

---

Charles Darwin University

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

Ibbett, M.; Woinarski, J. C.Z.; Oakwood, M.

*Published in:*  
Australian Mammalogy

*DOI:*  
[10.1071/AM17011](https://doi.org/10.1071/AM17011)

Published: 01/01/2018

*Document Version*  
Peer reviewed version

[Link to publication](#)

### *Citation for published version (APA):*

Ibbett, M., Woinarski, J. C. Z., & Oakwood, M. (2018). Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia. *Australian Mammalogy*, 40(2), 181-187. <https://doi.org/10.1071/AM17011>

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

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<sup>A,B,C</sup>, J.C.Z. Woinarski<sup>A,D,G</sup>, and M. Oakwood<sup>E,F</sup>

<sup>A</sup> Department of Natural Resources Environment and the Arts, PO Box 496, Palmerston, Northern Territory 0831, Australia.

<sup>B</sup> Charles Darwin University, Northern Territory 0909, Australia.

<sup>C</sup> Queensland Parks and Wildlife Service, PO Box 2066, Cairns, Queensland 4870, Australia

<sup>D</sup> 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

<sup>E</sup> Evolutionary Ecology Group, Division of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia.

<sup>F</sup> Envirotek Ecological Services, PO Box 4022, Coffs Harbour Jetty, NSW 2450, Australia

<sup>G</sup> 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 km<sup>2</sup>, 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 km<sup>2</sup>) 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