

1
2 **Demographic evaluation of translocating the threatened northern quoll to two**
3 **Australian islands**

4
5 Anthony D. Griffiths^{1,2,*}, Brooke Rankmore^{1,3}, Kym Brennan¹ and John C. Z.
6 Woinarski^{1,2,4}

7 *¹Department of Environment and Natural Resources, PO Box 496 Palmerston, NT 0831*
8 *Australia*

9 *²Research Institute for Environment and Livelihoods, Charles Darwin University, Casuarina,*
10 *NT 0909, Australia*

11 *³Greening Australia, PO Box 1, Berrimah, NT 0828, Australia*

12 *⁴Threatened Species Recovery Hub, National Environmental Science Programme, The*
13 *University of Queensland, St Lucia, QLD 4072 Australia*

14
15
16 Running title: Evaluating translocation success of the northern quoll

17
18 *Corresponding author: Tony Griffiths, Department of Land Resource Management, PO Box
19 496 Palmerston, NT 0831 Australia; ph +618 89955004, fax +618 89955099, E-mail

20 tony.griffiths@nt.gov.au

21

22 **Abstract**

23 **Context.** Translocation is widely used to help avoid extinction of species from threatening
24 processes. A fundamental objective of translocation is to establish self-sustaining populations
25 and estimating demographic parameters is critical to assessing success of these programs and
26 can also be used to support future management actions.

27 **Aims.** We estimated demographic parameters to assess the success of translocating the
28 northern quoll *Dasyurus hallucatus* to two islands (Astell and Pobassoo) in response to the
29 threat posed by the introduced cane toad *Rhinella marina* on the Australian mainland.

30 **Methods.** We used capture-mark-recapture methods to monitor both populations at regular
31 intervals from initial release in 2003 until 2009 and a one-off survey in 2014.

32 **Key results.** Relative abundance (trap success) increased exponentially in the first four
33 years, declined and then stabilised in subsequent years. The population of female northern
34 quolls on Astell Island peaked in 2006 with an estimate of 3,640 (95% CI 3022 – 4257) and
35 on Pobassoo Island the peak was 2007 with 617 (95% CI 531 – 703) females. In 2014 the
36 population had decreased to 2193 (95% CI 1920 – 2467) on Astell and 451 (95% CI 359 –
37 543) on Pobassoo. Apparent survival and body condition decreased significantly following
38 the population peak, possibly related to density-dependence.

39 **Conclusion.** Both populations of northern quolls reached their regulation phase after going
40 through establishment and growth phases, which included exceeding carrying capacity. The
41 pattern was similar between the populations.

42 **Implications.** Increased survival and recruitment at predator-free translocation sites
43 contributes to successful establishment of self-sustaining populations.

44

45 **Introduction**

46 Translocation is the intentional movement of organisms from one area to another, in an
47 attempt to establish or re-establish viable, free-ranging populations of imperilled species
48 (IUCN/SSC 2013) and it is an important and increasingly applied tool to conserve threatened
49 species (Armstrong *et al.* 2015). However, many translocations have failed or been
50 characterised by poor conception (Griffith *et al.* 1989; Wolf *et al.* 1998). From analyses of
51 the fate of many translocations, several factors are recognised to contribute to the success of
52 these programs: the number of animals released, habitat quality, the location of the release
53 area and the threat environment in the release sites(s) (Griffith *et al.* 1989; Fischer and
54 Lindenmayer 2000; Perez *et al.* 2012; Sheean *et al.* 2012). From such reviews, there have
55 been attempts to adopt a more integrated, standardised and theoretically sound approach to
56 translocations (Seddon *et al.* 2007; Armstrong and Seddon 2008), including population
57 monitoring, modelling and structured decision making (Armstrong and Reynolds 2012;
58 Converse *et al.* 2013).

59 The establishment of a self-sustaining population is a fundamental objective of any
60 translocation. While there is no single definition of how to determine whether this objective
61 has been met (Robert *et al.* 2015; Shier 2015), it is necessary to obtain accurate estimates of
62 demographic parameters for the translocated population to be able to assess success. These
63 parameters can be used to assess the establishment of self-sustaining populations using
64 population viability analysis (e.g. Lindenmayer *et al.* 1993) and development of models to
65 guide management of populations (e.g. McCarthy *et al.* 2012). In addition, they can provide
66 important information on the dynamics of the translocated population and help identify
67 problems where management intervention may be needed.

68 Translocations have been used extensively to help conserve Australia's mammal fauna and
69 success has typically focussed on measures of population persistence or trends (Fischer and
70 Lindenmayer 2000; Clayton *et al.* 2014; Morris *et al.* 2015). Australian mammals have had

71 an extraordinary extinction rate over the last 200 years (Short and Smith 1994; Woinarski *et*
72 *al.* 2014): at least 30 Australian terrestrial mammal species have become extinct over this
73 period, representing well over a third of the world's recent mammal extinctions (Sattler and
74 Creighton 2002). Many threatening processes have been linked to this decline, including
75 predation by introduced vertebrates, habitat loss, habitat modification from the introduction
76 of exotic herbivores, disease and changed fire regimes (Burbidge and McKenzie 1989;
77 Woinarski and Braithwaite 1990; Short and Smith 1994; Smith and Quin 1996; Johnson
78 2006).

79 Here we estimate demographic parameters using capture-mark-recapture methods for an
80 island translocation for the northern quoll *Dasyurus hallucatus*. This omnivorous marsupial is
81 extremely susceptible to toxins ingested during predation on the exotic cane toad *Rhinella*
82 *marina*. Consequently, populations of northern quolls have drastically declined in many areas
83 of mainland Australia following the invasion of those areas by cane toads (Burnett 1997;
84 Shine 2010). Cane toads are spreading rapidly across mainland northern Australia and their
85 eventual range is likely to encompass almost entirely that of the northern quoll (Sutherst *et al.*
86 1996; Kearney *et al.* 2008). Cane toads have also naturally colonised (and may be
87 inadvertently introduced to) some islands, where they have also caused substantial local
88 losses of some predatory animals, including northern quoll (Woinarski *et al.* 2011). In the
89 medium term, it is unlikely that there will be any mechanism available to effectively slow the
90 spread or reduce the population of cane toads in northern Australia. In addition, the species
91 has experienced population declines and range contraction in parts of its distribution prior to
92 the arrival of cane toads (Braithwaite and Griffiths 1994). Because of these factors, the
93 northern quoll is listed as endangered under Australia's *Environment Protection and*
94 *Biodiversity Conservation Act*.

95 The objective of this paper is to demonstrate, using demographic parameters, whether the
96 translocation program established at least one secure island population of northern quolls.
97 Importantly, translocations to islands provide a unique opportunity to undertake natural
98 experiments, as they act as closed populations to threats and resources may vary between
99 islands used as translocation sites. In this case, given some risk of catastrophe (notably
100 invasion of the translocated sites by cane toads and tropical cyclones), we use two separate
101 translocation destinations, and hence can compare population trends across these two sites.
102 For both island sites, we simultaneously monitored demographic parameters to examine
103 difference between sites, evidence of density dependence (Armstrong *et al.* 2005) and
104 variation caused environmental covariates such as rainfall. This information will inform
105 future management of the populations and provides insight into future translocations of other
106 mammal species.

107 **Materials and methods**

108 *Island selection*

109 Broadly following established IUCN criteria for translocations (IUCN/SSC 2013), we
110 developed a candidate set of potentially suitable Northern Territory islands. The selection
111 criteria included the following: adequate size for persistence for at least 30 years ($> 1 \text{ km}^2$,
112 but preferably $> 10 \text{ km}^2$); occurrence of suitable habitat (areas of rugged sandstone); absence
113 of human habitation; relatively low risk of cane toad colonisation (limited visitation by
114 humans, distant from mainland, not in the outflow area of mainland rivers); moderate
115 accessibility; and absence of other conservation values susceptible to predation or
116 competition from translocated quolls. These criteria restricted the candidate set to about ten
117 islands. The final selection was made after a period of detailed consultation with the islands'
118 Aboriginal landowners.

119 Two islands were selected as translocation sites: Astell (area =1268 ha, max. elevation =
120 74 m and distance to mainland = 5.4 km) and Pobassoo (area =392 ha, max. elevation = 78 m
121 and distance to mainland = 2.3 km), both in the English Company group off north-eastern
122 Arnhem Land (Fig. 1). Both islands are rugged and dominated by eucalypt (particularly
123 *Eucalyptus tetradonta*) woodlands, with small fringing areas of coastal vine thicket and
124 mangroves (Woinarski *et al.* 2000).

125 INSERT FIG 1

126 Translocations may have impacts on other species present at the destination site, and these
127 impacts may be particularly severe when the translocated species is a predator such as the
128 northern quoll. Previous detailed surveys had indicated that these islands did not support any
129 plant (Woinarski *et al.* 2000), ant (Woinarski *et al.* 1998), herpetofauna (Woinarski *et al.*
130 1999a), bird (Woinarski *et al.* 2001) or mammal (Woinarski *et al.* 1999b) species of
131 conservation significance likely to be affected by a quoll translocation. Indeed, there were no
132 marsupials and only one species of rodent (*Hydromys chrysogaster*) recorded from these two
133 islands (Woinarski *et al.* 1999b). Furthermore, unlike many islands in this group they also
134 lacked significant nesting sites for marine turtles (Chatto and Baker 2008) and shorebirds
135 (Chatto 2003).

136 *Founder population and translocation procedure*

137 Founder stock was drawn from a range of sites across mainland Northern Territory,
138 particularly from lowland areas on the Darwin rural fringe and Kakadu National Park.
139 Collections were timed to immediately precede the cane toad invasion front, and coincided
140 with the time when juvenile quolls became independent (February-March 2003). This age
141 class was considered most likely to adapt to translocation, especially since adults (especially
142 males) have a short life expectancy. Animals were collected using Elliott (10 × 10 × 33 cm)

143 and cage ($15 \times 15 \times 60$ cm) traps and held in purpose-built enclosures for 1 to 9 days before
144 being transported to translocation sites. Nineteen animals (8 males; 11 females) were released
145 at Pobassoo Island in February 2003, and then 45 animals (11 males; 34 females) were
146 released at Astell Island in March 2003. The sizes of founder populations were set to account
147 for some initial post-release mortality and what we believed to be the minimum number of
148 animals for successful establishment. No further translocations were made during the
149 program.

150 *Monitoring*

151 The translocated quoll populations were monitored on ten occasions following release, with
152 all surveys conducted in collaboration with the islands' Aboriginal owners. The earlier
153 surveys (2003 to 2005) occurred in the early to mid-Dry season (April to July). Subsequent
154 surveys (2006 to 2009) took place in October or December, when adult males were largely
155 absent and the weaned young of the year were entering the trappable population. We also
156 conducted a survey in October 2014 to confirm the persistence of the quoll populations.

157 In the earlier monitoring surveys, sampling used either (or both) grids (an array of 7×10
158 traps, spaced 20 m apart) or transects (a line of 10 traps spaced 20 m apart) over 3 or 5 nights
159 with multiple surveys occurring in some years. In later surveys, permanent trapping grids (an
160 array of 5×5 traps, spaced 20 m apart) were established and sampled over five nights, with
161 ten grids used on Astell and eight on Pobassoo. The survey in 2014 used half the permanent
162 grids on each island (due to funding constraints). The change in survey methodology post-
163 2006 was due to a need to collect more robust capture-mark-recapture data once the
164 population had become established. All traps used were cage traps ($13 \text{ cm} \times 13 \text{ cm} \times 40 \text{ cm}$),
165 baited with a mixture of peanut butter, honey and oats. In total, there were 7,776 trap nights
166 on Astell Island and 6,431 trap nights on Pobassoo Island over the entire monitoring program.

167 Traps were set and baited in the late afternoon and checked (and then closed) in the early
168 morning. For every quoll caught, we recorded its sex, body mass (g) and head length (mm).
169 We marked all individuals by microchip (Destron PIT tags) except in the 2007 survey where
170 eartags (Model 1005-1 self-piercing ear tag, National Band and Tag Co.) were used. All
171 quolls were released at the grid immediately after processing.

172 *Statistical analysis*

173 We used two methods to assess changes in abundance. The first used the rate of trap success
174 (captures per 100 trap nights) of all individuals (males and females) over all surveys. We
175 used generalised linear regression to estimate long-term linear trend in northern quoll trap
176 success for both island populations. The response variable was log transformed trap success
177 and island and year were fixed-effects. In years when two surveys occurred, we pooled the
178 data into a single value for each island. To account for temporal correlation we used a first
179 order autocorrelation term and a log link (Chaloupka and Limpus 2001), and models were
180 fitted using maximum likelihood estimation to allow comparison between models with
181 different fixed effects (Pinheiro and Bates 2000).

182 The second method used capture-mark-recapture data from the later surveys (2006 to 2009
183 and 2014) to estimate the density of female northern quolls. We used the closed-captures
184 component within the Pradel Robust Design model for the 2006 to 2009 and a single closed-
185 capture model for the 2014 survey using Program MARK v8.0 (White and Burnham 1999).
186 Using the full likelihood model we estimated the probability of initial capture (p) and the
187 probability of recapture (c) of female quolls over five nights (Williams *et al.* 2002). We
188 constructed a candidate set of models that included parameters representing no variation
189 (null), linear trend, year and island for both p and c , which were combined with constant
190 survival and recruitment models. Model selection was based on Akaike's Information

191 Criterion, corrected for small sample size (AIC_c: (Burnham and Anderson 2002). The
192 likelihood of each model, relative to others in the candidate set, was estimated with AIC_c
193 weights (w) and models were ranked according to this measure (Burnham and Anderson
194 2002). To estimate density we calculated the effective trapping area of the 0.64 ha trapping
195 grid by adding a boundary area around its perimeter of half of the average home range size of
196 an individual (Williams *et al.* 2002). This resulted in an effective trapping area of 5.63 ha
197 (based on a home range of 2.3 ha for females in rocky habitat (Schmitt *et al.* 1989)). To
198 estimate the population size of female quolls we divided the density estimate on each island
199 for each year by the effective trapping area. There was considerable homogeneity across all
200 trapping grids on both islands therefore the extrapolations are considered accurate.

201 Body condition for each individual was estimated using the scaled mass index (Peig and
202 Green 2009; Peig and Green 2010). The index is the predicted body mass for individual i
203 when the linear body measurement (head length, mm) is standardised to the mean value of
204 the study population and scaled to the slope of standardised major axis regression of body
205 mass and head length. We used linear regression model differences in scaled mass index
206 among years (2005 to 2009 and 2014), between the two islands and sexes and compared them
207 using AIC model selection.

208 To estimate apparent annual survival and recruitment between 2006 and 2009 we used
209 Pradel temporal symmetry Robust Design models (Pradel 1996) using Program MARK v8.0
210 (White and Burnham 1999). By analysing the encounter history of all marked individuals in
211 the population going backwards in time, it is possible to estimate the probability of an
212 individual entering the population. Apparent survival (ϕ) is the probability that an animal that
213 has not emigrated from the population is alive at time $i + 1$ given it was alive at time i
214 (Williams *et al.* 2002). Recruitment (f) is defined as a per capita recruitment probability (i.e.,
215 net new animals per animal alive at occasion i entering the marked population between

216 occasions i and $i + 1$). The link function was logit for survival and log for recruitment. The
217 temporal symmetry model assumes the area sampled does not change during the study and all
218 animals have some probability of being captured, there is no response to being trapped and
219 there is little difference among animals in being captured. In addition, the Pradel model is an
220 extension of the Cormack-Jolly-Seber (CJS) model that assumes that every marked animal
221 has the same probability of survival, tags are not lost or misidentified, emigration is
222 permanent and the fate of each animal is independent of other animals (Williams *et al.* 2002).

223 We analysed the effect of the two islands, annual rainfall, density dependence, temporal
224 variation and body size on apparent survival and recruitment based on the method of linear
225 modelling of explanatory covariates originally proposed by Lebreton *et al.* (1992) (see
226 Appendix A). We modelled rainfall (mm) as a time-specific covariate over the interval
227 between two primary periods. Temporal variations were represented by year and linear trend,
228 and were expressed as time-specific covariates. Density dependence was modelled as a time-
229 specific covariate and we used the total number of quolls captured on each island from the
230 previous year. Body mass was modelled as an individual covariate. We constructed a priori
231 candidate sets of models from these variables based on known biology and the published
232 ecological literature, comprising additive and, for some models, interactive combinations.
233 Each temporal covariate was scaled to range between positive and negative one. The best
234 capture-recapture model was used when comparing different apparent survival and
235 recruitment models. If the 95% confidence interval for the slope of the logit- or log-
236 explanatory covariate (β) did not include zero, the relationship was considered statistically
237 significant (Williams *et al.* 2002). There is no goodness-of-fit test for the robust-design
238 model, therefore we used separate tests for the open and closed parts of the model. For the
239 open model we collapsed each primary period and performed a median goodness-of-fit on a

240 model containing all temporal covariates with the CJS model in Program MARK (Cooch and
241 White 2014).

242 **Results**

243 *Survey effort and goodness-of-fit*

244 In total, we recorded 2,327 northern quolls captures from 13,507 trap nights across all
245 sampling periods (2003 to 2009 and 2014). The capture rate on Astell Island (1523 captures
246 from 7,776 trap nights: 19.6% trap success) was higher than for Pobassoo (804 captures from
247 6,431 trap nights: 12.5% trap success). For the capture-mark-recapture (CMR) data, there was
248 no evidence of over-dispersion: the median \hat{c} test estimated a \hat{c} of 1.16 and therefore we made
249 no adjustments to \hat{c} in the CMR modelling.

250 *Population trend*

251 From the initial release of 64 northern quolls in 2003, there was a rapid increase in trap
252 success for three years. On Astell Island, trap success peaked in 2005 whereas on Pobassoo
253 Island it remained high from 2005 to 2007 and then decreased (Figure 2a). At both islands,
254 trap success stabilised at a reduced level in later years. Trap success was significantly higher
255 on Astell than Pobassoo Island (Table 1). The best-supported model for variation in trap
256 success contained the factor Island and a quadratic linear trend, representing non-linear
257 change in trap success over the seven years (Table 1).

258 INSERT FIG 2

259 INSERT TABLE 1

260 The density estimates of female northern quolls followed a similar pattern to trap success:
261 a very rapid increase in density of female northern quolls for a few years after the
262 introductions and then a decline and finally stability (Figure 2b). Density was higher on

263 Astell than on Pobassoo Island and densities decreased on both islands after 2007 (Figure
264 2b). Initial capture (p) and recapture probabilities (c) differed over time and between islands
265 (Appendix Table A1). For the one-off survey in 2014 the density on Astell Island was similar
266 to that in 2009 but on Pobassoo the 2014 density was higher than in 2009. Extrapolation of
267 the density estimates showed that the population of female northern quolls on Astell Island
268 peaked in 2006 with an estimate of 3640 (95% CI 3022 – 4257) and in 2014 it was 2193
269 (95% CI 1920 – 2467). On Pobassoo Island the population peaked in 2007 with 617 (95% CI
270 531 – 703) and in 2014 was estimated to be 451 (95% CI 359 – 543). We note that the use of
271 different home range estimates will change these estimates by increasing or decreasing the
272 effective trapping area.

273 Body condition (represented by scaled mass index) varied considerably across the six
274 years and also differed between the two islands. The best-supported model for variation in
275 body condition contained only the parameter year and the next best model contained the
276 interaction between parameters year and island suggesting a different pattern in body
277 condition of quolls over time between Astell and Pobassoo Islands (Table 2). Inspection of
278 model coefficients showed a significant decrease in body condition on Astell Island for the
279 years 2006 to 2008 compared to 2005 (Fig 3a). A similar but less pronounced pattern was
280 observed on Pobassoo Island with body condition being significantly lower in 2006 and 2007
281 but not 2008 (Fig 3b).

282 INSERT FIG 3

283 INSERT TABLE 2

284 *Apparent survival and recruitment*

285 Apparent survival of female quolls varied over the period 2006-2009 and corresponded to the
286 population peak and subsequent decline. The best-supported model contained parameters

287 representing density dependence and the interaction of year and body mass of female quolls
288 (Table 3). Inspection of beta coefficients for the top ranked model showed that higher number
289 of northern quolls in the previous year was negatively related to apparent survival ($\beta = -1.17$,
290 95% CI -1.50 to -0.84). In addition, body mass influenced apparent survival. In 2006-2007
291 there was a negative but non-significant relationship ($\beta = -0.12$, 95% CI -0.45 to 0.21) and in
292 2007-2008 there was a significant negative relationship ($\beta = -0.84$, 95% CI -1.21 to -0.46).
293 However, in 2008-2009 the relationship was positive and non-significant ($\beta = 0.24$, 95% CI -
294 13 to 0.62). Model-averaged estimates of apparent survival on Astell and Pobassoo were 0.42
295 (95% CI 0.34-0.50) and 0.28 (95% CI 0.22-0.34) in 2006-2007, 0.10 (95% CI 0.06-0.15) and
296 0.12 (95% CI 0.08-0.18) in 2007-2008 and 0.63 (95% CI 0.51-0.73) and 0.57 (95% CI 0.46-
297 0.67) in 2008-2009.

298 INSERT TABLE 3

299 Recruitment of female northern quolls varied over the four years of monitoring. The best-
300 supported model included terms that related to rainfall over the previous 12 months.
301 Inspection of beta coefficients showed that increasing rainfall had a negative but non-
302 significant effect on recruitment in ($\beta = -0.36$, 95% CI -0.7 to 0.4). There was no evidence
303 that recruitment differed between the two island populations ($\beta = 0.15$, 95% CI -0.08 to 0.40).
304 Model-averaged estimates of recruitment on Astell and Pobassoo were 0.56 (95% CI 0.46-
305 0.65) and 0.55 (95% CI 0.43-0.73) in 2006-2007, 0.61 (95% CI 0.49-0.73) and 0.59 (95% CI
306 0.43-0.73) in 2007-2008, and 0.41 (95% CI 0.24-0.61) and 0.40 (95% CI 0.25-0.58) in 2008-
307 2009.

308 **Discussion**

309 Based on the demographic parameters presented here there is clear evidence that the
310 translocation program to date has been able to establish two independent northern quoll

311 populations. The translocated island populations exhibited extraordinary rates of increase in
312 the first four years followed by a decline and stabilisation of the population. Both populations
313 appear to have reached their regulation phase within six years after going through
314 establishment and growth phases (Sarrazin and Barbault 1996). The pattern was similar for
315 both islands though there was evidence that the pattern was more pronounced on the larger
316 island (Astell).

317 Several demographic factors are likely to have contributed to the successful establishment
318 of the northern quoll populations. The species has a high maximum annual population growth
319 rate of 1.35 (95% CI 0.11 – 5.46) and short generation length (Hone *et al.* 2010) and this
320 resulted in very high rates of increase in the first four years following the initial release on
321 both islands. This was despite there being a number of catastrophic events within the first
322 four years: approximately 70% of Astell Island was burnt in 2003 and two Category 5
323 tropical cyclones passed directly over both islands on 2005 and 2006, with wind gusts to 325
324 km hr⁻¹ and >300 mm of rainfall (Gove Airport: Bureau of Meteorology). Furthermore, both
325 apparent survival and recruitment were higher on both islands than for (pre-cane toad)
326 mainland sites. Comparable estimates of maximum apparent annual survival for female
327 quolls on the mainland (Kakadu National Park) was 0.49 (Griffiths and Brook 2015)
328 compared to 0.63 in this study. Per capita recruitment rates were higher in the translocated
329 populations on both islands compared to the mainland. Recruitment rates on both islands
330 ranged from 0.40 to 0.60 compared to 0.25 to 0.35 on the mainland (Griffiths and Brook
331 2015). This indicates that the absence of predators and presence of high quality habitat (rocky
332 woodland) contributed to the high deterministic growth rate. Based on this information, both
333 populations appear to have avoided early reintroduction failure due to the high population
334 growth rate in a predator and threat (i.e. cane toad) free environment despite the founder
335 populations being relatively small.

336 There was evidence suggesting negative density-dependence within five years of the initial
337 translocation with female apparent survival decreasing with increasing abundance of northern
338 quolls. In age-structured populations of large herbivores, recruitment (juvenile survival,
339 proportion of females breeding) is considered more sensitive to density dependence than
340 adult survival (Gaillard *et al.* 1998). In this study, there was little variation in recruitment and
341 lower survival of females with larger body mass during the years with high density. Female
342 northern quolls are relatively short-lived (maximum life expectancy 4 years), have high
343 fecundity (average litter size of six young per year) and the majority of females reproduce
344 each year (Braithwaite and Griffiths 1994; Oakwood 2000). It is plausible that the population
345 increased initially in response to lack of predation and an unexploited abundant food
346 resource, but then declined to stabilise at a lower level due to the impacts of the quoll-
347 induced food depletion. Variation among years in body condition supports this hypothesis as
348 the scaled mass index was lowest when relative abundance (i.e., trap success) was highest in
349 2007 then increased when relative abundance levelled off in 2009 and 2014. The pattern was
350 similar between the two islands but more pronounced on the larger island (Astell), possibly
351 caused by the higher density and therefore competition for food. The observed stabilisation of
352 the populations from 2006 to 2014 suggests there has been no significant and sustained
353 habitat degradation. Availability of food resources has probably declined (unsurprisingly
354 given high densities of a novel predator) but now stabilised. It is unclear why larger females
355 had lower apparent survival during periods of high population density. Body size may be
356 related to age but this was not examined in this study.

357 The study raises some important issues for future management of the northern quoll. The
358 translocation was timely for the northern quoll as alternative conservation management
359 options such as building cane toad-proof enclosures were either too expensive or risky
360 (Brook and Whitehead 2005) or had not been developed (O'Donnell *et al.* 2010). As evident

361 in the fate of important populations of other mammal species on some other Northern
362 Territory islands following the spread of introduced species (Woinarski *et al.* 2011), the most
363 critical factor relates to biosecurity, particularly ensuring that cane toads do not colonise or
364 are introduced to these two islands or other islands containing at-risk species. To some extent,
365 this will require the ongoing involvement and interest of the islands' Aboriginal owners. A
366 feature of this program to date has been the full involvement of these landowners, and these
367 landowners have developed a strong sense of responsibility for these translocated
368 populations. Reintroduction of individuals from the translocated island populations to the
369 mainland is another management option. Based on demographic data from mainland
370 populations, a carrying capacity of $\sim 1.0 \text{ ha}^{-1}$ female northern quolls is required for long-term
371 population viability in mainland populations (Griffiths *et al.* 2015). Prior to release, this
372 demographic information could be used to model the number of animals to be released and
373 the potential impact of predators. Conversely, reintroduction of northern quolls to mainland
374 predator exclosures could result in overabundance and demographic parameters presented in
375 this study could be used to develop appropriate release strategies to minimise risk to other
376 species. Future translocation of northern quolls to islands should target threat-free islands that
377 do not contain threatened species that may be preyed upon by quolls. We note that a
378 reduction in genetic diversity of the translocated populations occurred after only three
379 generations but was higher than endemic island populations (Cardoso *et al.* 2009). Future
380 management actions should incorporate maintaining and monitoring genetic diversity of the
381 translocated populations.

382 In conclusion, we have demonstrated the need to collect detailed demographic information
383 for translocated populations to determine that the fundamental objective of establishing self-
384 sustaining populations. Given the relatively small size of the founder populations in this
385 study, it is likely that the high intrinsic growth rate of the species due to high survival and

386 recruitment in a predator- and toad-free translocation sites contributed to both populations
387 reaching their regulation phase and persisting into the future. The results may also contribute
388 to a more unified approach in the use of demographic parameters, such as carrying capacity,
389 in developing universal criteria for defining reintroduction success (Robert *et al.* 2015; Shier
390 2015).

391 **Acknowledgements**

392 Funding was provided by the Natural Heritage Trust, Australian Geographic, Threatened
393 Species Network of Worldwide Fund for Nature, and the Tropical Savannas Cooperative
394 Research Centre. The Territory Wildlife Park provided temporary housing of the founder
395 population. The endorsement, interest and cooperation of traditional owners of the areas from
396 which the quoll's founder populations as well as the destination islands was vital to the
397 success of this project, and we acknowledge particularly the Gumarr Marthakal and
398 Dhimurru ranger groups, Terry Yumbulul and Bruce Lirrwa Ganambarr. The Gumarr
399 Marthakal ranger group has maintained an enduring involvement in this program. In addition,
400 the Northern Land Council, Kakadu National Park, and Arafura Pearls provided much needed
401 support, and many people contributed to fieldwork over the course of the project. All research
402 was conducted under Charles Darwin University Animal Ethics Permits: A03017, A13026
403 and A01001.

404 **References**

405 Armstrong, D. P., Davidson, R. S., Perrott, J. K., Roygard, J., and Buchanan, L. (2005).
406 Density-dependent population growth in a reintroduced population of North Island
407 saddlebacks. *Journal of Animal Ecology* **74**, 160-170.

- 408 Armstrong, D. P. and Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in*
409 *Ecology & Evolution* **23**, 20-25.
- 410 Armstrong, D. P. and Reynolds, M. H. (2012). Modelling reintroduced populations: the state
411 of the art and future directions. In 'Reintroduction Biology: integrating science and
412 management'. (Eds J. Ewen, D. P. Armstrong, and K. A. Parker) pp. 165-222. (John
413 Wiley & Sons Ltd.: Chichester.)
- 414 Armstrong, D. P., Hayward, M., Moro, D., and Seddon, P. (Eds) (2015). 'Advances in
415 Reintroduction Biology of Australian and New Zealand Fauna.' (CSIRO Publishing:
416 Collingwood.)
- 417 Braithwaite, R. W. and Griffiths, A. D. (1994). Demographic variation and range contraction
418 in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research*
419 **21**, 203-217.
- 420 Brook, B. W. and Whitehead, P. J. (2005). Exclosures as a means of controlling the impact of
421 cane toads. In 'A review of the impact and control of cane toads in Australia with
422 recommendations for future research and management approaches'. (Eds R. Taylor and
423 G. Edwards). (A report to the Vertebrate Pests Committee from the National Cane Toad
424 Taskforce: Canberra.)
- 425 Burbidge, A. A. and McKenzie, N. L. (1989). Patterns in the modern decline of Western
426 Australia's vertebrate fauna: causes and conservation implications. *Biological*
427 *Conservation* **50**, 143-198.
- 428 Burnett, S. (1997). Colonizing cane toads cause population declines in native predators:
429 reliable anecdotal information and management implications. *Pacific Conservation*
430 *Biology* **3**, 65-72.
- 431 Burnham, K. P. and Anderson, D. R. (2002) 'Model selection and multimodel inference: a
432 practical information-theoretic approach.' 2nd edn. (Springer: New York.)

- 433 Cardoso, M. J., Eldridge, M. D. B., Oakwood, M., Rankmore, B., Sherwin, W. B., and
434 Firestone, K. B. (2009). Effects of founder events on the genetic variation of translocated
435 island populations: implications for conservation management of the northern quoll.
436 *Conservation Genetics* **10**, 1719-1733. doi: 10.1007/s10592-008-9774-z.
- 437 Chaloupka, M. and Limpus, C. (2001). Trends in the abundance of sea turtles resident in
438 southern Great Barrier Reef waters. *Biological Conservation* **102**, 235-249.
- 439 Chatto, R. (2003). The distribution and status of shorebirds around the coast and coastal
440 wetlands of the Northern Territory. Parks and Wildlife Commission of the Northern
441 Territory1920772103. (Palmerston.)
- 442 Chatto, R. and Baker, B. (2008) 'The distribution and status of marine turtle nesting in the
443 Northern Territory.' (Parks and Wildlife Services of the Northern Territory.)
- 444 Clayton, J. A., Pavey, C. R., Vernes, K., and Tighe, M. (2014). Review and analysis of
445 Australian macropod translocations 1969-2006. *Mammal Review* **44**, 109-123.
- 446 Converse, S. J., Moore, C. T., and Armstrong, D. P. (2013). Demographics of reintroduced
447 populations: estimation, modeling, and decision analysis. *The Journal of Wildlife*
448 *Management* **77**, 1081-1093.
- 449 Cooch, E. G. and White, G. C. (2014). Program MARK: A gentle introduction. (Cornell
450 University and Colorado State University.)
- 451 Fischer, J. and Lindenmayer, D. (2000). An assessment of the published results of animal
452 relocations. *Biological Conservation* **96**, 1-11.
- 453 Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. (1998). Population dynamics of large
454 herbivores: variable recruitment with constant adult survival. *Trends in Ecology &*
455 *Evolution* **13**, 58-63.
- 456 Griffith, B., Scott, J. M., Carpenter, J. W., and Reed, C. (1989). Translocation as a species
457 conservation tool: status and strategy. *Science* **245**, 477-480.

- 458 Griffiths, A. D. and Brook, B. W. (2015). Fire impacts recruitment more than survival of
459 small-mammals in a tropical savanna. *Ecosphere* **6**, art99-art99.
- 460 Griffiths, A. D., Garnett, S. T., and Brook, B. W. (2015). Fire frequency matters more than
461 fire size: Testing the pyrodiversity-biodiversity paradigm for at-risk small mammals in
462 an Australian tropical savanna. *Biological Conservation* **186**, 337-346.
- 463 Hone, J., Duncan, R. P., and Forsyth, D. M. (2010). Estimates of maximum annual
464 population growth rates (rm) of mammals and their application in wildlife management.
465 *Journal of Applied Ecology* **47**, 507-514.
- 466 IUCN/SSC (2013). Guidelines for reintroductions and other conservation translocations.
467 IUCN Species Survival Commission. (Gland, Switzerland.)
- 468 Johnson, C. (2006) 'Australia's mammal extinctions: a 50,000 year history.' (Cambridge
469 University Press: Port Melbourne, Victoria.)
- 470 Kearney, M., Phillips, B. L., Tracy, C. R., Christian, K. A., Betts, G., and Porter, W. P.
471 (2008). Modelling species distributions without using species distributions: the cane toad
472 in Australia under current and future climates. *Ecography* **31**, 423-434.
- 473 Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival
474 and testing biological hypotheses using marked animals: a unified approach with case
475 studies. *Ecological Monographs* **62**, 67-118.
- 476 Lindenmayer, D. B., Clark, T. W., Lacy, R. C., and Thomas, V. C. (1993). Population
477 viability analysis as a tool in wildlife conservation policy: with reference to Australia.
478 *Environmental Management* **17**, 745-758.
- 479 McCarthy, M. A., Armstrong, D. P., and Runge, M. C. (2012). Adaptive management of
480 reintroduction. In 'Reintroduction Biology: integrating science and management'. (Eds J.
481 G. Ewen, D. P. Armstrong, K. A. Parker, and P. J. Seddon) pp. 256-289. (Wiley-
482 Blackwell: Oxford, UK.)

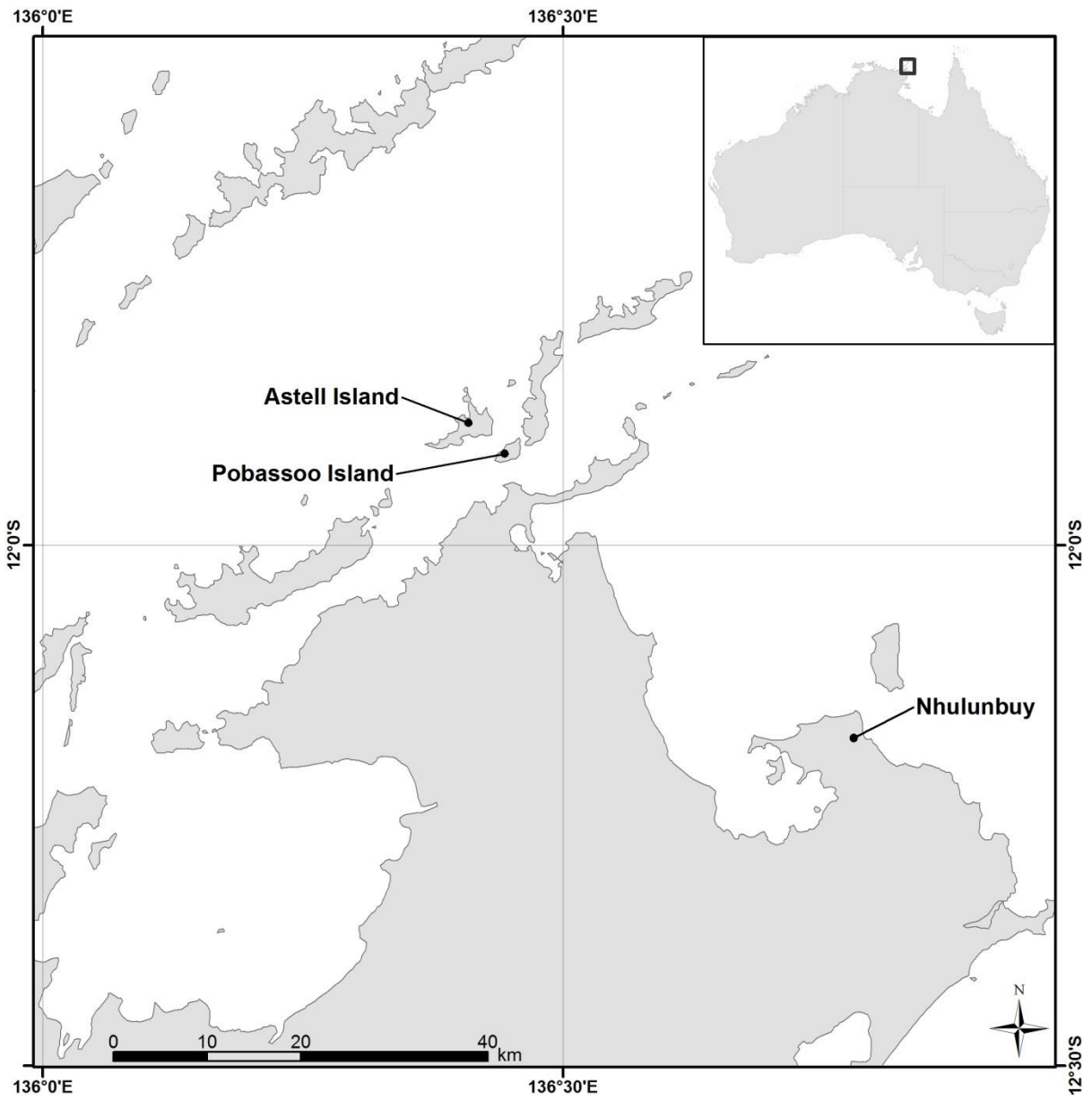
- 483 Morris, K., Page, M., Kay, R., Renwick, J., Desmond, A., Comer, S., Burbidge, A., Kuchling,
484 G., and Sims, C. (2015). Forty years of fauna translocations in Western Australia: lessons
485 learned. In 'Advances in Reintroduction Biology of Australian and New Zealand Fauna'.
486 (Eds D. Armstrong, M. W. Hayward, D. Moro, and P. J. Seddon) pp. 217. (CSIRO
487 Publishing: Melbourne.)
- 488 O'Donnell, S., Webb, J. K., and Shine, R. (2010). Conditioned taste aversion enhances the
489 survival of an endangered predator imperilled by a toxic invader. *Journal of Applied*
490 *Ecology* **47**, 558-565. doi: 10.1111/j.1365-2664.2010.01802.x.
- 491 Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus*
492 *hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology*
493 **48**, 519-539.
- 494 Peig, J. and Green, A. J. (2009). New perspectives for estimating body condition from
495 mass/length data: the scaled mass index as an alternative method. *Oikos* **118**, 1883-1891.
496 doi: 10.1111/j.1600-0706.2009.17643.x.
- 497 Peig, J. and Green, A. J. (2010). The paradigm of body condition: a critical reappraisal of
498 current methods based on mass and length. *Functional Ecology* **24**, 1323-1332. doi:
499 10.1111/j.1365-2435.2010.01751.x.
- 500 Perez, I., Anadon, J., Diaz, M., Nicola, G. G., Tella, J. L., and Gimenez, A. (2012). What is
501 wrong with current translocations? A review and a decision-making proposal. *Frontiers*
502 *in Ecology and the Environment* **10**, 494-501.
- 503 Pinheiro, J. C. and Bates, D. M. (2000) 'Mixed effects models in S and S-PLUS.' (Springer:
504 New York.)
- 505 Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and
506 population growth rate. *Biometrics* **52**, 703-709.

- 507 Robert, A., Colas, B., Guigon, I., Kerbiriou, C., Mihoub, J.-B., Saint Jalme, M., and Sarrazin,
508 F. (2015). Defining reintroduction success using IUCN criteria for threatened species: a
509 demographic assessment. *Animal Conservation* **18**, 397-406.
- 510 Sarrazin, F. and Barbault, R. (1996). Reintroduction: challenges and lessons for basic
511 ecology. *Trends in Ecology & Evolution* **11**, 474-478.
- 512 Sattler, P. and Creighton, C. (2002). Australian Terrestrial Biodiversity Assessment 2002.
513 National Land and Water Resource Audit. (Canberra.)
- 514 Schmitt, L. H., Bradley, A. J., Kemper, C. M., Kitchener, D. J., Humphries, W. F., and How,
515 R. A. (1989). Ecology and physiology of the northern quoll, *Dasyurus hallucatus*
516 (Marsupialia, Dasyuridae), at Mitchell Plateau, Kimberley, Western Australia. *Journal of*
517 *Zoology, London* **217**, 539-558.
- 518 Seddon, P. J., Armstrong, D. P., and Maloney, R. F. (2007). Developing the science of
519 reintroduction biology. *Conservation Biology* **21**, 303-312.
- 520 Shean, V. A., Manning, A. D., and Lindenmayer, D. B. (2012). An assessment of scientific
521 approaches towards species relocations in Australia. *Austral Ecology* **37**, 204-215.
- 522 Shier, D. M. (2015). Developing a standard for evaluating reintroduction success using IUCN
523 Red List indices. *Animal Conservation* **18**, 411-412. doi: 10.1111/acv.12242.
- 524 Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia.
525 *The Quarterly Review of Biology* **85**, 253-291.
- 526 Short, J. and Smith, A. (1994). Mammal decline and recovery in Australia. *Journal of*
527 *Mammalogy* **75**, 288-297.
- 528 Smith, A. P. and Quin, D. G. (1996). Patterns and causes of extinction and decline in
529 Australian conilurine rodents. *Biological Conservation* **77**, 243-267.

- 530 Sutherst, R. W., Floyd, R. B., and Maywald, G. F. (1996). The potential geographical
531 distribution of the cane toad, *Bufo marinus* L in Australia. *Conservation Biology* **10**, 294-
532 299.
- 533 White, G. C. and Burnham, K. P. (1999). Program MARK: survival estimation from
534 populations of marked animals. *Bird Study* **46**, 120-138.
- 535 Williams, B. K., Conroy, M. J., and Nichols, J. D. (2002) 'Analysis and management of
536 animal populations: modeling, estimation, and decision making.' (Academic Press: San
537 Diego, CA.)
- 538 Woinarski, J., Reichel, H., and Andersen, A. (1998). The distribution of ants on the Wessel
539 and English Company Islands, in the seasonal tropics of Australia's Northern Territory.
540 *Australian Journal of Zoology* **46**, 557-579.
- 541 Woinarski, J., Horner, P., Fisher, A., Brennan, K., Lindner, D., Gambold, N., Chatto, R., and
542 Morris, I. (1999a). Distributional patterning of terrestrial herpetofauna on the Wessel and
543 English Company Island groups, northeastern Arnhem Land, Northern Territory,
544 Australia. *Australian Journal of Ecology* **24**, 60-79.
- 545 Woinarski, J., Brennan, K., Cowie, I., Fisher, A., Latz, P., and Russell-Smith, J. (2000).
546 Vegetation of the Wessel and English Company Islands, North-eastern Arnhem Land,
547 Northern Territory, Australia. *Australian Journal of Botany* **48**, 115-141.
- 548 Woinarski, J., Fisher, A., Brennan, K., Morris, I., and Chatto, R. (2001). Patterns of bird
549 species richness and composition on islands off Arnhem Land, Northern Territory,
550 Australia. *Austral Ecology* **26**, 1-13.
- 551 Woinarski, J., Ward, S., Mahney, T., Bradley, J., Brennan, K., Ziembicki, M., and Fisher, A.
552 (2011). The mammal fauna of the Sir Edward Pellew island group, Northern Territory,
553 Australia: refuge and death-trap. *Wildlife Research* **38**, 307-322.

- 554 Woinarski, J., Burbidge, A., and Harrison, P. (2014) 'Action Plan for Australian Mammals
555 2012.' (CSIRO Publishing: Canberra.)
- 556 Woinarski, J. C. Z. and Braithwaite, R. W. (1990). Conservation foci for Australian birds and
557 mammals. *Search* **21**, 65-68.
- 558 Woinarski, J. C. Z., Palmer, C., Fisher, A., Southgate, R., Masters, P., and Brennan, K.
559 (1999b). Distributional patterning of mammals on the Wessel and English Company
560 islands, Arnhem Land, Northern Territory, Australia. *Australian Journal of Zoology* **47**,
561 87-111.
- 562 Wolf, C. M., Garland, T., and Griffith, B. (1998). Predictors of avian and mammalian
563 translocation success: reanalysis with phylogenetically independent contrasts. *Biological*
564 *Conservation* **86**, 243-255.
- 565
- 566
- 567

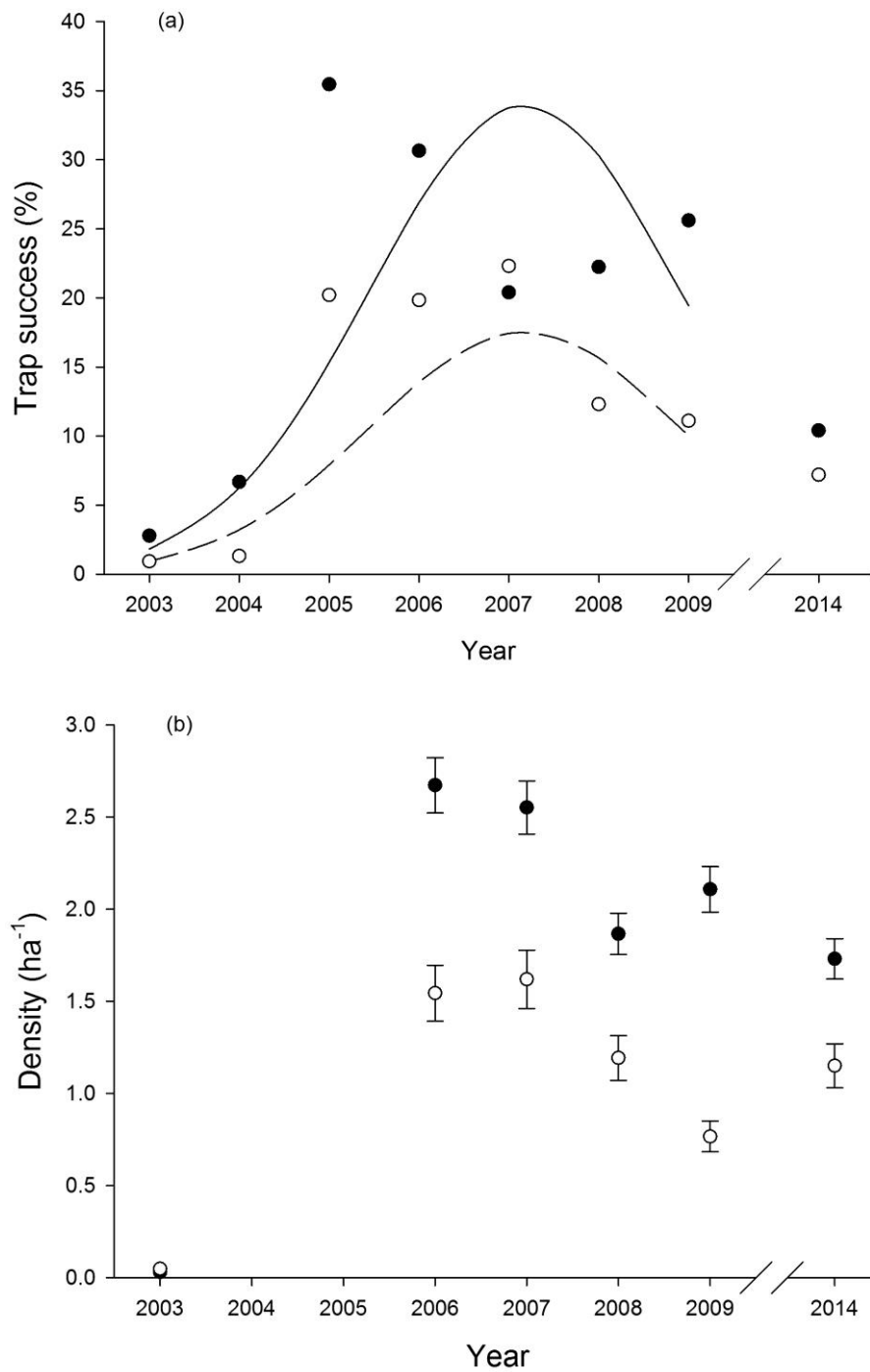
568



569

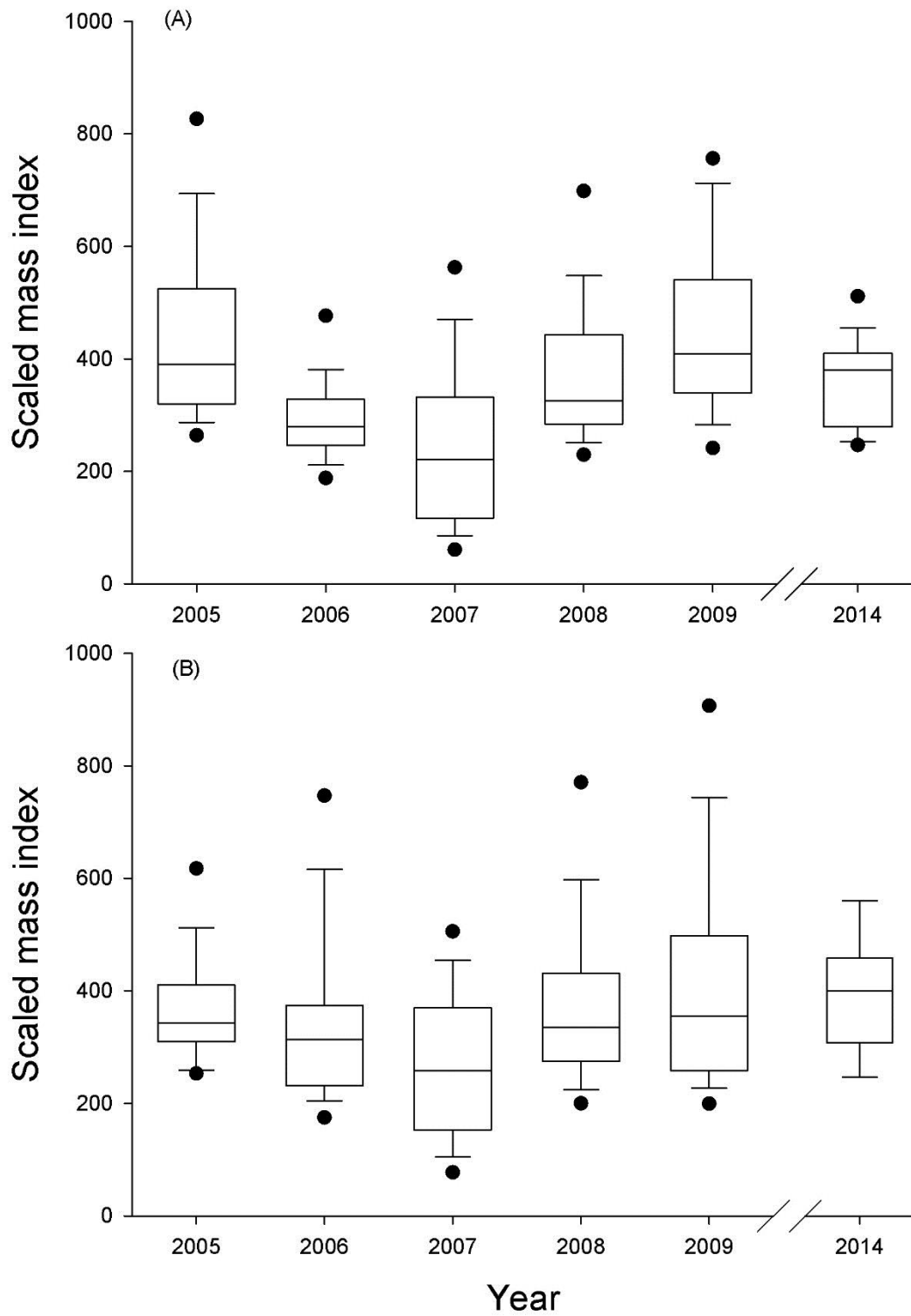
570

Fig. 1. Location of Astell and Pobassoo Islands, Northern Territory.



571

572 **Fig. 2.** Time series of (a) trap success of all northern quolls and (b) density of female
 573 northern quolls on the two islands (open circles – Pobassoo, closed circles – Astell). Error
 574 bars are one standard error.



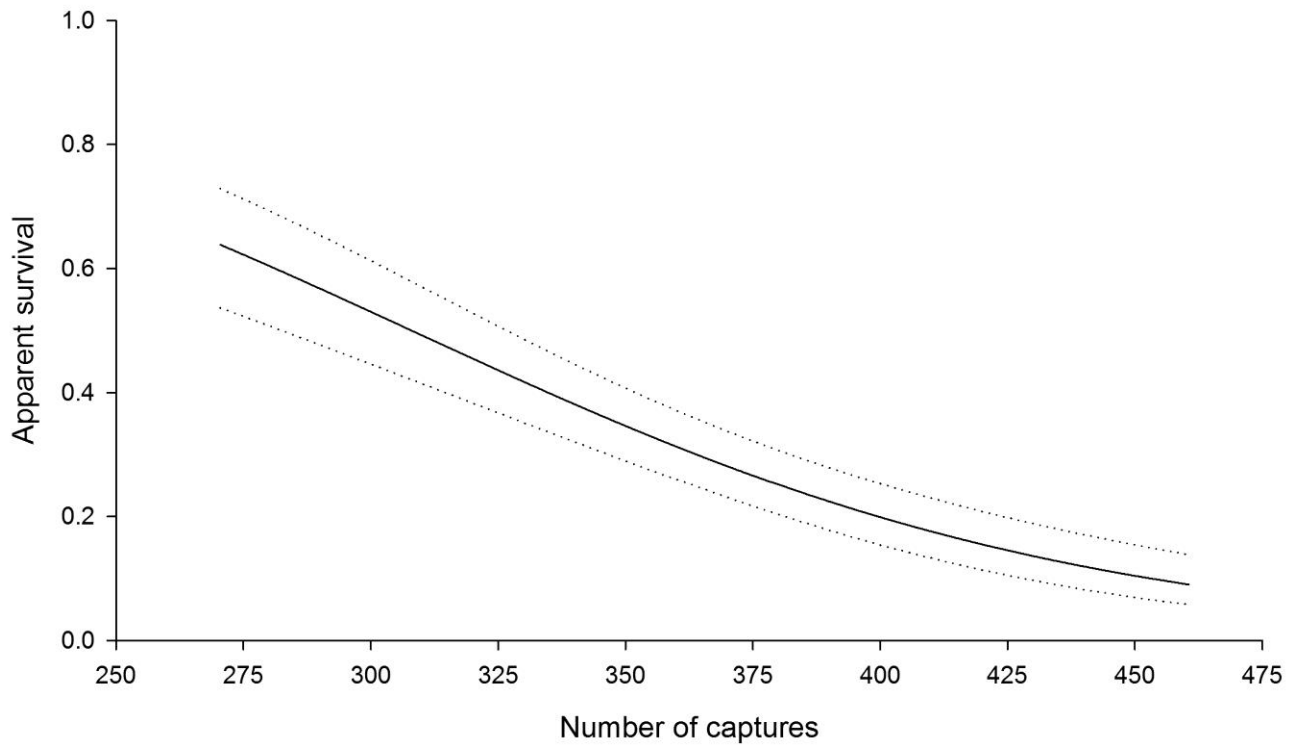
575

576 **Fig. 3.** Boxplots of body condition (scaled mass index) of northern quolls over time on (a)

577 Astell and (b) Pobassoo Islands. Band inside the box represents the median value, box

578 boundaries the 25th and 75th percentiles, whiskers the 10th and 90th percentiles and filled
579 circles are the 5th and 95th percentiles outliers.

580



581

582 **Fig. 4.** Predicted relationship between apparent survival of female northern quolls and the
583 number of captures in the previous year based on the top-ranked model. Dashed lines
584 represent 95% confidence intervals.

585

586

587

588 **Table 1.** Summary of model-selection results for northern quoll trap success on Astell and
 589 Pobassoo Islands from 2003 to 2009. All models contain a temporal autocorrelation
 590 parameter representing captures in the previous year on each island. K is the number of
 591 parameters. AIC_c is Akaike's Information Criterion, corrected for small sample size. ΔAIC_c
 592 shows the difference between the model AIC_c and the lowest AIC_c out of the set of models.
 593 AIC_c weights (w_i) are the relative likelihood of model i (normalised to sum to 1). The bigger
 594 the delta the smaller the weight and the less plausible model i .

Models	K	AIC_c	ΔAIC_c	w_i	Model likelihood
~ Island + Year + Year ²	5	30.20	0	0.77	1
~ Year + Year ²	4	32.85	2.65	0.20	0.27
~ Year	3	37.97	7.77	0.16	0.02
~ Island + Year	4	39.80	9.60	0.00	0.01
~ Null	2	40.58	10.38	0.00	0.01
~ Island	3	42.77	12.57	0.00	0

595

596

597 **Table 2.** Summary of model-selection results for northern quoll body condition linear models
 598 (scaled mass index) on Astell and Pobassoo Islands over six years of monitoring. See Table 1
 599 for explanation of table column headings.

Models	<i>K</i>	AIC_c	ΔAIC_c	<i>w_i</i>	Model likelihood
~ Year	7	9232.99	0	0.51	1
~ Year * Island	13	9234.05	1.06	0.30	0.59
~ Year + Island	8	9235.02	2.03	0.18	0.36
~ Null	2	9364.58	131.59	0	0
~ Island	3	9365.62	132.63	0	0
~ Sex	4	9360.82	127.83	0	0

600

601

Table 3. Summary of model-selection results for female northern quoll apparent survival and recruitment (Pradel Robust Design). All models fitted with $p(\text{Island} * 4=5)$ $c(\text{Island} * 3=4)$ $N(t)$ parameterisation. See Table 1 for explanation of table column headings.

Model	K	AIC_c	ΔAIC_c	w_i	Model likelihood
Phi(density + body mass * year) $f(\text{rain})$	29	1647.32	0.00	0.55	1.00
Phi(island + density + body mass * year) $f(\text{rain})$	30	1649.39	2.07	0.19	0.36
Phi(density + body mass * year) $f(\text{island})$	29	1649.98	2.66	0.14	0.26
Phi(density + body mass * year) $f(\text{rain} + \text{density} + \text{trend})$	32	1651.37	4.06	0.07	0.13
Phi(density + body mass * year) $f(\text{island} + \text{year})$	32	1652.47	5.15	0.04	0.08
Phi(density) $f(\text{density})$	26	1664.09	16.77	0.00	0.00
Phi(island * t) $f(.)$	29	1664.68	17.36	0.00	0.00
Phi(rain + density) $f(.)$	26	1664.80	17.48	0.00	0.00
Phi(density + body mass * year) $f(\text{island} * t)$	30	1665.66	18.34	0.00	0.00
Phi(island + rain + density + body mass + trend) $f(\text{density})$	30	1665.66	18.34	0.00	0.00
Phi(island + rain + density + body mass + trend) $f(\text{year})$	31	1665.74	18.42	0.00	0.00
Phi(Island * t) $f(\text{Island} * t)$	34	1666.42	19.10	0.00	0.00

Phi(island + rain + density + body mass + trend) f (island + rain + density + trend)	33	1667.86	20.54	0.00	0.00
Phi(t) f (t)	28	1668.69	21.37	0.00	0.00
Phi(rain + body mass * year) f (island)	29	1672.01	24.69	0.00	0.00
Phi(rain) f (rain)	26	1674.78	27.46	0.00	0.00
Phi(rain) f (.)	25	1676.74	29.42	0.00	0.00
Phi(island + rain) f (island + rain)	28	1676.74	29.42	0.00	0.00
Phi(.) f (Island * t)	29	1713.35	66.03	0.00	0.00
Phi(.) f (.)	24	1715.26	67.94	0.00	0.00
Phi(.) f (island)	25	1715.50	68.18	0.00	0.00
Phi(body mass * year) f (island + rain + density + trend)	31	1716.67	69.35	0.00	0.00
Phi(body mass * year) f (.)	27	1718.98	71.66	0.00	0.00

Appendix A

Parameters used and their biological significance to construct capture-mark-recapture models of apparent survival (ϕ), recruitment rate (f), derived from binomial likelihood-based models for female northern quolls on the translocation to Astell and Pobassoo islands. Category relates to how each parameter was used in the design matrix.

Name	Category	Used in	Apparent survival, or recruitment is ...	Notes
Null		ϕ, f	constant	
Island	Category	ϕ, f	different among the two islands	Area of each island: Astell (1292 ha) and Pobassoo (392 ha)
Body mass	Individual covariate	ϕ	related to body mass of individual	Body mass (g) at first capture
Rainfall	Time - specific covariate	ϕ, f	influenced by total rainfall in the previous 12 months	Previous 12 monthly total rainfall (mm) in primary trapping occasion (taken from Gove Airport, 40 km south)
Year	Time - specific covariate	ϕ, f	different among each year of sampling	Period between the four years (2006 to 2007, 2007 to 2008, 2008 to 2009)
Linear trend	Time -	ϕ, f	constrained by either	Capture intervals

	specific		a positive or	numbered from 1 to 4
	covariate		negative linear trend	
			over the study	
Density	Time - specific	ϕ, f	Influenced by the number of northern quolls in the previous year	Number of captures of all quolls on each island in the previous year

Table A1

Summary of model selection results for initial capture (p) and recapture (c) probability as part of the Pradel Robust Design modelling. All models contained the parameters $\Phi(\text{Island} * t)$, $f(\text{Island} * t)$ and $N(t)$.

Model	K	AICc	ΔAICc	w_i	Model likelihood
$p(\text{Island} * 4=5) c(\text{Island} * 3=4)$	34	1666.42	0	0.99	1
$p(\text{Island}) c(\text{Island})$	24	1677.15	10.73	0.01	0.005
$p(4=5) c(3=4)$	27	1688.37	21.95	0	0
$p(4=5) c(3=4)$	27	1691.23	24.81	0	0
$p(.) c(.)$	22	1704.97	38.55	0	0
$p(t) c(=p)$	25	1799.07	132.65	0	0
$p(t) c(=p)$	24	1820.51	154.09	0	0
$p(\text{Island}) c(=p)$	22	1838.31	171.89	0	0
$p(.) c(=p)$	21	1851.12	184.70	0	0