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9 Interpreting long-term trends in bushmeat harvest in southeast

10 Cameroon

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44 **Highlights**

45 • Long-term monitoring of hunting offtake in tropical forests is fundamental to
46 achieve sustainability.

47 • Catch per hunter per day and mean body mass indicator of hunted prey can be
48 used to document extraction patterns over time.

49 • Notwithstanding some caveats, these measures can still be used as a good
50 indication of changes in prey offtake.

51

52

53 **Abstract**

54 Measuring hunting sustainability across West/Central African forests remains a
55 challenge. Long-term assessment of trends is crucial. Via hunter-reported surveys we
56 collected offtake data in three villages near the Dja Biosphere Reserve (southeast
57 Cameroon). During four months (March–June) in 2003, 2009 and 2016, we gathered
58 information on hunters, prey species and number of carcasses brought to the three
59 settlements. Because it was not possible to record hunter effort i.e. the time a hunter
60 spent pursuing animals or setting traps, to calculate catch per unit effort (CPUE), we
61 used catch per hunter per day (CPHD) to document hunter returns. We then used the
62 changes in the mean body mass indicator (MBMI) throughout the study period to test
63 for defaunation in the three villages. Differences in CPHD and MBMI by month and
64 year, between villages and hunting method, were investigated using Tweedie regression
65 models. For all species pooled, we found that the mean CPHD remained relatively
66 constant between 2003 and 2016. There was an observed shift from traps to firearms
67 during the study period. CPHD for each of the seven most hunted species did not vary
68 significantly during the entire study period, and a similar change from traps to firearms
69 was observed. MBMI also remained stable for all species pooled, but significantly
70 declined in the remotest village. Starting MBMI values for this village were higher than
71 for the other two settlements perhaps because wildlife here is less depleted. Although
72 hunter effort data may be difficult to obtain over long time periods, CPHD and MBMI
73 may be useful tools as a measure of impact of hunters on prey populations.

74 *Keywords:* bushmeat, hunter offtake, mean body mass indicator, mammals, tropical
75 rainforests

76 **1. Introduction**

77 It is now widely recognized that hunting above sustainable levels is one of the main
78 causes of worldwide biodiversity loss (Robinson & Bennett 2000; Milner-Gulland et al.
79 2002). In tropical forest regions, where standing biomass of wildlife is significantly
80 lower than in more open habitats, overhunting of wild animals for their flesh (bushmeat)
81 may lead to the depletion of local populations and even contribute to the extinction of
82 some species (Abernethy et al. 2013).

83 Uncontrolled bushmeat hunting in African rainforests results in large-bodied
84 species, species with slower life histories, often frugivores, and those with high hunter
85 or black market value to disappear first. As a result, more smaller-bodied taxa are then
86 targeted; the latter (large rodents and small duikers) possess higher reproductive
87 potentials that confer them greater resilience to heavy hunting pressure. Although
88 evidence for the universality of such pattern of defaunation is still debated, given
89 confounding effects such as hunter choice (see Luiselli et al. 2017), some studies have
90 shown that potentially overexploited hunting catchment areas are characterized by a
91 preponderance of smaller-bodied game species (Fa et al. 2015). This phenomenon has
92 been measured by the ‘mean body mass indicator’ (MBMI) in different sites and time
93 scales where the MBMI drops as the proportion of small-bodied species in the offtake
94 increases (Ingram et al. 2015). This index can arguably be employed (assuming a linear
95 relation between percent of small prey and large species loss) as a proxy of defaunation
96 (Dirzo et al. 2014) in a habitat. The MBMI can be seen as analogous to the ‘large fish
97 index’ (LFI), which reveals changes over time in the contribution of large-bodied fish to
98 the biomass of the catch (Greenstreet et al. 2011; Shephard et al. 2011).

99 Sustainability of hunted game populations is often impractical to assess directly
100 given that the estimation of game populations in the field requires considerable
101 investment of time and money. Consequently, indices such as ‘catch per unit effort’

102 (CPUE) are useful for comparative studies, i.e. to indicate that hunting pressure is
103 higher in a site in contrast to another (Puertas & Bodmer 2004; Rist et al. 2010; Grande-
104 Vega et al. 2015). Furthermore, data reported by hunters themselves, can be used to
105 investigate exploitation levels, gain insights into the status of a harvested population,
106 and approximate sustainability of hunting. Despite some potential biases due to
107 misreporting or unwilling hunter participation, self-reporting hunter data provide useful
108 information and is often the most cost-effective option for assessing hunting impacts
109 (Rist et al. 2010). However, a major limitation in measuring hunting impact is linked to
110 the difficulty of recording the time dedicated to hunting, since gathering such
111 information requires intensive monitoring of hunters via hunter follows (e.g. Kümpel et
112 al. 2008) or the reporting by hunters of the time spent engaged in the pursuit of prey
113 (e.g. Grande-Vega et al. 2015). However, the number of hunted animals brought to a
114 camp or village can often be counted more easily, and in some cases quarry can be
115 ascribed to specific hunters. This type of data, although a measure of hunter returns
116 only, can with some caution still be used to assess whether the catch per hunter over a
117 set period is diminishing, stable or increasing. Like CPUE and MBMI indices, hunter
118 returns are proxies of hunting impact.

119 Over a 13-year period, we recorded the species and number of individual
120 animals killed by known hunters in three villages in southeastern Cameroon. Using
121 these data, we described changes in hunter returns (catch per hunter per day, CPHD) for
122 all species pooled and for the more frequently hunted species. Since hunter effort was
123 not logged, because of the inherent difficulties in accurately obtaining this information,
124 offtake per hunting trip could not be calculated as a proxy for changes in prey
125 abundance. However, we estimated the average number of animals a hunter brought
126 back to the village in a day over the entire study period. To determine if there was

127 evidence of faunal depletion within the three study villages, we used the MBMI for all
128 animals hunted to assess whether hunters relied increasingly on smaller species over
129 time. We test whether there were spatial and temporal differences in the CPHD and
130 MBMI between villages, and hunting methods. Finally, we argue that the offtake data
131 gathered in our study, despite potential shortcomings, can be used as an indirect
132 measure of offtake in the study area.

133

134 **2. Methods**

135 *2.1. Study area*

136 The three study villages, Malen V (MV), Duomo-Pierre (DP) and Mimpala (MIM), are
137 situated at the northeastern periphery of the Dja Biosphere Reserve (DBR) in
138 southeastern Cameroon (Fig. 1); the DBR encompasses a total area of 5,260 km² and is
139 noted for its rich biodiversity (Betti 2004). The main type of habitat in the region is
140 near-primary forest and secondary forest, ranging from areas with closed canopy and
141 little undergrowth to zones with a relatively open canopy and dense undergrowth
142 (Dupain et al. 2004; Tagg et al. 2015; Tagg & Willie 2013). Swampy areas are also
143 found near the River Dja. Rainfall is around 1500 mm/year, divided into two rainy
144 seasons and two dry seasons (Willie et al. 2012). Mean temperatures are fairly constant,
145 around 24 °C (McSweeney et al. 2010).

146 MV is the largest of the three villages (Table 1) and the most accessible by
147 motorized vehicles; the closest markets are at Messamena (60km away), and Abong
148 Mbang (100km away). MV is comprised of three smaller settlements (MV, Diassa and
149 Palestine), which we treat here as one (Luyten 2009). Total population size for the three
150 villages was around 300 inhabitants and settlement sizes did not vary substantially
151 during the study period (Table 1).

152 Most inhabitants of the three villages are Badjoué, but a small number of Baka
153 pygmies also reside there. Villagers are generally poor, with an average income of less
154 than \$1 per capita per day. These communities are amongst the least developed (i.e.,
155 infrastructure such as roads, schools and health centers is lacking in most villages) and
156 least educated in the country (Tagg et al. 2011; Tagg & Willie 2013). Most people fish,
157 hunt, harvest or gather forest products and many are engaged in some form of
158 subsistence agriculture. Bushmeat is hunted mainly for subsistence; only a small
159 proportion is sold (Epanda et al. 2005).

160 The three study villages have been involved with the Association de la
161 Protection de Grands Singes (APGS) of the Zoological Society of Antwerp (Tagg et al.
162 2011) since 2001. Through awareness raising, education and creation of alternative
163 income, APGS has tried to discourage the use of firearms and hunting of protected
164 species such as elephant and great apes (A or B categories of the Cameroonian Wildlife
165 Law) within clearly delimited community hunting areas (Fig. 1). The law also prohibits
166 the use of wire snares, but this hunting method has been common practice since the
167 1940s and impossible to control (Epanda et al. 2005).

168 Ecoguards, employed by the Cameroonian Ministry of Forestry, regularly patrol
169 inside the DBR and its periphery (including the APGS sites) to ensure hunting laws are
170 respected, including sanctioning of perpetrators if caught (Epanda et al. 2005).

171

172 2.2. *Bushmeat surveys*

173 In each study village, we gathered data during three distinct study periods: August
174 2002–August 2003, March–June 2009 and February–September 2016. We employed a
175 research assistant in each village (thus familiar with the community, the area and the
176 dialect) to build trust, avoid biases, and maximize reliability of the data collected. To

177 allow for inter-annual comparisons we only used data gathered during March–June,
178 since records for these four months were available for all study years. This period
179 encompassed the end of the long dry season, the entire short rainy season (from mid-
180 March to mid-June), and the start of the short dry season.

181 We employed data collectors in each village to document all bushmeat brought
182 to their village at the end of each study day. Hunters willingly brought their catch to the
183 data collectors when returning from a hunting trip. For each carcass, the data collectors
184 recorded the identity of the hunter, species, hunting method used (trap, firearm, dog, net
185 or collected by hand), and in some cases the condition of the carcass (dried, smoked,
186 fresh or alive) and its weight. We were not able to document the time spent by a hunter
187 either setting traps or pursuing animals to shoot.

188

189 2.3. *Measuring offtake*

190 *Hunter returns*

191 We calculated average monthly hunter returns by dividing the total number of carcasses
192 recorded for each hunter by the total number of days in which a hunter reported prey
193 items in a month:

194

$$195 \quad \text{CPHD} = \frac{MNC}{UE} \quad (1)$$

196

197 where *MNC* is the monthly number of carcasses and *UE* is the number of hunter days
198 per month.

199

200 *Mean body mass indicator*

201 We employed the mean body mass indicator (MBMI) to investigate temporal changes in
202 the composition of hunted species (Ingram et al. 2015). We estimated MBMI only for
203 mammal species since this group represented the majority of animals hunted (Appendix
204 S1). We used the species' mean body weight (adult males and females pooled) available
205 from the literature (Kingdon et al. 2013). We calculated the MBMI as follows:

206

$$207 \quad \text{MBMI} = \frac{\sum(MBWi * ni)}{N}, \quad (2)$$

208

209 where $MBWi$ is a species' body weight, n_i is the number of carcasses recorded for that
210 species, and N is the total number of carcasses of all species. MBMI was estimated for
211 each hunter each month, for each village, and for each hunting method.

212

213 **3. Statistical Analyses**

214 We assessed temporal changes in CPHD and MBMI over the three study periods. We
215 also tested the effect of the covariates: village (MV, DP and MIM), study year (2003,
216 2009 and 2016), month (March, April, May and June) and hunting method (firearms
217 and traps). We used eight CPHD response variables corresponding to the sum of all
218 species and for those species that had more than 100 carcasses. We also fitted an
219 additional model for the response variable MBMI.

220 We fitted nine independent Tweedie regression models (Bonat & Kokonendji
221 2016) using hunter data (1027 observations). In all models, the linear predictor was
222 composed of the effect of the four main covariates with interaction effects up to a
223 second order. We adopted the orthodox logarithm link function. We fitted the models
224 using the maximum likelihood method. We used the statistical software R (R Core
225 Team 2015). Since our nine response variables are continuous, but with a probability

226 mass at zero (Appendix S2), Tweedie regression models are suitable to deal with these
227 types of data (Shono 2008; Arcuti et al. 2013).

228 We were also interested in certain comparisons, such as differences between
229 villages in terms of hunting method, or over time. For this, we employed procedures for
230 multiple comparisons. The R package doBy (Højsgaard & Halekoh 2016) was used to
231 compute differences between villages, years, hunting methods, as well as possible
232 interactions between these effects. For such multiple comparisons tests, Bonferroni
233 corrections are recommended for the associated p -values. In this paper, we employed
234 the multcomp package (Hothorn et al. 2008) to compute such corrections.

235 For each response variable we fitted a saturated model, i.e. a model with all main
236 and interaction effects, and subsequently performed a Wald-ANOVA type test to
237 remove all non-significant effects. We use 95% confidence levels. We then fitted a
238 second model with the linear predictor composed only from the significant effects of the
239 previous model and interpreted the results using multiple comparison techniques. By
240 removing the non-significant terms, we simplified the presentation of our results, thus
241 making them easier to interpret. Furthermore, we gained more power to test the
242 remained effects.

243

244 **4. Results**

245 *4.1. General patterns*

246 A total of 27 mammals, one bird and three reptile species were hunted during the study
247 (Appendix S1). More than 50% of carcasses recorded in all villages were ungulates,
248 followed by rodents (20–28%) and then primates (8–11%). Pangolins (one species)
249 amounted to 5–7% of all carcasses, small carnivores around 5%, while birds and reptiles

250 less than 2%. The number of hunted species for the three villages ranged between 26 in
251 2016 and 31 in 2003.

252 For the three villages pooled, the total numbers of recorded animals hunted and
253 number of reporting hunters varied between years (Table 1). Only 17 (8%) of the total
254 214 recorded hunters in the three villages remained active during all year-periods. Out
255 of the total of number of carcasses for the three villages (Table 1), almost half (48%)
256 were hunted in MV, 26% in DP, and 26% in MIM.

257 Animals were trapped (both foot and neck traps) and killed by firearms
258 (shotguns), nets, dogs, or by hand. A total of 1471 animals (56%) were trapped and
259 1003 shot (38%) (Table 1); the rest (6%) were taken with other methods. Around half of
260 all ungulates were trapped, the other half shot. However, more than 80% of primates
261 were shot and almost 80% of rodents were trapped. The most commonly hunted species
262 (>100 carcasses), all mammals, were: brush-tailed porcupine (*Atherurus africanus*),
263 Peter's duiker (*Cephalophus callipygus*), Bay duiker (*Cephalophus dorsalis*),
264 mustached guenon (*Cercopithecus cephus*), giant pouched rat (*Cricetomys emini*), long-
265 tailed pangolin (*Phataginus tetradactyla*) and blue duiker (*Philantomba monticola*). Of
266 these, the blue duiker was the most frequently hunted species in all study years and
267 villages (see data in Appendix S3).

268

269 4.2. Changes in CPHD

270 Mean monthly CPHD for the entire study period was 1.55 ± 0.08 (range 1–2.86). CPHD
271 for the three villages over the study period did not drop significantly (Fig. 2). Year and
272 Method, but not Month, were significant predictors of CPHD (Fig. 3). However, there
273 were significant interactions for Village/Year, Village/Method, and Method/Month
274 (Table 2).

275 During the entire study period, CPHD increased significantly for firearms (by a
276 factor of 6.52, p -value < 0.00), but decreased by 2.77 (p -value < 0.00) for traps during
277 the same period (Fig. 3, Appendix S4, Table S1). Firearm use differed between villages
278 MV and DP, and MV and MIM (Appendix S4, Table S2) but no difference appeared
279 between villages in trap use. CPHD for firearms was on average 1.57 times (p -value =
280 0.02) greater in March than in June, but 1.97 times lower in March than in June for traps
281 (p -value < 0.00) (Appendix S4, Table S3).

282 The interaction Village/Year was significant for five species (*C. callipygus*, *C.*
283 *dorsalis*, *Cer. cephus*, *C. emini*, *P. monticola*); Village/Method for two species (*A.*
284 *africanus*, *Cer. cephus*); Method/Month for *A. africanus* and *P. monticola*; and
285 Year/Method for six of the seven species considered (the exception being *Cer. cephus*
286 where no interaction was found). The same four interaction effects were also significant
287 for all species pooled (Table 2).

288 We found evidence of a significant and strong Year and Method interactions for
289 the three most hunted ungulates: *P. monticola*, *C. dorsalis* and *C. callipygus*. For all
290 ungulate species, the CPHD for firearms between 2003 and 2016 increased by a factor
291 of 9.00 (p -value < 0.00) for *P. monticola* (Appendix S4, Table S15), by 11.19 (p -value
292 < 0.00) for *C. callipygus* (Appendix S4, Fig. S2 and Table S8), and by 7.99 (p -value $<$
293 0.00) for *C. dorsalis* (Appendix S4, Fig. S3 and Table S9, S10). In contrast, CPHD for
294 traps decreased by 6.45 (p -value < 0.00) for *P. monticola*, 10.42 (p -value < 0.00) for *C.*
295 *callipygus* and by 7.89 (p -value < 0.00) and 3.35 (p -value 0.01), between 2003 and
296 2009, and 2003 and 2016, for *C. dorsalis*, respectively. Village and Year CPHD
297 differences for *P. monticola* were higher in MV than MIM and DP, but only in 2009
298 (Appendix S4, Table S14). On the other hand, for *C. callipygus* there were differences
299 between DP and MIM, but only in 2016 (Appendix S4, Table S7). Lastly, Month

300 differed only for *P. monticola* where CPHD for traps increased from March to June
301 (Appendix S4, Fig. S7 and Table S16). No species showed any significant interaction
302 between Method/Month.

303 There were no significant temporal changes according to hunting method
304 observed for *C. emini* (Appendix S4, Fig. S5). However, in the case of *A. africanus*,
305 CPHD for firearms increased by a factor of 9.87 (p -value < 0.00) from 2003 to 2016,
306 but CPHD for traps decreased by 2.71 for the same period. For *A. africanus*, MV
307 differed significantly from DP and MIM in the use of firearms (Appendix S4, Table S4)
308 but trap use increased from March to June in all villages, in all years (Appendix S4, Fig.
309 S1 and Tables S5, S6). On the other hand, for *C. emini* we found a significant
310 interaction between Village/Year (Appendix S4, Table S12) with the only significant
311 difference between MV and MIM in 2016.

312 For *P. tetradactyla* we found only a significant interaction effect between
313 Year/Method. CPHD values increased between 2003 and 2016 for firearms and
314 decreased for the same period for traps. No difference between Village/Month was
315 detected for this species (Appendix S4, Fig. S6 and Table S13).

316 Only the interaction Year and Method was significant for the only recorded
317 primate (*Cer. cephus*) (Table 2). There was a significant increase in CPHD between
318 2003 and 2009, but not between 2003 and 2016 for firearms (Appendix S4, Table S11).
319 For traps, CPHD decreased between 2003 and 2016. No evidence of differences
320 between Village/Month was observed for this species (Appendix S4, Fig. S4).

321

322 4.3. Changes in MBMI

323 Average monthly MBMI was 5.98 ± 0.25 kg (range 2.82–9.40) and did not vary
324 significantly between study years (Fig. 4).

325 We found no significant interaction effects for Village/Method, Village/Month,
326 Year/Method and Year/Month. Only in 2009 did we find significant differences
327 between DP and MIM, and between MV and MIM (Fig. 5 and Appendix S5, Table S1).
328 On average, MIM had MBMI values 1.83 (p -value < 0.00) and 1.50 (p -value < 0.00)
329 larger than DP and MV, respectively. For 2003 and 2016 we found no evidence of
330 significant differences between villages.

331 For both hunting methods, we detected a significant difference only between the
332 months April and May. The MBMI increased for animals taken with firearms, but
333 decreased for traps. We found no significant differences for all other comparisons
334 (Appendix S5, Tables S2–S3).

335

336 **5. Discussion**

337 A main goal of the APGS program is to instate a self-management system of
338 wildlife resources that would contribute to the livelihoods of people without
339 endangering animal populations or their ecological functions. Hunters in the three study
340 villages were asked to comply with the memorandum of understanding signed between
341 the villages and APGS (Epanda et al. 2005; Luyten 2009). As part of this agreement,
342 hunters allowed APGS to record daily numbers of animals killed in each village.
343 Although hunters were active within community hunting zones defined by the APGS
344 agreement, hunting with firearms could not be controlled or trapping regulated (Luyten
345 2009).

346 Our results show that the average CPHD and MBMI in the study villages did not
347 drop over time. From a hunter's perspective, the number of animals brought to the
348 villages every day was similar throughout the study period, although substantial
349 variation existed between hunters. However, our metrics may mask the possibility that

350 hunting trips may have become longer if prey populations around the villages became
351 more depleted. We have no evidence that hunters were moving out of the mapped
352 community hunting areas. Moreover, hunting effort data gathered for the study villages
353 in 2002, 2005 and 2009 indicate that most trap hunters only undertook day-long trips
354 spending on average 4.60 hours per week hunting (Epanda et al. 2005; Luyten 2009).
355 Day-long trips are usual in subsistence hunting situations, typical in our study villages,
356 since men who hunt for their home consumption are also engaged in other activities
357 such as farming so they do not spend multiple days away from the village. Furthermore,
358 there is no evidence that hunters were venturing further from their villages over time. In
359 fact, the contrary may have been the case since the overall hunting area for the three
360 villages was 111.5 km² in 2002 and significantly smaller (43.8 km²) in 2009 (Luyten
361 2009), even though CPHDs remained stable. Moreover, despite an increase in hunters,
362 the lack of variation in CPHD and MBMI throughout the 13-year period may be an
363 indication that the forests around the three study villages possess relatively high animal
364 densities, as suggested in Luyten (2009), and that hunting pressure from the villagers
365 was probably still relatively low.

366 Our study highlights some warning signs. The most important is arguably the
367 observation that increasingly larger animals were taken using firearms by the end of the
368 study period. This is confirmed by the rise in the overall MBMI values for animals
369 taken with firearms, but not for those caught in traps. This change in hunter choice of
370 methods could be a response to either hunters having more money to buy weapons, or
371 an increased opportunity to buy cheaper guns. There is evidence that from 2005/2006
372 shotguns have become more numerous in the three villages (Willie 2006; Tagg et al.
373 2011) and that bushmeat traders began to supply hunters with cartridges in exchange for
374 hunted animals (Luyten 2009). This penetration of the study villages by middlemen

375 (who use motorbikes), can explain the higher offtake observed in the road-accessible
376 Malen V and the greater amounts of bushmeat sold, as reported by Luyten (2009).
377 However, a decline in MBMI was only detected in Mimpala, the furthest village from
378 the road. This drop is probably attributable to the fact that starting MBMI values
379 recorded for this village were highest in 2003, explicable by the village's closer
380 proximity to the DBR (see Fig. 1). That larger-bodied animals have become scarcer
381 around this village could be explained by the influx of more shotguns in more recent
382 years.

383 We are aware that there are limitations to the type of data gathered in this study
384 and that caution should be exercised when interpreting the observation of constancy in
385 hunter returns. However, it is possible that, as suggested by Luyten (2009), the self-
386 management of natural resources and economic development in the three villages has
387 had positive impacts between 2002 and 2004, but has floundered after 2009. The main
388 support for this argument is the apparent increase in the bushmeat trade and the upsurge
389 in firearm use; the latter being strictly forbidden in the APGS hunting management
390 plan. Despite this, wildlife surveys in forest blocks adjacent to the study villages have
391 indicated that wildlife did not drastically vary between 2002, 2006 and 2009 (Luyten
392 2009) and between recent surveys (Tagg, unpublished data).

393 Community-based monitoring is particularly relevant in countries where
394 investment in research is limited. Participatory systems may shorten decision-making
395 time frames promote local autonomy in resource management and strengthen
396 community resource rights (Brook and McLachlan 2008; Danielsen et al. 2009).
397 Participatory, adaptive management of wildlife use requires efficient monitoring
398 systems designed to address impacts at appropriate temporal and spatial scales, while
399 involving both scientific experts and local resource users (Luzar et al. 2011). Ideally,

400 metrics that allow conservation managers or communities themselves to understand
401 patterns, track changes, and revise and update regulations affecting hunting, are
402 fundamental. However, collecting data on spatial and temporal changes in hunting
403 offtake to assist a community to regulate their impact on prey numbers can be
404 demanding if hunters are required to provide daily data on hunter effort and number of
405 animals killed. The difficulty of convincing hunters to partake in self-monitoring
406 activities is exemplified by a study of hunters in five communities in the Piagaçu-Purus
407 Sustainable Development Reserve in Brazil in which only 37 out of 74 (50%) potential
408 monitors, and 36% of initially interested families, participated (Vieira et al. 2015). If
409 monitoring of hunters is to be assisted by researchers (e.g. Coad et al. 2013) the costs of
410 this would increase dramatically, especially if hunter follows are undertaken. Data on
411 each hunting event such as time dedicated to hunting and location of hunt are more
412 time-consuming to collect for every hunter especially if long-term trends are required to
413 assess. Thus, more cost-effective means of recording and using data on hunter offtake
414 are required for hunting monitoring systems to be maintained over long periods. A
415 practical way forward may comprise describing hunting offtake by gathering data that
416 are simpler to collect, pertaining to animals hunted (number of animals taken by
417 species, sex and relative age of animals) and hunter identity within a village or camp.
418 We argue that CPHD and MBMI can be used alongside more basic hunter interviews at
419 different intervals to ascertain whether hunters are increasing their hunting effort by
420 using indirect methods such as those employed by Parry and Peres (2016). Testing how
421 much the coarser CPHD index differs from the more costly to obtain CPUE measures
422 may provide the information required to allow practitioners and communities to
423 sustainably manage their wildlife resources.

424

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430

431 **Authors' contribution**

432 Eva Ávila, analyzed the data and drafted the first version of this article.

433 Nikki Tagg, revised the manuscript.

434 Jacob Willie, revised the manuscript.

435 Donald Mbohli, collected field data.

436 Miguel Ángel Farfán, revised the manuscript.

437 J. Mario Vargas, revised the manuscript.

438 Wagner H. Bonat, led the statistical analyses and revised the manuscript.

439 Jef Dupain, revised the manuscript.

440 Manfred A. Epanda, collected field data.

441 Inge Luyten, revised the manuscript.

442 Luc Tedonzong, collected field data.

443 Martine Peeters, revised the manuscript.

444

445 **Supporting Information**

446 The list of hunted species (Appendix S1), number of carcasses recorded per species,
447 village, month and year (Appendix S2), raw data (Appendix S3), statistical results for
448 CPUE (Appendix S4) and for MBMI analyses (Appendix S5). The authors are solely

449 responsible for the content and functionality of these materials. Queries (other than
450 absence of the material) should be directed to the corresponding author.

451

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555 patchiness and sample grain size. *Acta Oecologica* **45**:31-41.

556

557 Table 1 - Summary of offtake results per village and year.

Variables	Village/Year									Total		
	Duomo Pierre			Malen V			Mimpala					
	2003	2009	2016	2003	2009	2016	2003	2009	2016	2003	2009	2016
Total village population size ¹	82	71	85	143	163	152	98	81	71	323	315	308
Total number of hunters	12	18	29	23	38	36	18	27	18	53	79	82
Total number of recorded carcasses	412	105	174	377	598	283	247	259	170	1036	962	627
Numbers hunted/traps	376	34	61	359	179	75	203	128	56	938	341	192
Numbers hunted animals with firearms	19	62	77	10	405	195	29	98	108	58	565	380
Total number of hunted species	19	22	19	22	23	22	27	25	20	31	30	26

558

559 ¹Demographic data for each village obtained for 2002, 2009 and 2015 (unpublished data).

560

561

562

563 Table 2 - Wald statistics (W), degrees of freedom (df) and *p*-values for the components of the saturated model for each species.

564

Effects	df	W (<i>p</i> -value)							
		All species	<i>Atherurus africanus</i>	<i>Cephalophus callipygus</i>	<i>Cephalophus dorsalis</i>	<i>Cercopithecus cephus</i>	<i>Cricetomys emini</i>	<i>Phataginus tetradactyla</i>	<i>Philantomba monticola</i>
Village	2	2.19 (0.34)	7.51 (0.02)	10.01 (0.01)	2.08 (0.35)	5.20 (0.07)	0.02 (0.99)	1.93 (0.38)	9.65 (0.01)
Year	2	19.33 (< 0.00)	2.02 (0.36)	0.09 (0.95)	9.93 (0.01)	0.61 (0.74)	1.88 (0.39)	6.47 (0.04)	4.96 (0.08)
Method	1	33.48 (< 0.00)	19.33 (< 0.00)	1.50 (0.22)	13.43 (< 0.00)	0.05 (0.82)	0.00 (1.00)	10.49 (< 0.00)	6.92 (0.01)
Month	3	4.14 (0.25)	3.74 (0.29)	1.12 (0.77)	4.77 (0.19)	1.96 (0.58)	0.00 (1.00)	3.10 (0.38)	4.61 (0.20)
Village/Year	4	27.72 (< 0.00)	5.45 (0.24)	21.73 (< 0.00)	10.43 (0.03)	12.26 (0.02)	10.86 (0.03)	6.11 (0.19)	27.61 (< 0.00)
Village/Method	2	14.55 (< 0.00)	13.56 (< 0.00)	3.59 (0.17)	5.34 (0.07)	6.22 (0.04)	0.06 (0.97)	5.34 (0.07)	5.47 (0.06)
Village/Month	6	7.57 (0.27)	4.50 (0.61)	12.74 (0.05)	3.65 (0.72)	4.66 (0.59)	6.49 (0.37)	8.25 (0.22)	10.29 (0.11)
Year/Method	2	134.87 (< 0.00)	32.29 (< 0.00)	27.01 (< 0.00)	31.02 (< 0.00)	25.27 (< 0.00)	0.32 (0.85)	6.86 (0.03)	110.90 (< 0.00)
Year/Month	6	1.17 (0.98)	11.33 (0.08)	4.61 (0.59)	6.83 (0.34)	8.26 (0.22)	8.88 (0.18)	7.09 (0.31)	2.53 (0.87)
Method/Month	3	29.42 (< 0.00)	14.71 (< 0.00)	6.55 (0.09)	2.60 (0.46)	5.14 (0.16)	0.00 (1.00)	2.92 (0.40)	11.29 (0.01)

565

566

567 **FIGURE LEGENDS**

568

569 Figure 1. a) Location of the research site and study villages, southeast Cameroon; b)
570 Zonation of land use by the three study villages, as instigated by the APGS according to
571 Epanda et al. (2005).

572

573 Figure 2. Monthly changes in average CPHD (catch per hunter per day) for all hunted
574 animal species in three Cameroonian villages (Duomo Pierre, Malen V, Mimpala)
575 during March-June in 2003, 2009 and 2016. Box plots show the distribution of CPHD
576 (median, interquartile range, and whiskers indicating 95% confidence intervals).
577 Tweedie regression lines are also shown.

578

579 Figure 3. Monthly changes in average CPHD (catch per hunter per day, \pm 95%
580 confidence intervals) according to hunting method (firearms, traps) in three
581 Cameroonian villages (Duomo Pierre, Malen V, Mimpala) during March-June in 2003,
582 2009 and 2016.

583

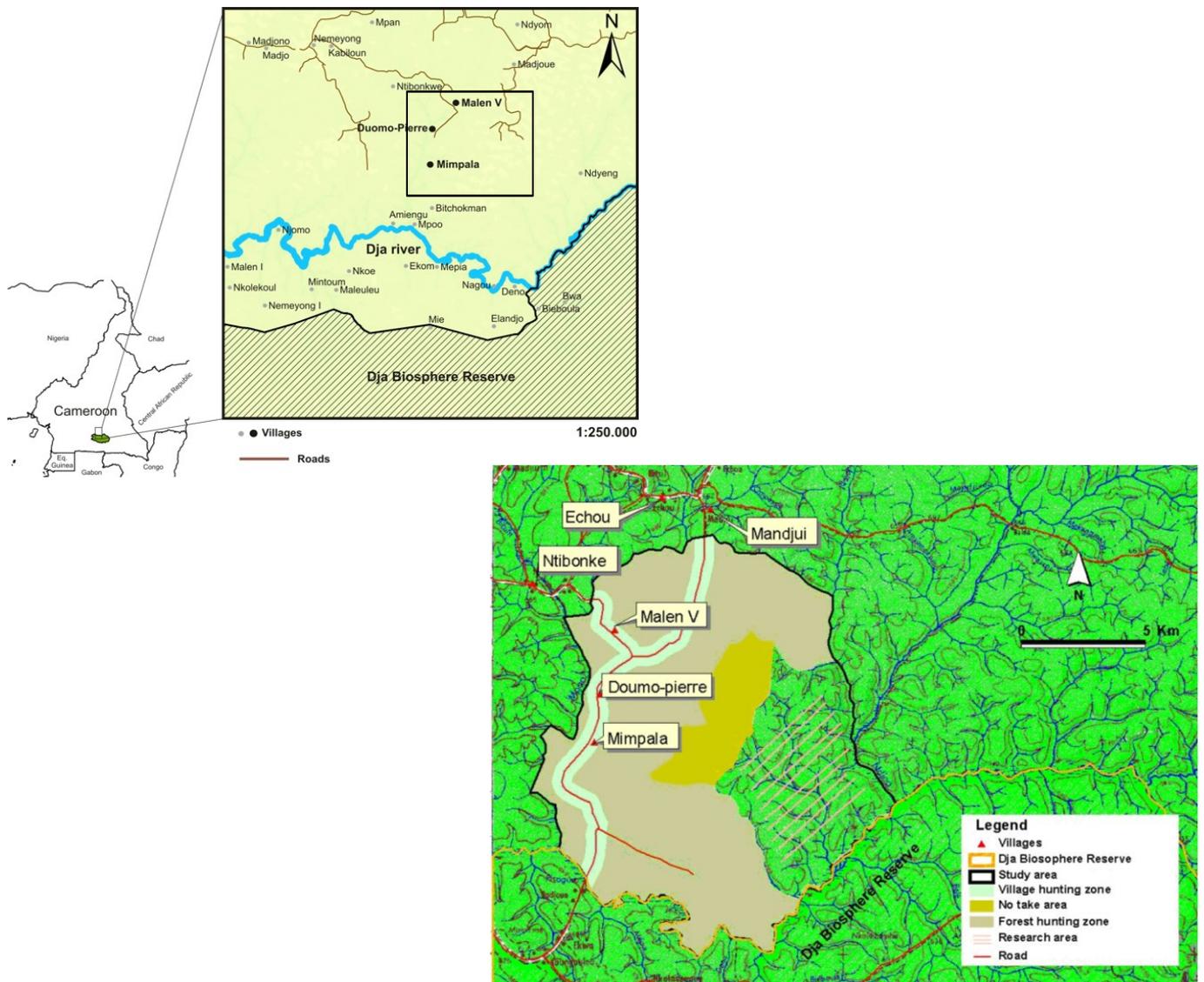
584 Figure 4. Monthly changes in average MBMI (kg, \pm 95% confidence intervals)
585 according to hunting method (firearms, traps) in three Cameroonian villages (Duomo
586 Pierre, Malen V, Mimpala) during March-June in 2003, 2009 and 2016.

587

588 Figure 5. Monthly changes in average MBMI (kg) for all hunted animal species in
589 three Cameroonian villages (Duomo Pierre, Malen V, Mimpala) during March-June in
590 2003, 2009 and 2016. Box plots show the distribution of CPHD (median, interquartile

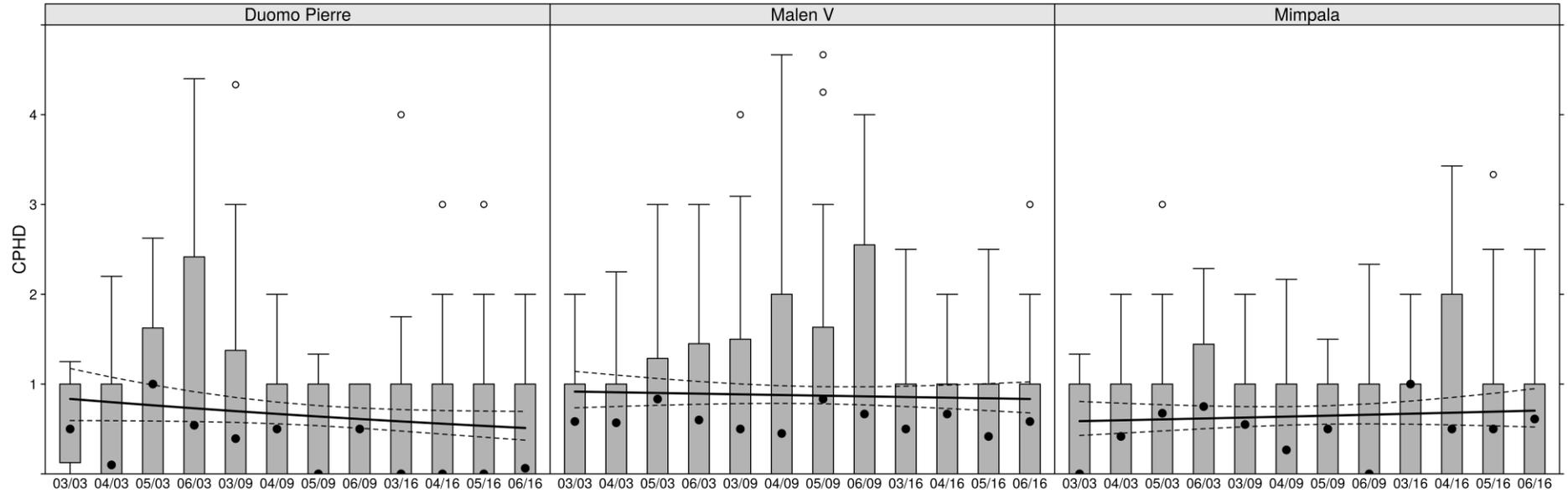
591 range, and whiskers indicating 95% confidence intervals). Tweedie regression lines are
592 also shown.

593 Fig. 1.



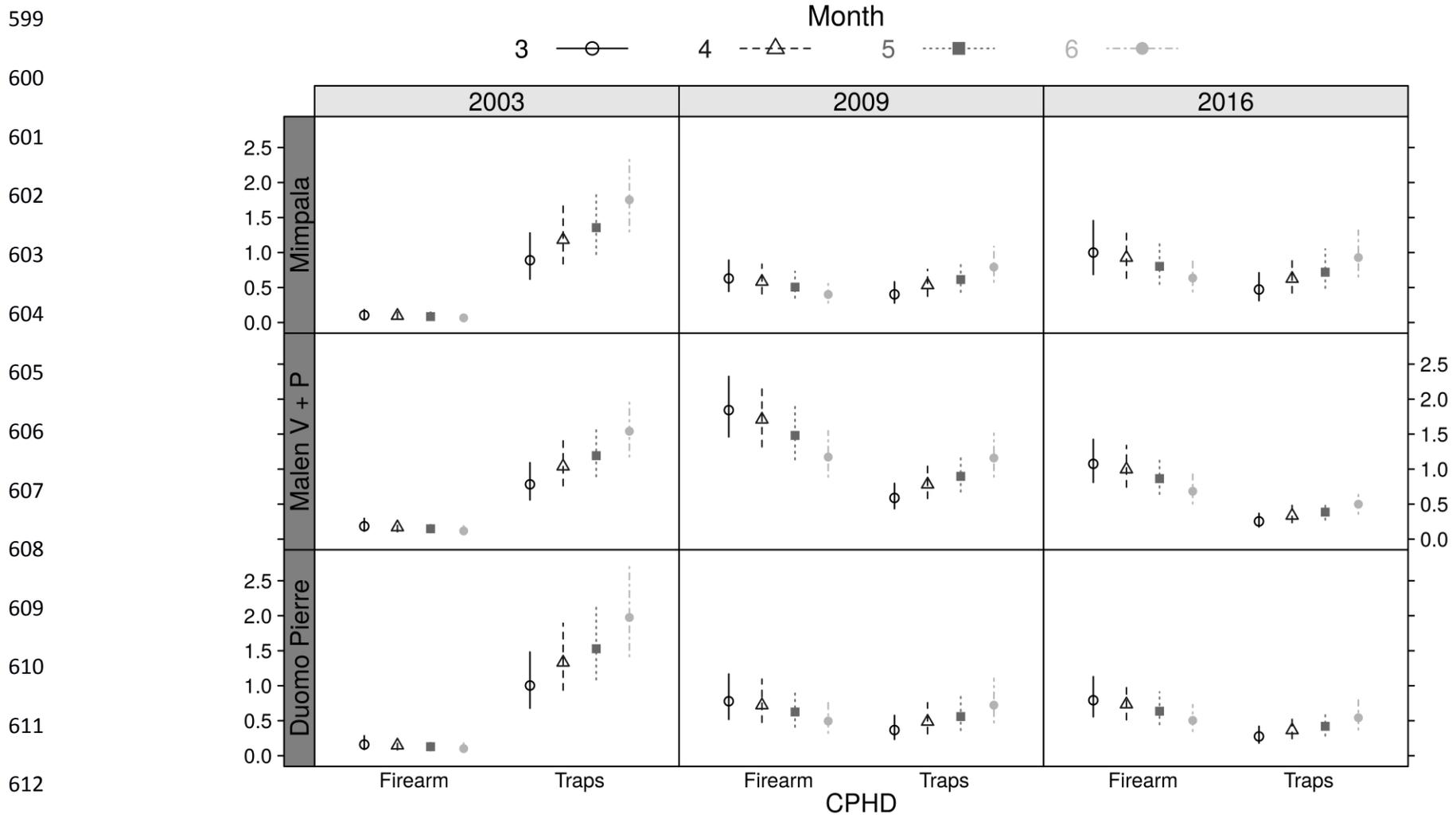
595 Fig. 2.

596



597

598 Fig. 3

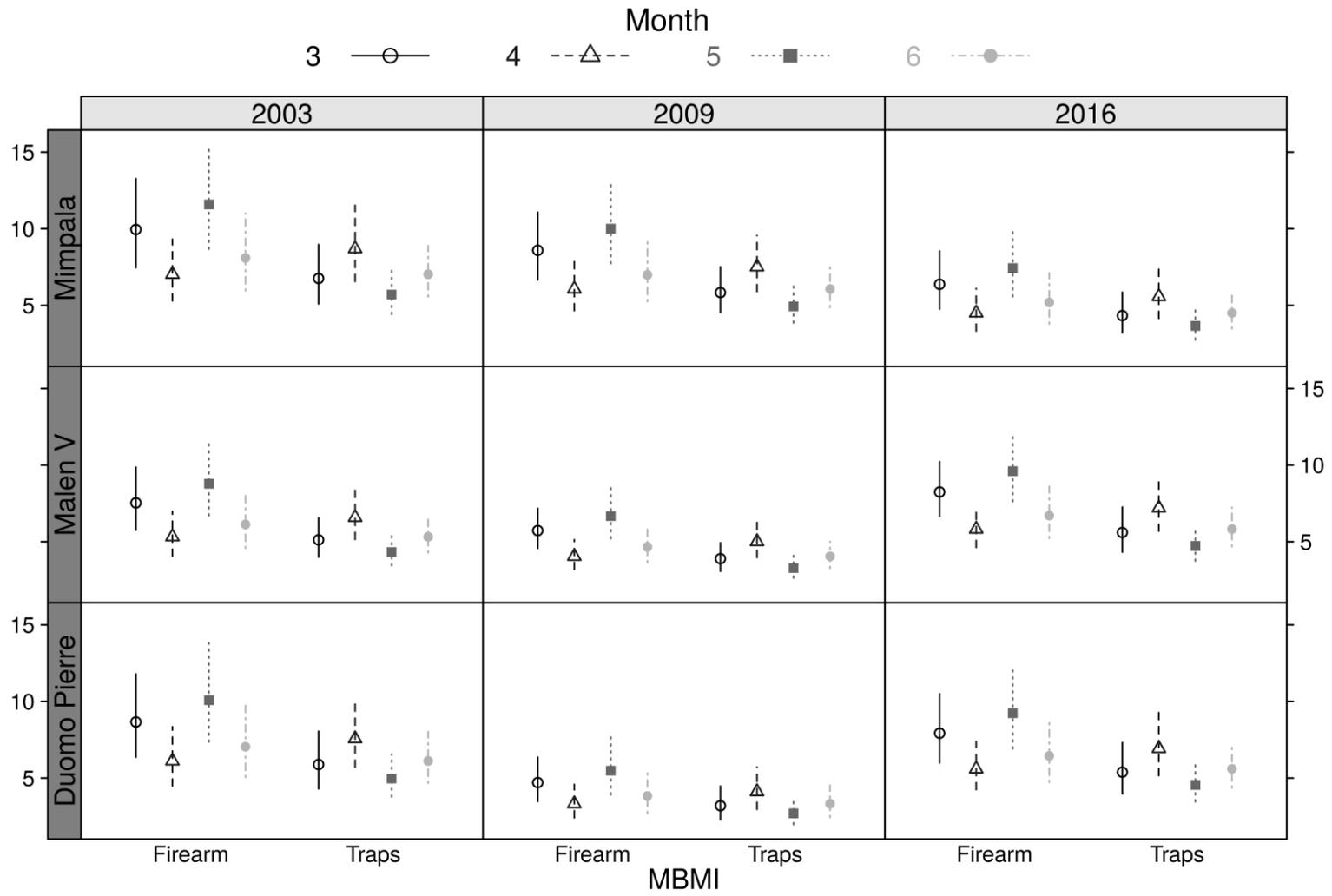


613 Fig. 4.

614

615

616



617 Fig. 5.

