Survival rates of *Rattus verecundus* and *Paramelomys platyops* in a murid rich tropical rainforest of Papua New Guinea

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Estimations of survival rates of small mammal populations that occur on the island of New Guinea are crucial for conservation and management strategies. Here, we used mark-recapture data in programme MARK to estimate apparent survival and detection of two murid species in a tropical rainforest in Papua New Guinea. The most parsimonious model allowed survival and recapture probability to vary by species. Across the two species, *Rattus verecundus* generally had lower survival rates, but higher recapture probabilities, whereas *Paramelomys platyops* had higher survival rates but lower recapture probabilities. Since many small mammal species that occur in New Guinea are already listed under the IUCN red list for Threatened Species, similar studies can be replicated targeting the threatened species to provide information to wildlife managers for management and conservation decision.

Key words and phrases: apparent survival, recapture probabilities, *Paramelomys platyops, Rattus verecundus,* New Guinea, small mammals.

INTRODUCTION

INDIVIDUAL survival within an animal population is an important determinant of population trends (Bond *et al.* 2000), and estimates of survival rate can help direct wildlife management. The understanding of specific survival estimates (Bond *et al.* 2000) of animal populations of management interest is crucial for conservation strategies, especially where a population is thought to be declining (Ryan *et al.* 2008; Sandercock *et al.* 2008; Van Noordwijk and Thomson 2008), endangered (Boyles *et al.* 2007; Bradshaw *et al.* 2007; Hamer and Mahony 2007; Hurd *et al.* 2004; Salvador and Fernandez 2008; Wittmer *et al.* 2007), or in danger of extinction (Bradshaw *et al.* 2007; Hurd *et al.* 2004; Wittmer *et al.* 2007).

Survival is one of the more difficult population parameters to measure, especially if the animals are elusive and nocturnal such as most small mammals that occur in tropical rainforests. The mark-recapture method, used in ecological studies since 1896 (Krebs 1999), has become one of the most commonly used methods for estimating survival rates across many animal taxa (Kendall *et al.* 1995; Lebreton *et al.* 1992; Pollock 2002). Despite the increasing use of mark-recapture methods in population ecology studies around the world, this method is yet to be adequately employed to assess population parameters of many taxa, including small mammals that occur in New Guinea.

Here, we estimate individual apparent survival rates of two rainforest dwelling New Guinean murid rodents, *Rattus verecundus* and *Paramelomys platyops*. *R. verecundus* is a small rainforest rodent; males weigh 120 ± 14 grams (n = 61) and females 102 ± 19 grams (n = 68). *R. verecundus* occurs from lowlands to 1 300 m in elevation (Flannery 1995), and is widely distributed in Papua New Guinea (PNG) and some parts of West Papua Province of Indonesia. *P. platyops* is also a small rodent with males weighing 95 ± 11 grams (n = 29) and females 86 ± 9 grams (n = 30). It inhabits lowlands throughout much of New Guinea as well as hill forest; it is most abundant at 200–300 m elevation (Flannery 1995). Both species are mostly nocturnal and terrestrial and nest in ground tunnels. The specific objectives for this study were: (1) to compare apparent survival between the two species and (2) compare apparent survival between males and females of each species. Incidental captures of other mammal species were documented to provide community ecology context for the findings.

METHODS

Study site

The study was conducted at the Crater Mountain Biological Research Station (CMBRS) within the Crater Mountain Wildlife Management Area (CMWMA). Crater Mountain is currently the known centre of murid diversity in New Guinea (Heads 2002). CMBRS was a field station managed for site-based conservation by the PNG Programme of the Wildlife Conservation Society. CMBRS is 10 km east of the village of Haia at 6° 43' S and 145° 05' E in Chimbu province in the Central Range of PNG. The site ranges in altitude from 850–1 300 m, and is predominantly hill forest, receiving mean annual rainfall of 6 400 mm (Wright *et al.* 1997). The study site is primary

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forest with Lauraceae, Myristicaceae and Moraceae being the most common tree families in both the understory and canopy (Wright *et al.* 1997). The area is a near pristine forest with a moratorium on hunting or vegetation cutting in place for 15 years since creation of CMBRS. Local topography is steep but there are no natural barriers such as big rivers surrounding or flowing within the trapping area that would limit rodent movements; in effect the site is an open system where small mammal movement is largely unrestricted.

Trapping protocol

Trapping of small mammals was conducted in a permanent trapping grid of seven by eight trapping stations. The 56 trapping stations were located at 40 m intervals and encompassed 6.7 ha (240 m x 280 m). Two Elliot live traps (375 x 105 x 105 mm) were set at each station. One was placed on the ground and one on a log or fixed on a tree trunk or twigs not higher than 2 m above ground to trap arboreal species. A Tomahawk trap (850 x 250 x 250 mm) was set at every 80 m within the grid to trap larger mammals that cannot be trapped in small Elliot traps. The Elliot traps were baited with peanut butter and rolled oats. Tomahawk traps were baited with a mixture of rolled oats, peanut butter, biscuits and tinned fish. The variety of baits used in the Tomahawk trap was to attract a greater variety of mammals. The traps were baited between 1600–1800 hrs daily and checked every morning beginning at 0600 hrs.

Four trapping sessions lasting eight consecutive weeks each with weekend breaks were conducted in 2005. Trapping session one was conducted from mid January to mid March, session two from April to June, session three from August to October and the final session from November to December. A total of 2 432 trap-nights (2 128 Elliot trap-nights and 304 Tomahawk trap-nights) were run for each session in the grid. This trapping effort was maintained for each trapping session throughout the study yielding 9 728 total trap-nights for the entire trapping from January to December consisting of 8 512 Elliot trap-nights and 1 216 Tomahawk trap-nights.

Capture-mark-recapture technique was employed in this study. Thus, to individually identify recaptures, PIT tags (Passive Integrated Transponder) were implanted on the back of each animal. A combination of different colored beads woven on strings as tags were sewn on each of the ears of small mammals as a back-up tagging strategy. All small mammals were handled without anesthesia to reduce stress on the study animals. Mortality due to handling was three out of 2 853 times in which study animals were handled. All live animals were handled according to the protocols of the American Society of Mammalogists (Gannon *et al.* 2007) and were released at the site of capture.

Data analysis

Data analysis was done using programme MARK version 6.1 (White and Burnham 1999). Cormack Jolly-Seber (CJS) models (Lebreton *et al.* 1992) for estimating survival for open populations were built in MARK using the parameter index charts of the software. Since the study was conducted on an open population, random immigration and emigration was assumed. The models were ranked using Akaike's Information Criteria with a second order bias correction for small sample size (AICc) in MARK. Lower values of AICc indicate the most plausible models while larger values indicate least supported models (White and Burnham 1999). AICc is the recommended model selection criteria for analysis and inference from capture-recapture data; it is both powerful in displaying a balance between underfitted and overfitted models, and also had a much smaller relative bias in parameters estimated than other model selection criterion (Anderson *et al.* 1998).

We estimated apparent survival ö, "(the probability that an individual lives and remains on the study area between the intervals i and i + 1) and recapture probability *p*, (the probability an individual is alive and available for capture at time i)" (Ryan *et al.* 2008). Apparent survival is the probability that the marked animal remains alive and is re-encountered (White and Burnham 1999), because mortality and emigration are indistinguishable (Ryan *et al.* 2008). The small mammals marked and recaptured for four consecutive sessions provided three cohorts of marked and encountered animals. We ran group models to elucidate and estimate any apparent survival and recapture probability differences between species and sexes. Of 16 possible candidate models the nine most likely models were tested plus an unlikely "null model" devoid of species or sex differences ((ö(.)p(.)). We adjusted for over-dispersion in the data using the median c-hat procedure available in programme MARK 6.1 under which AICc is replaced by quasi-AICc (QAICc) and then manually adjusted the parameter count adjusted upwards by one (Anderson 2008).

RESULTS

Community structure and ecology

Rattus verecundus and *P. platyops* were captured more frequently on the trapping grid than any other terrestrial mammals. A total of 201 individual *R. verecundus* and 85 individual *P. platyops* were handled a combined total of 2 355 times. Five other murid species (Table 1) and two dasyurid species, *Dasyurus albopunctatus* and *Antechinus melanurus* were also trapped. Fifty-five percent of *R. verecundus* were trapped on the ground while 45% in traps placed in arboreal positions. For *P. platyops*, 51% of the captures resulted from ground traps versus 49% from arboreal traps. Thirty percent of *Melomys rufescens* were trapped in traps placed on the ground traps while 70% were trapped in arboreal locations. Twenty-nine percent of *Melomys leucogaster* were trapped on the ground while 71% in arboreal positions. Thirty-eight percent of *Uromys caudimaculatus* were trapped on the ground versus 62% in arboreal traps.

R. verecundus was the dominant species among total captures in all sessions and was captured in approximately even numbers in each session. In contrast, captures of *P. platyops* fluctuated markedly over time from 51 individuals in session one to only four new individuals in session two. The number of new individuals of *P. platyops* increased in the final trapping session, at which time they exceeded new captures of *R. verecundus*.

Parameter estimates

Model ranking

Three parameters (species, sex and time variation) were initially considered within the MARK analysis, however, this global model was over-parameterized and subsequently a reduced global model of ö(species*sex)p(species*sex) became the basis for further analysis (Table 2). The most parsimonious model comprized 41% of the support and suggested that there were species specific survival and recapture probabilities. The three most plausible models (all with QAICc < 2) had species as a parameter in both survival and detection, thereby suggesting that species has a strong explanatory effect in the data. The forth ranked model was the unlikely "null model" which lacked both species and sex effects. The evidence ratio (Anderson 2008) between the top model and the null model (E = 5.17), suggests that the strength of evidence for there being a species effect for both survival and detection is five times more likely than there being no such effect.

Model averaging

When the ten models were averaged for each species, *R. verecundus* had lower apparent

Table 1. Total number of individuals trapped by species during the four trapping sessions in 2005. The numbers in the brackets are recaptures.

Species	Number of captures/trapping sessions			
	Session 1	Session 2	Session 3	Session 4
Lorentzymys nouhuysi			1 (0)	
Melomys leucogaster			4 (25)	1 (27)
*Paramelomys platyops**	51 (296)	4 (35)	11 (90)	19 (171)
Melomys rufescens	12 (21)	8 (16)	5 (93)	7 (90)
*Rattus verecundus**	61 (355)	71 (133)	58 (486)	11 (503)
Uromys caudimaculatus	5 (18)	3 (6)	9 (9)	12 (19)
Xenuromys barbatus			1 (3)	0 (2)

Table 2. Ranking of models used to estimate apparent survival rates of both males and females for *R. verecundus* and *P. platyops* from January to December 2005. Survival (*ö*) and recapture probability (*p*) were held constant in the models indicated by (.) and varied by sex (sex) or species (spp) or as an interaction (sex*spp). The models for each species are listed from most to least parsimonious based on a small sample quasi-Akaike Information Criteria (QAICc) and K is the number of parameters in each model.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	K	QDeviance
ö(spp)p(spp)	448.65	0	0.42	1	5	44.96
ö(sex*spp)p(spp)	450.1	1.45	0.2	0.49	7	42.25
ö(spp)p(sex*spp)	450.62	1.97	0.16	0.37	7	42.77
ö(.)p(.)	451.94	3.29	0.08	0.19	3	52.36
ö(sex)p(spp)	452.79	4.13	0.05	0.13	5	49.09
ö(sex*spp)p(sex*spp)	453.23	4.58	0.04	0.1	9	41.18
ö(spp)p(sex)	455.33	6.68	0.01	0.04	5	51.64
ö(sex)p(sex*spp)	455.58	6.92	0.01	0.03	7	47.73
ö(sex)p(sex)	455.8	7.15	0.01	0.03	5	52.11
ö(sex*spp)p(sex)	456.13	7.48	0.01	0.02	7	48.28

survival rates, but higher recapture probabilities, whereas *P. platyops* have higher apparent survival rates but lower recapture probabilities (Table 3). The recapture probability also was marginally higher in males than females of *P. platyops*.

R. verecundus is known to use a variety of habitats, from rainforests to gardens, and it occurs over a wider altitudinal range from 150 to 2 750 m (Flannery 1995) more than any other species captured during this study. As a habitat generalist, *R. verecundus* may also be advantaged over other species with narrower habitat requirements. Furthermore, members of the genus *Rattus* are known for their interspecific aggression (Towns *et al.* 2006) which could result in the behavioural suppression of other murid genera and might explain the apparent dominance of one species over others in a sympatric community (Rychlik and Zwolak 2006).

Table 3. Weighted average (in bold) of apparent survival (ö) and recapture probabilities (p) derived from the models (Table 2), unconditional standard errors and 95% confidence intervals for *R. verecundus* and *P. platyops*

Species	Sex	Estimates ö (SE) (95% CI)	 p (SE) (95% CI)
R. verecundus	male	**0.46** (0.36–0.57)	**0.81** (0.56–0.93)
	female	**0.48** (0.37–0.59)	**0.79** (0.56–0.92)
P. platyops	male	**0.65** (0.42–0.83)	**0.52** (0.27–0.75)
	female	**0.61** (0.39–0.80)	**0.47** (0.22–0.73)

DISCUSSION

Community structure and ecology

R. verecundus and *P. platyops* appeared to be equally foraging on the forest floor and in arboreal locations as revealed by the number of captures on the ground and in traps placed not more than 2 m above the ground. However, all individuals of both species either enter into ground tunnels or escape into thick vegetation on the forest floor when released. *M. rufescens*, *M. leucogaster* and *U. caudimaculatus* were mostly trapped in arboreal locations indicating the three species to be arboreal. According to Flannery (1995), *M. rufescens* is largely arboreal, utilising its long prehensile tail for climbing; *M. leucogaster* constructs leaf nest in pandanus and trees while *U. caudimaculatus* is reported to utilize several nesting types, including tree hollows and underground nests.

Although *R. verecundus* was the most commonly captured species with 201 individuals captured (compared to 85 for *P. platyops*) it's detection rate was more than 1.5 times greater than *P. platyops*. Consequently, the apparent high abundance of the former maybe an artefact of its high capture probabilities and the more cryptic *P. platyops* may exist at similar numbers at the study locations. The ecological factors controlling the proportional mixture of at least seven sympatric murid species at this study site are unknown. Menzies and Dennis (1979) reported that stomach contents of *R. verecundus* included many insects and some seeds. While this suggests that *R. verecundus* is a generalist feeder and may be able to switch its food preferences to take advantage of available food resources, the diets of other murid species remain unknown.

P. platyops was the second most frequently captured species in the 6.7 ha study area sampled, however, their numbers fluctuated markedly through the study period. Flannery (1995) indicated that *P. platyops* is more common in disturbed habitats than in primary forests and appears to be most abundant below 500 m elevation. The 1 200 m altitude at which this study was conducted maybe at the upper attitudinal limit for this species. The abrupt changes in the apparent abundance of *P. platyops* were unexpected given the apparent stability of both abiotic and biotic conditions in the study site. Small mammals are known for abrupt population crashes following changes in rainfall events (Julliard *et al.* 1999; Letnic *et al.* 2005; Meserve *et al.* 1995; Milstead *et al.* 2007), but the current study site receives consistent year-round rainfall (Wright *et al.* 1997). Moreover, there were no extreme weather conditions of the kind known to influence other small mammal populations (e.g., Parrott *et al.* 2007) and do not seem to be a reasonable explanation for the fluctuation observed in *P. platyops*.

Apparent survival and population dynamics

Analyses based on the mark-recapture data have revealed some interesting insights into the population dynamics of the two sympatric species studied. The data indicated that apparent survival and recapture probabilities varied across species but did not substantially differ between sexes, indicating that each sex has similar parameters for both survival and recapture. Given that *R.verecundus* and *P. platyops* occur in sympatry with other five murid rodents in the study area we would expected there to be a complex of niche specialization and competition and thus the result that species is an important parameter in our analysis is not surprising.

Apparent survival does not refer to the actual survival probability of the marked animal populations but refers to the probability that a marked animal remained alive and is re-encountered in a later recapture session (White and Burnham 1999). This is because mortality and emigration from the open population under study cannot be distinguished from local mortality (Ryan *et al.* 2008). In estimating apparent survival, White and Burnham (1999) point out that animals that emigrate out of the study area are assumed to be dead in CJS models; however, the actual fate of small mammals never recaptured cannot usually be determined. Thus, the apparent survival determined in this study for both species may be influenced by various factors affecting open populations, including source-sink dynamics (Doyle 1990; Ellison and Van Riper 1998), parasitism (Fichet-Calvet *et al.* 2004; Isaac 2005; Randolph 1995), predation (Pavey *et al.* 2008; Schmidt *et al.* 2008; Terry 2008) primary productivity (Jimenez *et al.* 1992; Lima *et al.* 1999; Meserve *et al.* 1995) and seasonal food availability (Banks and Dickman 2000; Batzli and Henttonen 1993).

Our results showed that *R. verecundus* had lower survival and higher recapture probabilities while *P. platyops* had higher survival rates and lower detection rates. The lower survival observed in *R. verecundus* indicates two possibilities: the differences in survival estimates are real or a number of *R. verecundus* are emigrating out of the study area and are therefore are less available for capture. The possibilities of our results being such an artefact are plausible under the following scenario. Since *R. verecundus* is generally heavier than *P. platyops* they may have higher energetic requirements and be more likely to investigate baited traps and emigrate when resources become restricted (Kelt and Vuren 1999). Indeed, Wright (2005) observed less fruit production by large numbers of plants and species in the period between December to March at the study site. Conversely, *P. platyops* may have small home ranges and strong site fidelity thus higher apparent survival. However, the lower recapture probability in *P. platyops* may indicate the species is trap shy, or has different resource utilization. In the later possibility the animal may be passively avoiding traps if it feeds on cached seed buried in ground tunnels (Price *et al.* 2000) or avoiding areas frequented by predators such as *Dasyurus albopunctatus* that were present in the study area. While these alternatives are speculative a radio-telemetry study could resolve the possibility of such artefacts existing.

Conservation implications

Many communities on the island of New Guinea continue to rely on forest sourced protein including small mammals such as rodents (Mack and West 2005) and a total of 41 species of mammals occurring in Papua New Guinea have been listed on the 2008 IUCN list of threatened species including four species of murids (IUCN 2011). However, virtually no attempt has been made to examine the population dynamics of small mammal populations in New Guinea. Human population growth in Papua New Guinea at 2.3% per annum (World Bank 2011) is high by world standards and thus the assemblages of small mammals fringing human settlements will likely be exposed to greater human perturbation in the near future.

Very little is known about the murid species of New Guinea and even less is known about the community ecology of these murid assemblages. In this study we have shown that robust measures of survival and detection can be achieved for some murid species. Survival estimates, such as were gathered here, when combined with information on murid reproductive rates and life histories will yield simple population matrix models. These matrices can, in turn, provide useful insights into population dynamics and identify sensitive life stages to direct conservation efforts (Caswell 2001). Declines in survival and recapture probabilities can also be measures of relative health and may indicate phenomena such as disease invasion (Ryan *et al.* 2008), decrease in habitat quality, movement rate or increase in predation. When factors responsible for population declines are determined, then parameter specific management (Bond *et al.* 2000) can be employed to prevent further decline of the population. Estimation of population parameters through such studies can also help to assess and assign individual species to IUCN categories (e.g., Salvador and Fernandez 2008) and thereby prioritize future conservation effort in Papua New Guinea.

Data on small populations in tropical systems generally are lacking (Rudd and Stevens 1996), in contrast to semi-arid and temperate regions. This may be attributed to the degree of difficulty experienced in trapping small mammals in tropical rain forests (Mares and Ernest 1995). Although this was only a year-long study, it is the longest study yet conducted in New Guinea and has produced new insights into the population ecology of the two small mammal species. Further long-term studies on small mammals in New Guinea, especially those listed under the IUCN red list are required in order to understand their population ecology, and to provide adequate information for wildlife management and conservation.

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