

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50

Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia.

M. Ibbett^{A,B,C}, J.C.Z. Woinarski^{A,D,G}, and M. Oakwood^{E,F}

^A Department of Natural Resources Environment and the Arts, PO Box 496, Palmerston, Northern Territory 0831, Australia.

^B Charles Darwin University, Northern Territory 0909, Australia.

^C Queensland Parks and Wildlife Service, PO Box 2066, Cairns, Queensland 4870, Australia

^D Threatened Species Recovery Hub of the National Environment Science Programme, Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia

^E Evolutionary Ecology Group, Division of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia.

^F Envirotek Ecological Services, PO Box 4022, Coffs Harbour Jetty, NSW 2450, Australia

^G Corresponding author. Email: john.woinarski@cdu.edu.au

51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81

Abstract. There has been marked recent decline in the terrestrial mammal fauna across much of northern Australia, with most documentation of such decline for lowland areas. Here we report changes in the assemblage of small mammals in a rugged sandstone environment (Nawurlandja, in Kakadu National Park) over intermittent sampling between 1977 and 2002. Four native mammal species were commonly recorded in the original sampling: sandstone antechinus (*Pseudantechinus bilarni*), northern quoll (*Dasyurus hallucatus*), Arnhem rock-rat (*Zyomys maini*) and common rock-rat (*Z. argurus*). Trap success rates declined significantly for the northern quoll, Arnhem rock-rat and all species combined, but increased for the common rock-rat. Despite being recorded commonly in the initial (1977-79) study, no Arnhem rock-rats were recorded in the most recent (2002) sampling. Trap success rates for northern quoll declined by ca. 90% from 1977-79 to 2002. The reasons for change are not clear-cut. Notably, all sampling occurred prior to the arrival of cane toads (*Rhinella marina*), a factor that has caused severe decline in northern quolls elsewhere. Fire was more frequent in the sampling area in the period preceding the 2002 sampling than it was in the period preceding the initial (1977-79) sampling, and this may have contributed to change in mammal abundance.

Running head: Mammal decline at a sandstone site

Additional keywords: monitoring, rock-rat, northern quoll, sandstone antechinus, fire.

82

83 **Introduction**

84

85 Several studies have suggested a pattern of recent broad-scale decline in components
86 of the terrestrial mammal fauna of northern Australia (Kitchener 1978; McKenzie
87 1981; Braithwaite and Muller 1997; Oakwood 2000; Woinarski *et al.* 2001; Pardon *et*
88 *al.* 2003; Firth *et al.* 2010; Woinarski *et al.* 2010, 2011a, 2011b; Ziembicki *et al.*
89 2013, 2015; Davies *et al.* 2017). These studies have mostly been conducted in the
90 extensive *Eucalyptus*-dominated lowland savannas. Many intensive demographic
91 studies undertaken in the 1980s and 1990s of individual mammal species or mammal
92 assemblages in lowland environments (e.g. Friend 1985; Friend and Taylor 1985;
93 Friend 1987; Friend 1990; Braithwaite and Brady 1993; Braithwaite and Griffiths
94 1994, 1996; Braithwaite and Muller 1997) provided a foundation against which more
95 recent studies can be compared to provide an assessment of the timing and extent of
96 subsequent mammal decline.

97

98 Far less attention has been paid to the rugged sandstone ranges that contrast sharply
99 with the relatively featureless lowlands, although some monitoring data indicate
100 declines of some mammal species in these environments, albeit less drastic than for
101 lowland sites (Woinarski *et al.* 2004, 2010). These sandstone areas support a diverse
102 set of mammal species, many of which are endemic to them (Woinarski *et al.* 2009);
103 and their topographic complexity has been presumed to offer refuge from some
104 threatening processes that may pervade the lowland environments (Freeland *et al.*
105 1988; Radford *et al.* 2014; Hohnen *et al.* 2016b). For example, whereas vegetation
106 change due to extensive pastoralism has been posited as a possible contributory agent
107 for faunal change in the lowlands (Woinarski *et al.* 2001; Woinarski and Ash 2002;
108 Woinarski and Fisher 2003; Legge *et al.* 2011), cattle and feral livestock generally are
109 largely absent from more rocky and rugged areas, and hence this factor would be
110 unlikely to be involved in any change in the fauna of the sandstone uplands.

111

112 Detection of a consistent pattern of change in the sandstone mammal fauna is
113 constrained by the relatively sparse set of quantitative studies that may serve as
114 foundations for monitoring. Some such foundation and subsequent monitoring has
115 been reported for rugged areas of the Kimberley (Start *et al.* 2007, 2012), but there
116 have been few relevant studies in the upland areas of monsoonal Northern Territory.
117 In this region, the first and most substantial mammal demographic study was from
118 1977 to 1980 at one sandstone site (Little Nourlangie Rock, now called Nawurlandja)
119 within what is now Kakadu National Park (Begg 1981a, 1981b, 1981c; Begg *et al.*
120 1981; Dunlop and Begg 1981b). This set of studies focused particularly on the four
121 small to medium-sized mammal species that were commonly caught at the site:
122 northern quoll (*Dasyurus hallucatus*) (weight *ca.* 600 g), sandstone antechinus
123 (*Pseudantechinus bilarni*) (weight *ca.* 25 g) (with name given as *Antechinus bilarni* in
124 Begg's papers), Arnhem rock-rat (*Zyomys maini*) (weight *ca.* 120 g) (with name
125 given as *Z. woodwardi* in Begg's papers) and common rock-rat (*Z. argurus*) (weight

126 *ca.* 50 g). A few other terrestrial small to medium-sized mammals were reported
127 rarely and incidentally in this initial study (Dunlop and Begg 1981b), and that study
128 did not consider macropods or bats.

129

130 Our paper reports on a re-sampling of this site in 1994 and in 2002 and assesses
131 change in these four mammal species since Begg's original study. There are two main
132 constraints in the interpretation of any such comparison. First, we provide only three
133 points in a temporal pattern, and as such we cannot readily disentangle monotonic
134 longer-term trends from oscillations without long-term trends. Second, this single site
135 may not be representative of the status of sandstone environments (and of their
136 mammal fauna) across the broader region. Such interpretive limitations could feasibly
137 be resolved through meta-analyses of results from a series of re-samplings of historic
138 studies (although we note that there are few such foundation studies) and/or through
139 broader-based long-term monitoring program: such a program has now been
140 established for this region (Russell-Smith *et al.* 2014).

141

142 Begg *et al.* (1981) provided one interpretive key to the population status of the
143 complement of mammals in his studies. Following his initial autecological studies
144 from 1977 to 1979, he burnt the study site and then assessed short-term (to 13 months
145 post-fire) responses of the four mammal species, reporting population declines
146 especially for the Arnhem rock-rat. In recognition of the possible influence of fire on
147 the mammal fauna considered in this study, we assessed the fire history of the site in
148 the seven years preceding our 2002 sampling. Unfortunately, this was the only
149 potential threat that was considered in the initial and subsequent sampling: other
150 potential factors (such as feral cats *Felis catus*) were not monitored. However, notably
151 the 1977-79 and our re-sampling of the study site occurred prior to the 2003 invasion
152 of this area by the cane toad (*Rhinella marina*), demonstrated to have caused severe
153 decline in northern quolls elsewhere (Burnett 1997; Oakwood 2004; Oakwood and
154 Foster 2008; O'Donnell *et al.* 2010).

155

156 The objective of this study is to extend and complement the previous substantial
157 studies of recent change in the lowland mammal fauna of northern Australia, through
158 re-sampling the upland sandstone site with the most substantial historical information,
159 and in doing so contribute towards further clarification of information on the timing,
160 extent and potential causality of mammal decline in the region. We assess the extent
161 and pattern of change in the assemblage of small mammals at this rugged site over a
162 period of *ca.* 25 years, and provide some inferences on factors that may have
163 contributed to any observed change.

164

165 **Methods**

166

167 *Study Site*

168 The study was undertaken at Nawurlandja (12°51'S, 132°47'E) in Kakadu National
169 Park (although the initial sampling commenced before the Park's declaration). This

170 sandstone block occupies 2 km², and is an outlier of the sandstone massif of the
171 Western Arnhem Land Plateau. Nawurlandja rises about 100 m from the surrounding
172 plain, which isolates it (by about 500 m) from the much larger (30 km²) Nourlangie
173 Rock (Burrungui), itself about 10 km from the main massif.
174

175 The study area has a strongly seasonal monsoonal climate, with ca. 90% of the annual
176 rainfall of ca. 1500 mm occurring during the December-March wet season. Numerous
177 small streams flow down the eastern face of Nawurlandja into an adjacent billabong.
178 Because of the rocky nature of the site it remains largely undisturbed by feral pigs
179 (*Sus scrofa*), cattle (*Bos taurus*), water buffalo (*Bubalus bubalis*) and horses (*Equus*
180 *caballus*) that occur (sometimes in high numbers) in the surrounding lowland habitats
181 (Dunlop and Begg 1981b; Bradshaw *et al.* 2007). There is also little disturbance from
182 weeds.
183

184 In the original study, Dunlop and Begg (1981b) defined, described and mapped four
185 distinct habitats for the study site (Rocky Crevices, Closed Forest, Rocky Slopes and
186 Scree Slopes), with these habitats differentiated mostly on vegetation structure, cover
187 and floristic composition, and geomorphology.
188

189 Although Dunlop and Begg (1981a) provided a list of plant species recorded at the
190 site at the time of the 1977-79 sampling, the non-quantitative nature of this
191 description prohibited an assessment of vegetation change over the subsequent 23
192 years to our 2002 re-sample.
193

194 *1977-79 mammal sampling*

195 The Begg study provides a good foundation for comparison with subsequent sampling
196 because of its highly explicit sampling protocol and the extent to which the data were
197 reported. The original trapping methodology was described in Begg (1981b) and is
198 summarised here. In each sampling period, 100 Elliott traps were set in each of the
199 four habitats, in two fixed transect lines of 50 traps. Traps were baited with peanut
200 butter, oats, mixed fruit and sardines. Traps were placed approximately 10 m apart
201 and the two lines were separated by 20-40 m, depending on the terrain. The traps were
202 set for three consecutive nights around the middle of every month from February 1977
203 to June 1979. Sampling effort totalled 34,800 trap-nights, with 300 trap-nights per
204 month in each of the four habitats. Using the same procedure and monthly sampling
205 effort, Begg extended the original study to August 1980 to examine the response of
206 the mammal fauna to his imposition of an experimental fire (in July 1979) (Begg *et al.*
207 1981).
208

209 *Re-sampling*

210 Since the location of the original trapping transects was not documented nor presented
211 in published maps it was impossible to relocate the 1977-79 study's transects
212 precisely. However, the four habitats identified in the original study were mapped in
213 Dunlop and Begg (1981b), were still easily identifiable on ground and provide only

214 limited possible options for transects of the dimensions described. As such the
215 locations of transects in the repeat sampling were assumed to be largely consistent
216 with that of the original study. Repeat sampling was conducted in 1994 (by MO) and
217 2002 (by MI) using methodology that largely replicated the original design (with
218 variations as described below).

219

220 The 1994 re-sample comprised one trapping session only, in mid-June. Because the
221 focus of this re-sampling was an assessment of the status of northern quoll, trapping
222 was carried out only at the two habitats deemed to be most relevant for this species –
223 Rocky Slopes and Rocky Crevices. One hundred Elliott traps were set in two lines in
224 each of the two habitats, following the spacing used by Begg, for three consecutive
225 nights. The total trapping effort was 600 trap-nights.

226

227 Re-sampling in 2002 comprised two trapping sessions, in April and July. In the April
228 2002 re-survey, 200 Elliott traps were laid out in two lines in each of the four habitats.
229 This effectively doubled the trapping effort of any one trapping episode in the original
230 survey, giving a total of 600 trap-nights in each habitat. In the July 2002 re-survey,
231 100 Elliott traps were laid out in every habitat, equalling the trapping effort of one
232 episode in the original survey. The total trapping effort in 2002 was 3600 trap-nights.

233

234 *Fire history*

235 For at least several years prior to the 1977-79 study, and during that study, fire had
236 largely been excluded from the study site, except for two relatively small individual
237 fires in 1973 and 1976 that affected less than 25% of the study area (Dunlop and Begg
238 1981b). As a result, Begg's study (Begg 1981a, 1981b, 1981c) mostly occurred in
239 areas that had been unburnt for at least 4-6 years. However, in July 1979, after the
240 completion of the initial sampling, the study area was deliberately burnt. Fires were
241 ignited using a combination of incendiaries dropped from a helicopter and ground-
242 based drip torches that were used to burn areas that remained unburnt after the aerial
243 burning (Begg *et al.* 1981). After the application of this fire, the populations of small
244 mammals were monitored for a further 12 months. As reported by Begg *et al.* (1981),
245 overall trapping rates declined over this period, although changes were inconsistent
246 between species, habitats and seasonal comparisons (Table 1).

247

248 We derived fire histories for the study area for the six years preceding (and the year
249 of) our 2002 re-survey. The locations of trapping transects used in 2002 were overlaid
250 on Landsat TM satellite imagery using ArcView 3.2a software (ESRI 2002), then, for
251 each transect, we counted the number of pixels burnt in each year from 1996-2002
252 and thence calculated the percentage of each transect burnt annually.

253

254 *Analysis*

255 The 1977-79 study reported percentage trap success for each of the four species in
256 each of the four habitats, for each of four seasons (March-May, June-August,
257 September-November and December-February) (Begg 1981a, 1981b, 1981c). Trap

258 success rates for our two 2002 re-samples (April, July) were compared with means for
259 the 1977-1979 sample years for March-May and June-August respectively, in all
260 cases with results from all four habitats combined. We also compare our results with
261 Begg's post-fire results of June-August 1980 and March-May 1980. The analysis we
262 used is a z-ratio test of proportions, testing whether the earlier trap success rate is the
263 same as or different to that of our 2002 re-sampling. Tests were performed for each of
264 the four species, and for all species combined. Given that this analysis involves 20
265 separate comparisons (i.e. four species and all mammal species combined, with two
266 seasonal comparisons, and with 2002 results compared with both 1977-79 and 1980
267 results), probability thresholds were adjusted by Bonferroni correction. Our analyses
268 are based on trap success rates, in part because the initial (1977-79) study design did
269 not allow for estimates of detectability or density. Trap success rates generally
270 provide a reasonable index of relative abundance or population size for individual
271 species, but (because of varying trappability between species) do not provide a good
272 indicator of relative abundance among different species (Slade and Blair 2000;
273 Hopkins and Kennedy 2004).

274

275 We also present results from our June 1994 sampling of two habitats relative to those
276 of sampling of the same two habitats in June-August 1977-79, June-August 1980 and
277 July 2002, but, given the smaller sample sizes involved, we do not test statistically for
278 differences among these samples.

279

280 Patterns in small mammal community composition were also examined using multi-
281 dimensional scaling in the program PRIMER (Clarke and Gorley 2001).

282 Untransformed abundance (trap success rate) data for all four species were included in
283 the ordination, with compositional similarity of paired cases (unique combinations of
284 habitat, sampling season and sampling year) assessed using the Bray-Curtis similarity
285 index. The influence of sampling year (four levels: Begg's 1977-79 study, the 1980
286 post-fire sampling, 1994 and 2002), habitat, and sampling season (March to May *cf.*
287 June to August) on this pair-wise similarity was examined using ANOSIM (Clarke
288 and Gorley 2001) with the significance of the resultant global R-statistic tested by
289 comparison with 1000 random configurations.

290

291

292 **Results**

293

294 Trap success rates in April 2002 were lower for Arnhem rock-rat (decline of 100%),
295 and significantly lower for northern quoll (decline of 95%) and sandstone antechinus
296 (decline of 96%) and for total mammals (decline of 73%) than in March-May 1977-
297 1979 (Table 1a). In contrast, trap success rate was significantly greater for common
298 rock-rat in April 2002 than in March-May 1977-1979 (increase of 126%). These
299 trends were generally consistent when our re-sampling was compared with results
300 from March-May 1980 (Table 1), 8-10 months after Begg's extensive experimental

301 fire, notwithstanding an overall decrease in capture rate from pre-fire (1977-79) to
302 post-fire (1980) (Begg *et al.* 1981).

303

304 Trap success rates in July 2002 were lower for northern quoll (88% decline) than in
305 June-August 1977-79 and significantly lower for Arnhem rock-rat (100% decline)
306 (Table 1b). Capture rates in July 2002 for sandstone antechinus were lower (by 24%)
307 than in June-August 1977-79, but significantly higher than for the June-August 1980
308 post-fire sampling. Capture rates in July 2002 were significantly higher for common
309 rock-rats compared to the June-August 1977-79 sampling (increase of 102%) but not
310 significantly different to rates in June-August 1980 post-fire sampling.

311

312 No Arnhem rock-rats were caught in either of the two 2002 re-sample periods,
313 whereas 30 captures would have been expected based on their 1977-1979 capture
314 rates and the trap effort in 2002. Only two northern quolls were captured during the
315 2002 re-samples, whereas the 1977-1979 capture rates would have predicted a tally of
316 28 given the trap effort in 2002. The expected tally for sandstone antechinus was 139
317 (whereas 41 were caught), and for common rock-rat was 33 (whereas 63 were
318 caught).

319

320 Trap success results for northern quoll and Arnhem rock-rat from the more limited
321 1994 sampling of two habitats were intermediate between the earlier (1977-79, 1980)
322 and later (2002) sampling, indicating decline for these species probably substantially
323 preceded our 2002 sampling.

324

325 Variation in mammal species composition was significantly related to sampling
326 period ($R=0.47$, $p=0.001$), with significant variation between the 1977-79 and 1979-
327 80 periods ($R=0.17$, $p<0.05$), 1977-79 and 1994 periods ($R=0.85$, $p<0.05$), 1977-79
328 and 2002 periods ($R=0.60$, $p<0.001$), 1979-80 and 1994 periods ($R=0.57$, $p<0.05$),
329 and 1979-80 and 2002 periods ($R=0.68$, $p<0.001$), but not between the 1994 and 2002
330 periods ($R=0.03$, $p>0.05$). In contrast to the strong influence of sampling period,
331 variation in mammal species composition was unrelated to either habitat ($R=0.058$,
332 $p>0.05$) or sampling season ($R=0.045$, $p>0.05$).

333

334 *Fire history*

335 The study area was burnt in 5 of the 7 years preceding the 2002 sampling, with an
336 average of 17% burnt per year: 1996 (fires burnt 17% of the study area), 1997 (17%),
337 2000 (24%), 2001 (31%) and 2002 (31%),

338

339

340 **Discussion**

341

342 This study considers only one site, Nawurlandja, and provides only a limited number
343 of points in a temporal sequence. Furthermore, we recognise that this site, due to its
344 small size and isolation, may be unrepresentative of rugged upland areas more

345 broadly: for example its isolation may reduce the likelihood of re-colonisation,
346 following local population decline or extirpation, from a larger population base in
347 more extensive sandstone environments.

348

349 The terrestrial small mammal assemblage of Nawurlandja is simple, with four species
350 comprising >99% of all captures (in every episode of sampling). Of these four
351 species, two (Arnhem rock-rat and northern quoll) unequivocally declined from 1977-
352 79 to 2002, and the absence of records of Arnhem rock-rats in 1994 and 2002
353 suggests that it may have become extirpated at this site. Both of these species are now
354 recognised as threatened nationally. In contrast, the common rock-rat increased, and
355 the trends for sandstone antechinus were inconsistent. These results may represent
356 long-term monotonic trends or they may simply be part of a dynamic system whose
357 pattern of oscillations cannot be interpreted from so few samples. There is some
358 evidence for short-term dynamism in this assemblage, most notably in the six-fold
359 increase in trap success for sandstone antechinus from April 2002 to July 2002
360 (possibly associated with changes in activity and dispersion during the mating
361 season), and to some fluctuations in populations across the three years of the intensive
362 initial study (Begg 1981a, 1981b, 1981c). But the influence of such seasonal
363 dynamism is dampened in our assessment, as our comparisons between the initial
364 sampling and re-sampling were restricted to comparable seasons.

365

366 A case can be made for the results reported here being representative of long-term
367 trends, and to be indicative of the status of mammal assemblages in sandstone
368 environments more broadly. First, trends in abundance for northern quoll and Arnhem
369 rock-rat from the initial sampling to the 1994 re-sampling are broadly consistent with,
370 and intermediate to, trends from the 1977-79 results to the 2002 re-sampling,
371 suggesting a directional change. Second, while recognising that this mammal
372 assemblage is very simple, there is some consistency in the pattern of change with that
373 reported for recent changes in the lowland mammals of northern Australia (Woinarski
374 *et al.* 2001): declines occurred mostly in the larger (and/or more specialised)
375 dasyurids and rodents, with increase or relative stability in the smaller (and/or more
376 disturbance favoured) dasyurids and rodents. Third, a broader monitoring program in
377 Kakadu (incorporating lowland and sandstone upland sites), and other nearby
378 reserves, also demonstrated significant declines for northern quoll over the period
379 spanned in this study, and subsequently (Woinarski *et al.* 2010; Russell-Smith *et al.*
380 2014). However other trends from this monitoring were less consistent with the results
381 reported here: the broader Kakadu monitoring program reported no overall change
382 for Arnhem rock-rat and some decrease for common rock-rat over the period 2001 to
383 2009, and comparable sampling at nearby Litchfield National Park reported no change
384 in abundance for northern quoll over the period 1995 to 2002 (Woinarski *et al.* 2010;
385 Russell-Smith *et al.* 2014).

386

387 This study offers some useful perspective in relation to the role of some factors
388 considered as possible causative agents in the decline of components of the mammal

389 fauna of northern Australia (Woinarski *et al.* 2011a). First, our re-sampling showed a
390 substantial decline (88-95%) for the northern quoll over a period immediately
391 preceding the arrival of cane toads, so demonstrates that toads alone are not
392 responsible for the full extent of recent declines in this species. Second, given that
393 feral stock were largely absent from the study area throughout the period spanned by
394 this study, the decline we report for northern quoll and Arnhem rock-rat is also likely
395 to be unrelated to habitat degradation due to introduced herbivores.

396

397 The study provides some, albeit weak, evidence that fire is implicated in the decline in
398 this mammal fauna. Fire is a pivotal factor in the ecology of these sandstone
399 environments. A series of studies has shown that recent regimes of frequent and
400 extensive fires are detrimentally affecting sandstone plant communities, most notably
401 heathlands (Russell-Smith *et al.* 1998, 2002) and monsoon rainforests (Russell-Smith
402 *et al.* 1993), and causing regional declines in fire-sensitive plant species, such as
403 *Callitris intratropica* (Trauernicht *et al.* 2013; Bowman *et al.* 2014), although
404 intensive management may have improved this regime in some sandstone areas of
405 Kakadu subsequent to our 2002 sampling (Murphy *et al.* 2015). Fire regimes that
406 degrade sandstone rainforests in particular, and less so sandstone heathlands, may be
407 disadvantageous for the Arnhem rock-rat, as this species is strongly associated with
408 sandstone rainforests and a substantial component of its diet comprises fleshy fruits
409 from savanna and rainforest plant species, such as *Owenia vernicosa*, *Canarium*
410 *australianum* and *Terminalia carpentariae* (Begg and Dunlop 1980, 1985), whose
411 abundance, stature and fruit productivity is likely to be reduced by frequent fire
412 (Russell-Smith *et al.* 2014).

413

414 In the Kakadu region generally, the mammal fauna at re-sampled sites has been
415 shown to have a greater rate of decline when those sites are burnt more frequently or
416 extensively (Griffiths and Brook 2015; Griffiths *et al.* 2015; Lawes *et al.* 2015),
417 although studies in other sandstone regions have not reported such relationships
418 (Radford 2012).

419

420 At Nawurlandja, trap success was significantly higher in 1977-79 (when the study
421 area had been largely unburnt for at least 3-5 years) than in our 2002 re-sampling
422 (when the study area had experienced more frequent and pervasive fire in the
423 preceding years). Begg's experimental fire also demonstrated that these mammal
424 assemblages respond strongly to fire, reporting decline in the abundance of most
425 species and some changes in habitat use following the imposition of an extensive fire
426 (Begg *et al.* 1981). Other studies have also shown that populations of northern quoll
427 (Oakwood 2000) and Arnhem rock-rat (Kerle and Burgman 1984) are adversely
428 affected by extensive and/or frequent fire.

429

430 Fire may be a direct cause of changes in mammal abundance (e.g. by causing a
431 reduction in food availability for some mammal species), or it may work indirectly or
432 in concert with other factors. Recent studies in the Kimberley region of northern

433 Australia have demonstrated that feral cats are attracted to recently burnt areas and
434 that their impacts on native mammal species are more intense in such areas, especially
435 where fires leave few unburnt patches (McGregor *et al.* 2014, 2016; Leahy *et al.*
436 2015). This compounding interaction of two threat factors may be responsible for the
437 decline that we report for this study area, however the incidence of cats, and change in
438 this incidence over time, was not evaluated in our study. There is some evidence from
439 other regions that cat densities may be lower, and/or their predation impacts may be
440 less, in rugged areas than nearby lowland areas (Hohnen *et al.* 2016b; Legge *et al.*
441 2017).

442

443 Much of the recent decline in the mammal fauna of northern Australia has occurred in
444 relatively featureless lowland areas (Woinarski *et al.* 2001), with the fauna of more
445 rugged sandstone areas showing more resilience (Hohnen *et al.* 2016a). This has led
446 to some speculation that these rugged areas may provide a robust refuge from those
447 threat factors that operate almost pervasively in lowland areas (Woinarski *et al.* 2009;
448 Start *et al.* 2012; Hohnen *et al.* 2016b;). Our results suggests that this hopeful
449 assumption may be valid only in part, and that at least some of the influential threat
450 factors operating in lowland areas are also affecting the mammal fauna of rugged
451 upland areas.

452

453

454 **Acknowledgements**

455

456 We thank the rangers and Traditional Owners of Kakadu National Park for their
457 interest in and assistance with this work. The 2002 study formed part of a consultancy
458 for Parks Australia to the Tropical Savannas Cooperative Research Centre. We thank
459 Rod Kennett for his input and Martin Armstrong for much help with that field work.
460 The 1994 re-sampling was funded by the Australian National University and a
461 Commonwealth Postgraduate Research Award (MO). We thank Andrew Cockburn,
462 Tony Spring and Lyn Lowe for their assistance during that survey. We also thank
463 Ross Goldingay, Brett Murphy and an anonymous referee for their helpful
464 suggestions on an earlier draft of this manuscript.

465

466 This study is indebted to the initial detailed research undertaken by Robert Begg, and
467 we acknowledge the value of that series of studies.

468

469

470 **Conflicts of Interest**

471

472 The 2002 study formed part of a consultancy for Parks Australia to the Tropical
473 Savannas Cooperative Research Centre.

474

475

476 **References**

477
478 Begg, R.J. (1981a). The small mammals of Little Nourlangie Rock, N.T. III.
479 Ecology of *Dasyurus hallucatus*, the northern quoll (Marsupialia: Dasyuridae).
480 *Australian Wildlife Research* **8**, 73-85.
481
482 Begg, R.J. (1981b). The small mammals of Little Nourlangie Rock, N.T. II. Ecology
483 of *Antechinus bilarni*, the Sandstone Antechinus (Marsupialia: Dasyuridae).
484 *Australian Wildlife Research* **8**, 57-72.
485
486 Begg, R.J. (1981c). The small mammals of Little Nourlangie Rock, N.T. IV. Ecology
487 of *Zyromys woodwardi*, the large rock-rat, and *Z. argurus*, the common rock-rat
488 (Rodentia: Muridae). *Australian Wildlife Research* **8**, 307-320.
489
490 Begg, R.J., and Dunlop, C.R. (1980) Security eating, and diet in the large rock-rat,
491 *Zyromys woodwardi* (Rodentia: Muridae). *Australian Wildlife Research* **7**, 63-70.
492
493 Begg, R.J., and Dunlop, C.R. (1985) Diet of the large rock-rat, *Zyromys woodwardi*,
494 and the common rock-rat *Z. argurus* (Rodentia: Muridae). *Australian Wildlife*
495 *Research* **12**, 19-24.
496
497 Begg, R.J., Martin, K.C., and Price, N.F. (1981). The small mammals of Little
498 Nourlangie Rock, N.T. V. The effects of fire. *Australian Wildlife Research* **8**, 515-
499 527.
500
501 Bowman, D.M., MacDermott, H.J., Nichols, S.C., and Murphy, B.P. (2014). A grass-
502 fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecology and*
503 *Evolution* **4**, 4185-4194.
504
505 Bradshaw, C.J.A., Field, I.C., Bowman, D.M.J.S., Haynes, C., and Brook, B.W.
506 (2007). Current and future threats from non-indigenous animal species in northern
507 Australia: a spotlight on World Heritage Area Kakadu National Park. *Wildlife*
508 *Research* **34**, 419-436.
509
510 Braithwaite, R.W., and Brady, P. (1993) The delicate mouse, *Pseudomys delicatulus*:
511 a continuous breeder waiting for the good times. *Australian Mammalogy* **16**, 94-98.
512
513 Braithwaite, R.W., and Griffiths, A.D. (1994) Demographic variation and range
514 contraction in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae).
515 *Wildlife Research* **21**, 203-217.
516
517 Braithwaite, R.W., and Griffiths, A.D. (1996) The paradox of *Rattus tunneyi*:
518 endangerment of a native pest. *Wildlife Research* **23**, 1-21.
519
520 Braithwaite, R.W., and Muller, W.J. (1997). Rainfall, groundwater and refuges:
521 predicting extinctions of Australian tropical mammal species. *Australian Journal of*
522 *Ecology* **22**, 57-67.
523
524 Burnett, S. (1997). Colonizing cane toads cause population declines in native
525 predators: reliable anecdotal information and management implications. *Pacific*
526 *Conservation Biology* **3**, 65-72.

527
528 Clarke, K.R., and Gorley, R.N. (2001). PRIMER v5: User manual/Tutorial. PRIMER-
529 E, Portsmouth.
530
531 Davies, H.F., McCarthy, M.A., Firth, R.S.C., Woinarski, J.C.Z., Gillespie, G.R.,
532 Andersen, A.N., Geyle, H.M., Nicholson, E., and Murphy, B.P. (2017). Top-down
533 control of species distributions: feral cats driving the regional extinction of a
534 threatened rodent in northern Australia. *Diversity and Distributions* **23**, 272-283.
535
536 Dunlop, C.R., and Begg, R.J. (1981a). A checklist of the plants of Little Nourlangie
537 Rock, Kakadu National Park, N.T. *Northern Territory Botanical Bulletin* **3**, 12-25.
538
539 Dunlop, C.R., and Begg, R.J. (1981b). The small mammals of Little Nourlangie Rock,
540 N.T. I. Description of study site. *Australian Wildlife Research* **8**, 51-56.
541
542 ESRI (2002) ArcView 3.2. (Environmental Systems Research Institute: Redlands,
543 CA)
544
545 Firth, R.S.C., Brook, B.W., Woinarski, J.C.Z., and Fordham, D.A. (2010). Decline
546 and likely extinction of a northern Australian native rodent, the Brush-tailed Rabbit-
547 rat *Conilurus penicillatus*. *Biological Conservation* **143**, 1193-1201.
548
549 Freeland, W.J., Winter, J.W., and Raskin, S. (1988). Australian rock-mammals: a
550 phenomenon of the seasonally dry tropics. *Biotropica* **20**, 70-79.
551
552 Friend, G.R. (1985) Ecological studies of a population of *Antechinus bellus*
553 (Marsupialia: Dasyuridae) in tropical northern Australia. *Australian Wildlife Research*
554 **12**, 151-162.
555
556 Friend, G.R. (1987) Population ecology of *Mesembriomys gouldii* (Rodentia:
557 Muridae) in the wet-dry tropics of the Northern Territory. *Australian Wildlife*
558 *Research* **14**, 293-303.
559
560 Friend, G.R. (1990) Breeding and population dynamics of *Isoodon macrourus*
561 (Marsupialia: Peramelidae): studies from the wet-dry tropics of northern Australia. In
562 'Bandicoots and Bilbies.' (Eds. JH Seebeck, PR Brown, RL Wallis and CM Kemper)
563 pp. 357-365. (Surrey Beatty & Sons: Chipping Norton)
564
565 Friend, G.R., and Taylor, J.A. (1985) Habitat preferences of small mammals in
566 tropical open-forest of the Northern Territory. *Australian Journal of Ecology* **10**, 173-
567 185.
568
569 Griffiths, A.D., and Brook, B.W. (2015). Fire impacts recruitment more than survival
570 of small-mammals in a tropical savanna. *Ecosphere* **6**, 1-22.
571
572 Griffiths, A.D., Garnett, S.T., and Brook, B.W. (2015). Fire frequency matters more
573 than fire size: Testing the pyrodiversity–biodiversity paradigm for at-risk small
574 mammals in an Australian tropical savanna. *Biological Conservation* **186**, 337-346.
575

576 Hohnen, R., Tuft, K., Legge, S., Walters, N., Johanson, L., Carver, S., Radford, I.J.,
577 and Johnson, C.N. (2016a). The significance of topographic complexity in habitat
578 selection and persistence of a declining marsupial in the Kimberley region of Western
579 Australia. *Australian Journal of Zoology* **64**, 198-216.

580
581 Hohnen, R., Tuft, K., McGregor, H.W., Legge, S., Radford, I.J., and Johnson, C.N.
582 (2016b). Occupancy of the invasive feral cat varies with habitat complexity. *PloS one*
583 **11**, e0152520.

584
585 Hopkins, H.L., and Kennedy, M.L. (2004). An assessment of indices of relative and
586 absolute abundance for monitoring populations of small mammals. *Wildlife Society*
587 *Bulletin* **32**, 1289-1296.

588
589 Kerle, J.A., and Burgman, M.A. (1984). Some aspects of the ecology of the mammal
590 fauna of the Jabiluka area, Northern Territory. *Australian Wildlife Research* **11**, 207-
591 222.

592
593 Kitchener, D.J. (1978). Mammals of the Ord River area, Kimberley, Western
594 Australia. *Records of the Western Australian Museum* **6**, 189-217.

595
596 Lawes, M.J., Murphy, B.P., Fisher, A., Woinarski, J.C.Z., Edwards, A., and Russell-
597 Smith, J. (2015). Small mammals decline with increasing fire extent in northern
598 Australia: evidence from long-term monitoring in Kakadu National Park.
599 *International Journal of Wildland Fire* **24**, 712-722.

600
601 Leahy, L., Legge, S.M., Tuft, K., McGregor, H., Barmuta, L., Jones, M.E., and
602 Johnson, C.N. (2015). Amplified predation after fire suppresses rodent populations in
603 Australia's tropical savannas. *Wildlife Research* **42**, 705-716.

604
605 Legge, S., Kennedy, M.S., Lloyd, R., Murphy, S., and Fisher, A. (2011). Rapid
606 recovery of mammal fauna in the central Kimberley, northern Australia, following
607 removal of introduced herbivores. *Austral Ecology* **36**, 791-799.

608
609 Legge, S., Murphy, B.P., McGregor, H., Woinarski, J.C.Z., Augusteyn, J., Ballard, G.,
610 Baseler, M., Buckmaster, T., Dickman, C.R., Doherty, T., Edwards, G., Eyre, T.,
611 Fancourt, B., Ferguson, D., Forsyth, D.M., Geary, W.L., Gentle, M., Gillespie, G.,
612 Greenwood, L., Hohnen, R., Hume, S., Johnson, C.N., Maxwell, N., McDonald, P.,
613 Morris, K., Moseby, K., Newsome, T., Nimmo, D., Paltridge, R., Ramsey, D., Read,
614 J., Rendall, A., Rich, M., Ritchie, E., Rowland, J., Short, J., Stokeld, D., Sutherland,
615 D.R., Wayne, A.F., Woodford, L., and Zewe, F. (2017). Enumerating a continental-
616 scale threat: how many feral cats are in Australia? *Biological Conservation* **206**, 293-
617 303.

618
619 McGregor, H.W., Legge, S., Jones, M.E., and Johnson, C.N. (2014). Landscape
620 management of fire and grazing regimes alters the fine-scale habitat utilisation by
621 feral cats. *PloS One* **9**, e109097.

622
623 McGregor, H.W., Legge, S.M., Jones, M.E., and Johnson, C.N. (2016).
624 Extraterritorial hunting expeditions to intense fire scars by feral cats. *Scientific*
625 *Reports* **6**, 22559.

626
627 McKenzie, N.L. (1981). Mammals of the Phanerozoic South-West Kimberley,
628 Western Australia: biogeography and recent changes. *Journal of Biogeography* **8**,
629 263-280.

630
631 Murphy, B.P., Cochrane, M.A., and Russell-Smith, J. (2015). Prescribed burning
632 protects endangered tropical heathlands of the Arnhem Plateau, northern Australia.
633 *Journal of Applied Ecology* **52**, 980-991.

634
635 O'Donnell, S., Webb, J.K., and Shine, R. (2010). Conditioned taste aversion enhances
636 the survival of an endangered predator imperiled by a toxic invader. *Journal of*
637 *Applied Ecology* **47**, 558-565.

638
639 Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus*
640 *hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of*
641 *Zoology* **48**, 519-539.

642
643 Oakwood, M. (2004). The case of the disappearing spots. *Nature Australia* **28**(2), 26-
644 35.

645
646 Oakwood, M., and Foster, P. (2008). Monitoring extinction of the northern quoll.
647 *Australian Academy of Science Newsletter* **71**, 6.

648
649 Pardon, L.G., Brook, B.W., Griffiths, A.D., and Braithwaite, R.W. (2003).
650 Determinants of survival for the northern brown bandicoot under a landscape-scale
651 fire experiment. *Journal of Animal Ecology* **72**, 106-115.

652
653 Radford, I.J. (2012). Threatened mammals become more predatory after small scale
654 prescribed fires in a high-rainfall rocky savanna. *Austral Ecology* **37**, 926-935.

655
656 Radford, I.J., Dickman, C.R., Start, A.N., Palmer, C., Carnes, K., Everitt, C., Fairman,
657 R., Graham, G., Partridge, T., and Thomson, A. (2014). Mammals of Australia's
658 tropical savannas: a conceptual model of assemblage structure and regulatory factors
659 in the Kimberley region. *PloS one* **9**, e92341.

660
661 Russell-Smith, J., Edwards, A., Woinarski, J., Fisher, A., Murphy, B.P., Lawes, M.,
662 Crase, B., and Thurgate, N. (2014). North Australian tropical savannas: the three
663 parks savanna fire-effects plot network. In 'Biodiversity and environmental change:
664 monitoring, challenges and direction.' (Eds. D. Lindenmayer, E. Burns, N. Thurgate
665 and A. Lowe.) Pp. 335-378. (CSIRO Publishing: Melbourne)

666
667 Russell-Smith, J., Lucas, D.E., Brock, J., and Bowman, D.M.J.S. (1993).
668 *Allosyncarpia*-dominated rain forest in monsoonal northern Australia. *Journal of*
669 *Vegetation Science* **4**, 67-82.

670
671 Russell-Smith, J., Ryan, P.G., and Cheal, D.C. (2002). Fire regimes and the
672 conservation of sandstone heath in monsoonal northern Australia: frequency, interval,
673 patchiness. *Biological Conservation* **104**, 91-106.

674

675 Russell-Smith, J., Ryan, P.G., Klessa, D., Waight, G., and Harwood, R. (1998). Fire
676 regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem
677 Plateau, monsoonal northern Australia. *Journal of Applied Ecology* **35**, 829-846.
678

679 Slade, N.A., and Blair, S.M. (2000). An empirical test of using counts of individuals
680 captured as indices of population size. *Journal of Mammalogy* **81**, 1035-1045.
681

682 Start, A.N., Burbidge, A.A., McDowell, M.C., and McKenzie, N.L. (2012). The status
683 of non-volant mammals along a rainfall gradient in the south-west Kimberley,
684 Western Australia. *Australian Mammalogy* **34**, 36-48.
685

686 Start, A.N., Burbidge, A.A., McKenzie, N.L., and Palmer, C. (2007). The status of
687 mammals in the North Kimberley, Western Australia. *Australian Mammalogy* **29**, 1-
688 16.
689

690 Trauernicht, C., Murphy, B.P., Tangalin, N., and Bowman, D.M.J.S. (2013). Cultural
691 legacies, fire ecology, and environmental change in the stone country of Arnhem
692 Land and Kakadu National Park, Australia. *Ecology and Evolution* **3**, 286-297.
693

694 Woinarski, J.C.Z., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A.D., Hill, B.,
695 Milne, D.J., Palmer, C., Ward, S., Watson, M., Winderlich, S., and Young, S. (2010).
696 Monitoring indicates rapid and severe decline of native small mammals in Kakadu
697 National Park, northern Australia. *Wildlife Research* **37**, 116-126.
698

699 Woinarski, J.C.Z., Armstrong, M., Price, O., McCartney, J., Griffiths, A.D., and
700 Fisher, A. (2004). The terrestrial vertebrate fauna of Litchfield National Park,
701 Northern Territory: monitoring over a 6-year period and response to fire history.
702 *Wildlife Research* **31**, 587-596.
703

704 Woinarski, J.C.Z., and Ash, A.J. (2002). Responses of vertebrates to pastoralism,
705 military land use and landscape position in an Australian tropical savanna. *Austral
706 Ecology* **27**, 311-323.
707

708 Woinarski, J.C.Z., and Fisher, A. (2003). Conservation and the maintenance of
709 biodiversity in the rangelands. *Rangeland Journal* **25**, 157-171.
710

711 Woinarski, J.C.Z., Legge, S., Fitzsimons, J.A., Traill, B.J., Burbidge, A.A., Fisher, A.,
712 Firth, R.S.C., Gordon, I.J., Griffiths, A.D., Johnson, C.N., McKenzie, N.L., Palmer,
713 C., Radford, I., Rankmore, B., Ritchie, E.G., Ward, S., and Ziemnicki, M. (2011a).
714 The disappearing mammal fauna of northern Australia: context, cause, and response.
715 *Conservation Letters* **4**, 192-201.
716

717 Woinarski, J.C.Z., Milne, D.J., and Wanganeen, G. (2001). Changes in mammal
718 populations in relatively intact landscapes of Kakadu National Park, Northern
719 Territory, Australia. *Austral Ecology* **26**, 360-370.
720

721 Woinarski, J.C.Z., Russell-Smith, J., Andersen, A., and Brennan, K. (2009). Fire
722 management and biodiversity of the western Arnhem Land plateau. In 'Culture,
723 ecology and economy of fire management in north Australian savannas: rekindling the

724 wurrk tradition.' (Eds. J. Russell-Smith, P.J. Whitehead and P. Cooke.) Pp. 201-228.
725 (CSIRO Publishing: Collingwood)
726
727 Woinarski, J.C.Z., Ward, S., Mahney, T., Bradley, J., Brennan, K., Ziembicki, M., and
728 Fisher, A. (2011b). The mammal fauna of the Sir Edward Pellew island group,
729 Northern Territory, Australia: refuge and death-trap. *Wildlife Research* **38**, 307-322.
730
731 Ziembicki, M.R., Woinarski, J.C.Z., and Mackey, B. (2013). Evaluating the status of
732 species using Indigenous knowledge: novel evidence for major native mammal
733 declines in northern Australia. *Biological Conservation* **157**, 78-92.
734
735 Ziembicki, M.R., Woinarski, J.C.Z., Webb, J.K., Vanderduys, E., Tuft, K., Smith, J.,
736 Ritchie, E.G., Reardon, T.B., Radford, I.J., Preece, N., Perry, J., Murphy, B.P.,
737 McGregor, H., Legge, S., Leahy, L., Lawes, M.J., Kanowski, J., Johnson, C.N.,
738 James, A., Griffiths, A.D., Gillespie, G., Frank, A., Fisher, A., and Burbidge, A.A.
739 (2015). Stemming the tide: progress towards resolving the causes of decline and
740 implementing management responses for the disappearing mammal fauna of northern
741 Australia. *Therya* **6**, 169-225.
742
743
744
745
746

747
748
749
750
751
752
753
754

Table 1a. April 2002 sampling results compared with March-May 1977-79 and March-May 1980 results. Values in body of table are % trap-success (per 100 trapnights), with z-ratio score (for comparison with 2002 results) and Bonferroni-adjusted probability in brackets: * $p < 0.0025$; ** $p < 0.0005$; *** $p < 0.00025$.

Species	1977-79	1980	2002
<i>trap-nights</i>	10,800	3600	2400
sandstone antechinus	3.68 (z=9.18, ***)	1.83 (z=6.08, ***)	0.13
northern quoll	0.82 (z=4.21, ***)	0.85 (z=4.27, ***)	0.04
Arnhem rock-rat	0.36 (z=2.95, ns)	0.80 (z=4.41, ***)	0
common rock-rat	0.57 (z=3.80, **)	0.33 (z=4.31, ***)	1.29
all species	5.43 (z=8.32, ***)	3.83 (z=5.84, ***)	1.46

755
756
757
758
759
760

Table 1b. July 2002 sampling results compared with June-August 1977-79 and June-August 1980 results. Conventions as for Table 1a.

Species	1977-79	1980	2002
<i>trap-nights</i>	8400	3600	1200
sandstone antechinus	4.27 (z=1.66, ns)	1.70 (z=3.27, *)	3.25
northern quoll	0.69 (z=2.52, ns)	0.67 (z=2.43, ns)	0.08
Arnhem rock-rat	1.77 (z=4.65, ***)	1.31 (z=3.98, ***)	0
common rock-rat	1.57 (z=3.92, ***)	2.25 (z=1.77, ns)	3.17
all species	8.31 (z=2.15, ns)	5.91 (z=0.73, ns)	6.50

761
762
763