use
846 change promotes *Opuntia stricta*'s invasion of pastoral rangelands in Kenya. *Journal of*
847 *Arid Environments*, 118, 37–47.

848 Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou,
849 Guinea. *American Journal of Physical Anthropology*, *124*, 154–165.

850 Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to
851 microclimate in the tropical forest. *American Journal of Physical Anthropology*, *124*,
852 81–92.

853 Tutin, C. E. G., Ham, R. M., White, L. J. T., & Harrison, M. J. S. (1997). The primate
854 community of the Lope Reserve, Gabon: diets, responses to fruit scarcity and effects on
855 biomass. *American Journal of Primatology*, *42*, 1–24.

856 Treves, A., Wallace, R.B., Naughton-Treves, L., & Morales, A. (2006). Co-managing
857 human-wildlife conflicts – a review. *Human Dimensions of Wildlife*, *11*, 383–396.

858 Valenta, K., Hopkins, M. E., Meeking, M., Chapman, C. A., & Fedigan, L. M. (2015).
859 Spatial patterns of primary seed dispersal and adult tree distributions: *Genipa americana*
860 dispersed by *Cebus capucinus*. *Journal of Tropical Ecology*, *31*, 491–498.

861 van Schaik, C. (2013). The costs and benefits of flexibility as an expression of behavioural
862 plasticity: a primate perspective. *Philosophical Transactions of the Royal Society B*, *368*,
863 20120339

864 Vidal, M. M., Pires, M. M., & Guimarães, P. R. (2013). Large vertebrates as the missing
865 components of seed-dispersal networks. *Biological Conservation*, *163*, 42–48.

866 Wang, B. C., Sork, V. L., Leong, M. T., & Smith, T. B. (2007). Hunting of mammals
867 reduces seed removal and dispersal of the afro-tropical tree *Antrocaryon klaineianum*
868 (Anacardiaceae). *Biotropica*, *39*, 340–347.

869 Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012) Diet of chimpanzees (*Pan*
870 *trogodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet
871 composition and diversity. *American Journal of Primatology*, 74, 114–129.

872 Webb, C. O., & Peart, D. R. (2001). High seed dispersal rates in faunally intact tropical rain
873 forest: theoretical and conservation implications. *Ecology Letters*, 4, 491–499.

874 Wong, B., & Candolin, U. (2015). Behavioural responses to changing environments.
875 *Behavioral Ecology*, 26, 665–673.

876 Woodroffe, R., Thirgood, S., & Rabinowitz, A. (2005). *People and wildlife: conflict or*
877 *coexistence?* Cambridge, UK: Cambridge University Press.

878 Wrangham, R. W., Chapman, C. A., & Chapman, L. J. (1994). Seed dispersal by forest
879 chimpanzees in Uganda. *Journal of Tropical Ecology*, 10, 355–368.

880 Wright, S.J. (2003). The myriad consequences of hunting for vertebrates and plants in
881 tropical forests. *Perspectives in Plant Ecology Evolution and Systematics*, 6, 73–86.

882 Wright, S. J. (2007). Seed dispersal in anthropogenic landscapes. In A. J. Dennis, E. W.
883 Schupp, R. J. Green, D. A. Westcott (Eds.), *Seed dispersal: theory and its application in*
884 *a changing world* (pp.599–614). Wallingford, UK: CAB International.

885 Yamakoshi, G. (2011). The ‘prehistory’ before 1976: looking back on three decades of
886 research on Bossou chimpanzees. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.),
887 *The chimpanzees of Bossou and Nimba* (pp. 35–44). Tokyo, Japan: Springer.

888 Zárate, D. A., Andresen, E., Estrada, A., & Serio-Silva, J. C. (2014). Black howler monkey
889 (*Alouatta pigra*) activity, foraging and seed dispersal patterns in shaded cocoa
890 plantations versus rainforest in southern Mexico. *American Journal of Primatology*, 76,
891 890–899.