Effects of El Niño on the population dynamics of the Malay civet east of the Wallace line

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Abstract

The effect of climate on the population dynamics of rainforest vertebrates is known only for a limited subset of species and study locations. To extend this knowledge, we carried out an 8-year population study of a Viverrid (Malay civet *Viverra tangalunga*) in the Wallacea biogeographical region (Buton Island, Sulawesi). Civets were trapped annually from 2003 to 2010, during which there were four weak to moderate El Niño events and one moderate La Niña event. In Indonesia, El Niño events are associated with drier than normal conditions, while La Niña is associated with wetter conditions. The number of individuals captured was strongly correlated with the 12-month summed Southern Oscillation Index (SOI) prior to trapping, with significantly fewer individuals caught in years with lower summed SOI (i.e. stronger El Niño conditions). Adult civet body mass was significantly higher in El Niño years; mean adult male and female body masses were 10.6% and 4.0% greater in El Niño years. There was support for a 1-year time lagged effect of El Niño on the apparent survival (1 − probability of disappearing from the study site due to death or emigration) of male (but not female) civets, which was approximately 50% higher in the year following El Niño events. Using spatially explicit capture–mark–recapture models, we were unable to detect any significant change in civet density between years, which was estimated as 1.36 ± 0.14 (SE) individuals km^{-2}. We suggest that increased apparent survival of males observed in the year after El Niño events was brought about by reduced dispersal (possibly associated with a change in mating tactic) rather than reduced mortality.

Introduction

Tropical rainforests have long been considered to be relatively stable environments with little temporal variation in climate (Stevens, 1989). But there is growing evidence that the interannual variability in climate that does occur can have a considerable effect on the dynamics of rainforest vertebrate populations (Foster, 1982; Wright *et al.*, 1999; Ferreira *et al.*, 2016; Ryder & Sillet, 2016). The El Niño–Southern Oscillation (ENSO) is the principal driver of interannual variability in temperature and rainfall in tropical rainforest ecosystems; in much of the wet tropics, the warm El Niño phase is associated with unusually dry conditions, while the cold La Niña phase is linked to increased rainfall (Malhi & Wright, 2004).

The El Niño phase has been shown to have a strong positive effect on rainforest primary productivity and fruit production (van Schaik, Terborgh & Wright, 1993; Wright *et al.*, 1999); this is particularly true in the dipterocarp forests of western Malesia (notably the Malay Peninsula, Sumatra and Borneo) which display large-scale synchronized masting during strong El Niño years (Appanah, 1985; Ashton, Givnish & Appanah,

1988; Curran & Leighton, 2000; Sakai, 2002). Dramatic reduction in fruit and seed availability have been observed in the year following El Niño events leading to starvation and reduced survival in some vertebrate frugivore populations in Borneo (Knott, 1998; Wong *et al.*, 2005; Fredriksson, Wich & Trisno, 2006). However, across the Wallace line on nearby Sulawesi (<150 km from Borneo at its nearest point), dipterocarps are virtually absent, and trees do not appear to fruit in synchrony (Whitten, Henderson & Mustafa, 2002). As a result, vertebrate populations on Sulawesi may be expected to respond differently to ENSO events than those on Borneo. However, there have been very few long-term studies of vertebrate populations on Sulawesi (or anywhere else in the Wallacea biogeographical region) and none that have examined the effect of ENSO on population dynamics.

The aim of this study was to examine the relationship between climate and population dynamics of the Malay civet (*Viverra tangalunga*) inhabiting lowland evergreen rainforest on Buton Island (<6 km off the coast of Sulawesi) in the heart of the Wallacea biogeographical region. The Malay civet is a medium-sized (3–7 kg) Viverrid which is largely nocturnal and

solitary (Colón, 2002; Jennings, Seymour & Dunstone, 2006), has a generalist diet that includes fruit, insects and small vertebrates and a wide geographical distribution encompassing Sumatra, the Malay Peninsula, Borneo, Sulawesi and the Philippines (Jennings & Veron, 2009). As part of a larger study investigating the ecology of the Malay civet on Buton Island, we conducted annual 7-week capture–mark–recapture campaigns from 2003 to 2010, which allowed us to estimate demographic vital rates including annual apparent survival [1 − P(permanent emigration from the study site) − P(mortality)] and population density, as well as obtain information on body condition. Over the 8-year period of this study, there were four weak to moderate El Niño events and one moderate La Niña event (NOAA, 2016a,b). Specifically, our goal was to evaluate the hypothesis that El Niño conditions alter the demography of a medium size omnivorous vertebrate in the heart of the Wallacea biogeographical region. Given the virtual absence of dipterocarps and other mast-fruiting trees in the Wallacea biogeographical region, we predict that El Niño will have a much reduced effect on apparent survival, population density and mean adult body mass on civets on Buton Island compared to populations of other omnivorous vertebrates on Borneo.

Materials and methods

Study site

Buton Island has a tropical monsoon climate with a dry season from June to September (Whitten *et al.*, 2002). Like Borneo, Sulawesi experiences significantly drier conditions during El Niño events and wetter conditions during La Niña events. On Sulawesi, the effects of ENSO are particularly pronounced from July to November (Lestari *et al.*, 2016). The study site consisted of a roughly rectangular grid of 25 traps situated in an area of lowland evergreen rainforest on steep coral karst straddling the border of the Lambusango Forest Reserve. The trapping grid was located within 2 km of two villages, and its northern limit was bordered by a small road (Fig. 1); contemporary and historic disturbances were evident, including selective logging and numerous human trails throughout the forest used by locals to harvest wildlife (typically targeting Red Jungle Fowl *Gallus gallus*, and Anoa *Bubalus* sp.) and to collect firewood. The effective survey area (ESA) changed between years (8.3–9.7 km^2) because of variation in the area of the trapping grid [100% minimum convex polygon (MCP)], which was increased in 2005 (an attempt to increase sample sizes), and reduced in 2007 and 2009 due to unavoidable restrictions in accessing parts of the forest.

Capture–mark–recapture

Trapping was carried out for a minimum 7-week period starting in late June or early July each year from 2003 to 2010 using locally made box traps baited with salt fish. Traps were checked twice daily, and captured civets were immobilised with an intramuscular injection of ketamine hydrochloride

(15 mg kg^{-1} body weight) and xylazine hydrochloride (1.5 mg kg^{-1} body weight); most civets were ataxic within 5 min and remained so for at least 20 min (Jennings *et al.*, 2006). All individuals caught for the first time in a trapping season were sexed, allocated to an age class, weighed and measured and if not already marked, fitted with plastic numbered ear tags. Individuals that had already been caught in a trapping season were released immediately after being identified. We classified individuals as juveniles (milk teeth present), subadults (adult teeth present, but no signs of sexual maturity – i.e. testes not descended in males; nipples very small and underdeveloped in females) and adults (testes descended in males; prominent nipples in females or females known to be at least 2 years old). Adults were sub-classified into young adults (very little tooth wear), medium-age adults (unremarkable tooth wear) and old adults (heavy tooth wear).

Weather

Daily rainfall measurements for the period January 2001 to December 2010 were obtained from the Badan Meteorologi Dan Klimatologi Geofisika meteorological station located approximately 50 km away from the study site in the town of Bau-Bau. The US National Oceanic and Atmospheric Administration (NOAA) criteria for an ENSO event is at least five consecutive months of sea surface temperature anomalies (measured as 3-month running means) in the central equatorial Pacific exceeding a threshold of plus (El Niño) or minus (La Niña) 0.5°C (NOAA, 2016a,b). The strength of ENSO conditions was measured using the Southern Oscillation Index (SOI). The SOI is one measure of the large-scale fluctuations in air pressure occurring between the western and eastern tropical Pacific during El Niño and La Niña episodes (see NOAA 2016a for methodology for calculating the SOI). We chose the SOI as a measure of ENSO strength because of its common use in other population studies of the effect of ENSO on rainforest vertebrate population dynamics (e.g. Wolfe, Ralph & Elizondo, 2015; Ferreira *et al.*, 2016; Ryder & Sillet, 2016). Monthly values of SOI were obtained from the NOAA website (2016a). All annual measurements of rainfall and SOI were summed from the first day of July (corresponds to start of dry season and the trapping operations) to the last day of June in the following year. ENSO events typically start in July or after and end no later than April, so the 12-month period between surveys always encompassed the entire ENSO event.

Statistical analyses

Estimating apparent survival

We estimated Malay civet annual apparent survival (φ) and abundance (N) using a closed robust capture–recapture model implemented in the program MARK (Kendall, Nichols & Hines, 1997; White & Burnham, 1999). We considered each year of the study as a primary occasion and each trapping day as a secondary occasion. By linking trapping efforts across years (using the robust design approach), we were able to
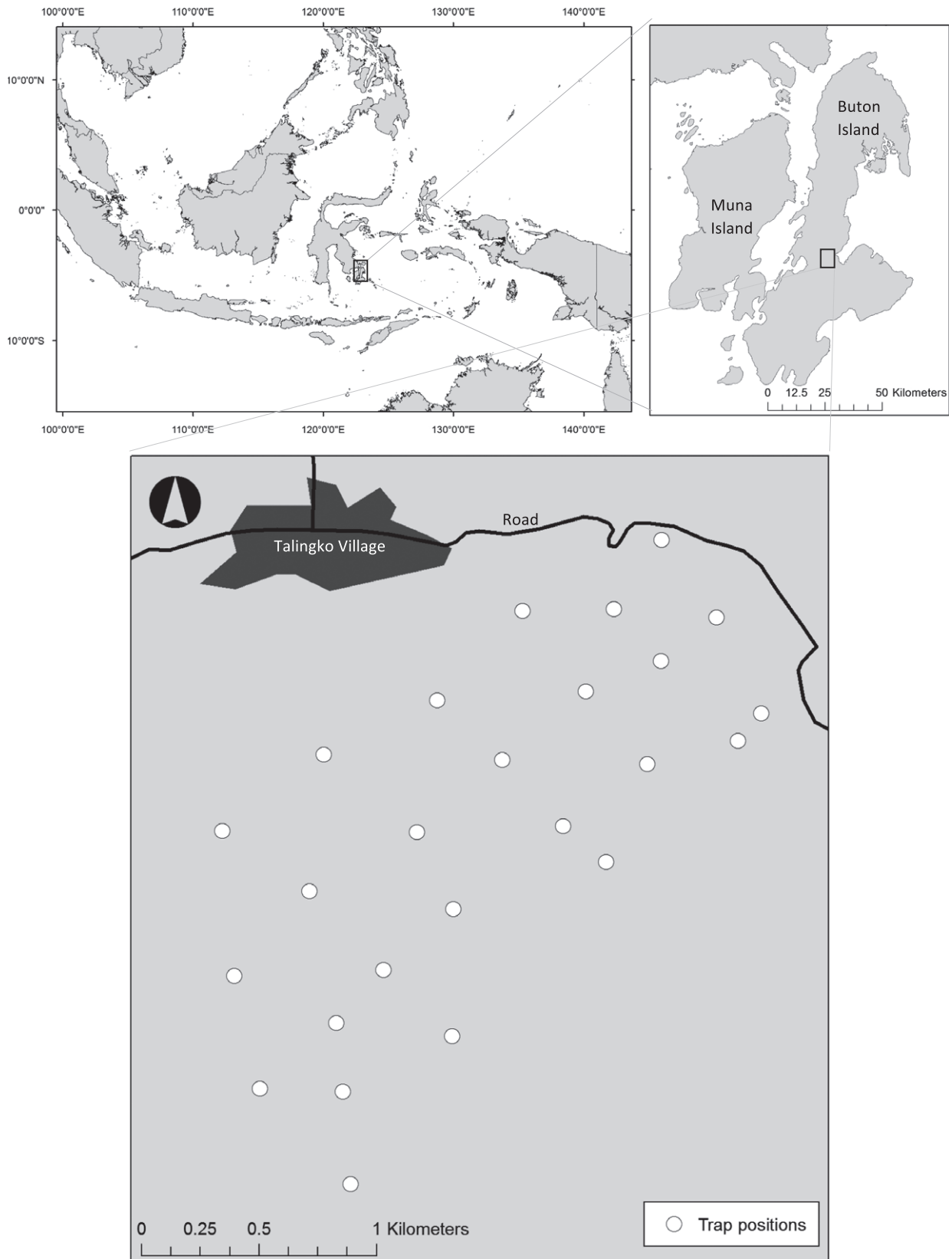
Figure 1 Location of study site and map of trapping grid. In the lower panel, the light grey area represents rainforest habitat.

model and account for variation in temporary emigration from the study area, which could otherwise bias survival (Kendall *et al.*, 1997); annual abundance is a derived parameter from this modelling approach. We considered models that included different combinations of effects of sex, year and climate on apparent survival. Sex was considered because of expected differences in philopatry between the sexes, where a higher proportion of males are likely to disperse from the study site, thereby reducing their apparent survival. We included the effect of climate in four different ways: (1) effect of El Niño year (*Nino t*), (2) effect of a 1-year time lag after an El Niño year (*Nino t + 1*), (3) a covariate describing the intensity of ENSO conditions (annual summed monthly SOI values: *SOI*) and (4) a rainfall covariate (annual summed rainfall at the nearest weather station: *Rain*). We also considered temporary emigration parameters to either be constant or vary by year. Lastly, we considered models with within-year detection probability to vary according to sex, year, a behavioural effect and/or following general individual heterogeneity; heterogeneity was either modelled using a finite mixture approach (Pledger, 2000) or using a random effect (Gimenez & Choquet, 2010). Data were too sparse to model survival by age class as well as sex and time variables, so age classes were pooled. In total, we compared 42 models, which were ranked using Akaike's information criterion with small sample size correction (AIC$_c$).

Estimating density

We estimated annual density in two ways. First, we used the derived abundance estimates from the closed robust capture–recapture modelling and divided by the ESA. The ESA was calculated as the 100% MCP of the trapping grid surrounded by a buffer strip whose width was measured as the mean-maximum-distance-moved (MMDM) between capture points (Sharma *et al.*, 2010; Gerber & Parmenter, 2015). The MMDM per year ranged from 501 m to 833 m. However, there was no significant difference in MMDM between years (one-way ANOVA: $F_{7,72} = 1.06$, $P = 0.39$), and no evidence for significant differences in home range size between years (based on radio-tracking data from 17 individuals tracked over four different trapping seasons 2005–2008; A. Seymour & M. Tarrant, unpublished data); the pooled MMDM (683 m) was used to estimate the ESA.

The second way we estimated annual Malay civet density was using a spatial capture–recapture (SCR) modelling approach (Borchers & Efford, 2008). SCR models explicitly consider the spatial layout of the trapping grid and the space-use of animals within and even beyond the grid. As such, SCR models can be more robust to variation in trapping array size and spacing, relative to animal movement (Sollmann, Gardner & Belant, 2012). We fit the Malay civet spatial capture–recapture data using a likelihood approach available in R through the package 'secr' (Efford, 2016). In total, we compared 25 models that varied in density according to *Nino t*, *Nino t + 1*, *Rain*, *SOI*, year or was constant. Spatial detection parameters were also modelled as constant or varied by climate (i.e. *Nino t*, *Nino t + 1*, *Rain*, *SOI*), year and/or a behavioural effect.

Body mass

We explored the effect of climate on civet body mass by fitting nine competing generalized linear models (GLM) and ranking by AIC$_c$. Only the body masses of adult age classes were included in the analysis. Male Malay civets are heavier than females (Jennings *et al.*, 2006), so a variable for sex (*Sex*) was included in all models. Each candidate model included a different one of the following time trends either as an additive or an interactive effect with *Sex*: *Year* (a category with eight levels corresponding to each year) or one of three annual climate variables (*El Nino*, *Rain* and *SOI*). One model included only *Sex* as a baseline. To test whether models accounted for a significant amount of variation in the data, we used *F* tests. We tested the significance of each model variable by comparing its estimated slope with zero using *t*-tests. All GLMs were fitted using R (R Core Team 2016).

All correlations were conducted using Spearman's rank correlation r_s (R Core Team 2016).

Results

Weather

Total annual rainfall varied considerably from year to year (Fig. 2), ranging from 1368 mm in 2005 to 2446 mm in 2006. There were no strong ENSO events during the study period. There were moderate El Niño conditions in 2002–2003 and 2004–2005, weak El Niños in 2006–2007 and 2009–2010, and moderate La Niña conditions in the 2007–2008 as reflected by the annual summed SOI (Fig. 2). There was a significant correlation between the annual number of days of rain and the summed annual SOI ($r_s = 0.78$, $P = 0.02$). There was on average 20 fewer rainy days during El Niño years compared to La Niña years (El Niño years: mean 118 ± 9.2 (SD) days of rain; La Niña years: mean 138 ± 3.8 days of rain). However, there was no clear correlation between annual rainfall and annual summed SOI.

Capture frequency

From 2003 to 2010, a total of 6430 trap nights of effort resulted in 532 capture events. We identified a total of 102 individuals, including 59 males, 40 females, and 3 juveniles, whose sex could not be identified. The most commonly encountered age class at first capture was medium-age adults (32 individuals) followed by young adults (26 individuals), juveniles (23 individuals), subadults (18 individuals) and old adults (3 individuals). The number of civets caught within a trapping period varied between years ranging from 15 in 2005 to 27 in 2008 (Table 1) and was not correlated with trap effort ($r_s = 0.10$, n.s.). There were significantly fewer individuals caught in El Niño years (annual summed SOI vs. number of individuals caught: $r_s = 0.95$, $P < 0.01$; annual number of rainy days vs. number of individuals caught: $r_s = 0.84$, $P < 0.01$). The capture rate also varied considerably between years, and was at its lowest in 2005 (3.1 captures per 100 trap nights) and at its highest in 2004 (11.3 captures per 100 trap nights; Table 1).
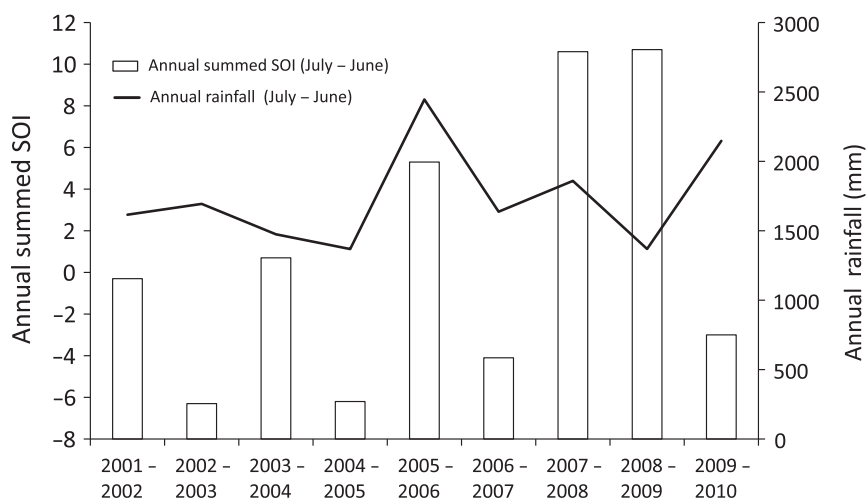
Figure 2 The sum of rainfall (mm) in southern Buton Island and the sum of monthly Southern Oscillation Indices (SOI) in the 12 months preceding the start of the trapping season.

Apparent survival

We found strong evidence of an effect of sex on apparent survival, as it appeared in each of the top nine best-ranked models (Table 2); the estimated apparent survival of females was greater than that of males in every year (Fig. 3). Apparent survival in the highest ranked model also included an interaction with the *Nino t* + 1; this model accounted for 53% of the total AIC_c weight, giving support for the effect of a 1-year time lag after El Niño events on the apparent survival of males but not females (Table 2). Male apparent survival was approximately 50% greater in years following an El Niño event (Fig. 3). Neither annual rainfall (*Rain*) nor annual summed SOI (*SOI*) appeared in any of the top 13 survival models (Table 2).

Density

Closed population model

Density estimates from the robust design closed population models varied between years, with the highest estimated density (2008: 3.10 ± 0.35 [SE] civets km^{-2}) 22% higher than the lowest estimated density (2003: 2.55 ± 0.56 civets km^{-2}; Table 3). There was no clear relationship between these estimates of civet density and annual rainfall or summed SOI.

SCR models

There was no support for any effect of El Niño or rainfall on civet density, or for any significant difference in civet density between years, and a model of constant density (but varying capture probability) between years explained 91% of the AIC_c weight (Table 4). The density of adult civets estimated by the best-supported model (i.e. constant density between years) was 1.36 ± 0.14 (SE) civets km^{-2} (95% CL: 1.12–1.65 civets km^{-2}).

Body mass

The highest ranked body mass GLM (i.e. the model which explained the most variation using the fewest terms) included an additive effect of *Sex* and *El Nino* (Table 5). This model explained a significant amount of variation in the data ($F_{2, 117} = 8.94$, $P < 0.0003$). Both *Sex* and *El Nino* had significant

Table 1 Summary of Malay civet captures per year

Year	Trap effort	No. civets captured		No. capture events		Capture rate[a]
		Males	Females	Males	Females	
2003	396	11	8	19	20	9.8
2004	855	14	8	60	37	11.3
2005	918	8	7	17	11	3.1
2006	866	9	15	20	37	6.6
2007	803	9	10	38	41	9.8
2008	917	17	10	52	49	11.0
2009	744	10	14	30	33	8.5
2010	931	11	12	21	33	5.8

[a]Per 100 trap nights.

Table 2 Top 20 robust design models of apparent survival

Model selection	Number of parameters	Deviance	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Model likelihood
Surv(*Sex* × *Nino t + 1*), RndMove(.), DetHet: μ(*Year*) σ(.)	14	3616.0	3644.9	0	0.53	1.00
Surv(*Sex*), RndMove(.), DetHet: μ (*Year*) σ(.)	12	3620.9	3645.5	0.6	0.39	0.73
Surv(*Sex*), RndMove(.), DetHet: μ(.) σ(.)	5	3640.0	3650.1	5.2	0.04	0.07
Surv(*Sex*), RndMove(.), DetHet: μ(.) σ(*Sex*)	6	3640.0	3652.2	7.3	0.01	0.03
Surv(*Sex*), RndMove(*Year*), DetHet: μ(*Year*) σ(.)	18	3618.0	3655.5	10.6	0.00	0.01
Surv(*Sex*), RndMove(*Sex*), DetHet: μ(.) σ(*Sex*)	8	3639.3	3655.6	10.7	0.00	0.00
Surv(*Sex* × *Nino t + 1*), RndMove(*Year*), DetHet: μ(.) σ(.)	13	3629.4	3656.2	11.3	0.00	0.00
Surv(*Sex*), RndMove(*Year*), DetHet: μ(.) σ(.)	11	3633.7	3656.3	11.4	0.00	0.00
Surv(*Sex+Nino t + 1*), RndMove(*Year*), DetHet: μ(.) σ(.)	12	3631.7	3656.3	11.4	0.00	0.00
Surv(*Nino t + 1*), RndMove(*Year*), DetHet: μ(.) σ(.)	9	3638.1	3656.5	11.6	0.00	0.00
Surv(Transience), RndMove(*Year*), DetHet: μ(*Year*) σ(.)	10	3636.8	3657.3	12.4	0.00	0.00
Surv(*Year* × *Sex*), RndMove(.), DetHet: μ(.) σ(.)	17	3622.1	3657.4	12.5	0.00	0.00
Surv(*Sex* × *Nino t + 1*), RndMove(*Year*), DetHet: μ(*Year*) σ(.)	21	3613.5	3657.5	12.6	0.00	0.00
Surv(*Sex+Rain*), RndMove(*Year*), DetHet: μ(.) σ(.)	12	3633.1	3657.8	12.8	0.00	0.00
Surv(*Sex+Rain*), RndMove(*Year*), DetHet: μ(.) σ(.)	12	3633.2	3657.9	12.9	0.00	0.00
Surv(*Sex*), RndMove(*Year*), DetHet: μ(Behav) σ(.)	12	3633.3	3658.0	13.1	0.00	0.00
Surv(*Sex+Nino t*), RndMove(*Year*), DetHet: μ(.) σ(.)	12	3633.6	3658.3	13.3	0.00	0.00
Surv(*Sex+SOI*), RndMove(*Year*), DetHet: μ(.) σ(.)	12	3633.7	3658.3	13.4	0.00	0.00
Surv(*Sex* × *Rain*), RndMove(*Year*), DetHet: μ(.) σ(.)	13	3632.9	3659.7	14.8	0.00	0.00
Surv(*Sex* × *Rain*2), RndMove(*Year*), DetHet: μ(.) σ(.)	13	3633.0	3659.8	14.9	0.00	0.00

Surv, Survival; RndMove, a model term describing temporary movement from the study site; DetHet, a model term describing detection heterogeneity that includes μ (mean detection rate) and σ (variability in detection rate); *Year*, the effect of year; *Nino t*, the effect of an El Niño year; *Nino t + 1*, the effect of an El Niño year with a 1-year time lag; *Sex*, males versus females; *SOI*, time trend of annual summed SOI; *Rain*, time trend of total annual rainfall; '.', indicates a constant value.
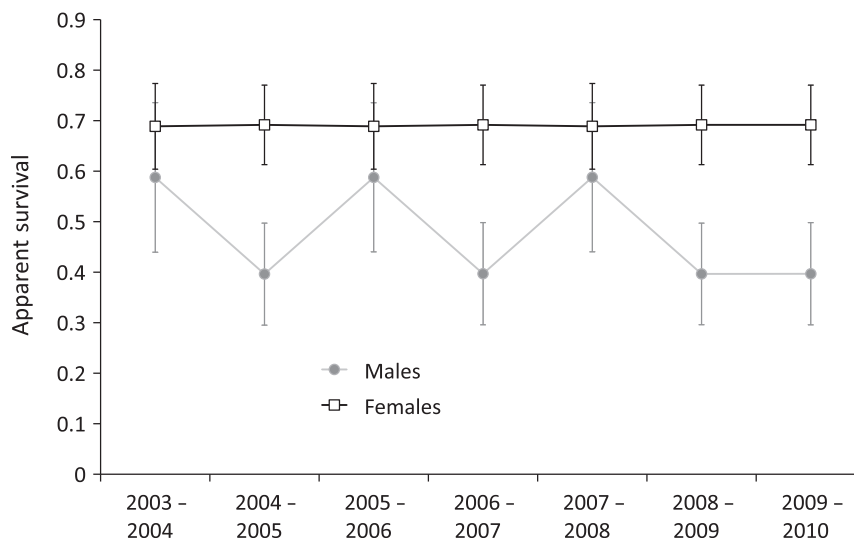
Figure 3 Estimates of annual apparent survival of male and female civets from the top-ranked CMR model.

effects on adult civet body mass (tests that slope of linear model is significantly different from zero: *Sex*, $t = 2.35$, $P < 0.026$; *El Nino*, $t = 3.56$, $P < 0.006$). In El Niño years, mean adult male and female civet weights were 10.6% and 4.0% greater than in other years (males: 3.87 ± 0.08 kg in El Niño years vs. 3.50 ± 0.07 kg in other years; females: 3.57 ± 0.07 kg in El Niño years vs. 3.43 ± 0.07 kg in other years). Mean adult weight was lowest for both males and females in 2004 (males: 3.35 ± 0.08 (SE) kg; females: 3.14 ± 0.25 kg), and for males, it was highest in 2010 (4.10 ± 0.18 kg) and for females, it was highest in 2007 (3.75 ± 0.20 kg).

Table 3 Civet density estimated using robust design closed population models with standard errors (SE) and lower and upper 95% confidence limits (LCL and UCL respectively), and the effective survey area (ESA)

Year	ESA (km²)	Population density (civets km⁻²)	SE	LCL	UCL
2003	8.86	2.55	0.56	1.44	3.65
2004	9.07	2.60	0.29	2.03	3.17
2005	9.67	2.97	0.91	1.19	4.76
2006	9.67	3.06	0.53	2.01	4.10
2007	8.31	2.59	0.37	1.85	3.32
2008	9.67	3.10	0.35	2.42	3.79
2009	8.52	2.71	0.40	1.92	3.50
2010	9.65	2.87	0.59	1.71	4.02

Discussion

Our principle findings were (1) male civets disappeared (probably emigrated) from the study site more frequently than females regardless of year; (2) the disappearance rate of males was lower over the year after El Niño events compared to other years, (3) adult civet body mass (especially that of males) was significantly higher in surveys made in El Niño years and (4) civet capture frequency and estimated capture probability were lower in El Niño years. Results 3 and 4 suggest that on Buton Island, food availability is enhanced during El Niño events, and that this then leads to higher body mass and reduced capture probability in the survey immediately following an El Niño event. Unfortunately, we did not measure food availability (e.g. fruit or small mammal abundance) so we do not know how El Niños actually affected food resources on Buton. However, given that El Niño events have been linked to community-wide increases in fruit production in other parts of the wet tropics, not only just in the dipterocarp forests of Peninsular Malaysia and Borneo (Ashton *et al.*, 1988; Curran & Leighton, 2000) but also on Barro Colorado Island (BCI) in Panama (Wright *et al.*, 1999; Wright & Calderón, 2006), and Taiwan (Chang-Yang *et al.*, 2016) increased food availability is a plausible explanation for our results. The low capture rates we observed in surveys immediately following El Niño events is also consistent with the hypothesis of higher food availability. For example, in temperate hardwood forests in North America, capture rates of American martens *Martes americana* was dramatically lower during masting events (Jensen *et al.* 2012). Our results are consistent with observations made by Ryder & Sillet (2016), who found an increase in the apparent survival of territorial male wire-tailed manakins *Pipra filicauda* in El Niño years in the Ecuadorian Amazon, which was also attributed to increased fruit production.

However, if El Niño events are linked to an increase in fruit production on Buton, we might expect the increase in apparent survival to occur over an El Niño year rather than over the following year as we found. The increased body mass observed in the post-El Niño survey might feasibly lead to increased survival in the following year if this higher body mass persisted for a significant proportion of the following year. By the next survey taken at the end of the following year, body masses were always much lower, and as no measurements of body mass were taken between surveys, we do not know how far through the year the decline in body mass began. Reduced mortality in the year following an El Niño is not consistent with studies of partially frugivorous carnivores on Borneo (sun bears *Helarctos melayanus*, Wong *et al.*, 2005) and BCI (coatis *Nasua narica*, Foster, 1982; Wright *et al.*, 1999), in which episodes of starvation were observed in some years following El Niños. In the 2004 survey (16 months after the end of the 2002–2003 El Niño), when the lowest body masses and highest capture rates were observed, there were signs of starvation (emaciation and/or unusually slow and wobbly movement after exiting traps) in 4 (17%) of the civets captured. This observation suggests an increased rather than decreased mortality in the year following the 2002–2003 El Niño. However, 2004 was the only year in which such signs of starvation were observed. There was nothing exceptional about the intensity of the 2002–2003 El Niño, nor was the rainfall in the following year extreme.

We suggest that the increased apparent survival occurring over the year after El Niño events is more likely to have been

Table 4 Top 10 SCR density estimation models

Model selection	Number of parameters	Log likelihood	AIC	AIC_c	ΔAIC_c	AIC_c weight
D(.) Hazard rate g₀(*Year* × *bk*) σ(*Year*) z(.)	26	−2776.36	5604.73	5613.67	0.00	0.91
D(*Year*) Hazard rate g₀(*bk*) σ(*Year*) z(.)	19	−2788.36	5614.72	5619.35	5.68	0.05
D(*Sex*) Hazard rate g₀(*Year* × *bk*) σ(*Year*) z(.)	27	−2778.21	5610.41	5620.10	6.43	0.04
D(*Year*) Hazard rate g₀(*Year* × *bk*) σ(.) z(.)	26	−2781.47	5614.94	5623.88	10.21	0.00
D(*Rain*) Hazard rate g₀(*Rain* × *bk*) σ(*Rain*) z(.)	9	−2804.79	5627.57	5628.61	14.94	0.00
D(*Year*) Hazard rate g₀(*Year* × *bk*) σ(*Year*) z(.)	33	−2775.06	5616.13	5631.09	17.42	0.00
D(*SOI*) Hazard rate g₀(*SOI* × *bk*) σ(*SOI*) z(.)	9	−2806.90	5631.81	5632.84	19.17	0.00
D(*El Nino*) Hazard rate g₀(*El Nino* × *bk*) σ(*El Nino*) z(.)	9	−2807.69	5633.38	5634.41	20.74	0.00
D(*El Nino t−1*) Hazard rate g₀(*El Nino t−1* × *bk*) σ(*El Nino t−1*) z(.)	9	−2808.76	5635.53	5636.56	22.89	0.00
D(.) Hazard rate g₀(.) σ(.) z(.)	4	−2814.32	5636.63	5636.86	23.19	0.00

El Nino, the effect of El Nino years versus other years; *El Nino t + 1*, the effect of El Nino + 1 years (i.e. time lag effect) versus other years; *Year*, the effect of year; *Rain*, the effect of summed annual rainfall; *SOI*, the effect of summed annual SOI; *bk*, the effect of a trap-specific behavioural response to capture; *Sex*, males versus females; '.', indicates a constant value; D, density; g₀, detection probability at a home range centre; σ, spatial scalar describing detection probability away from a home range centre; z, shape parameter.

Table 5 GLMs of adult body mass ranked by AIC$_c$

Model	Number of parameters	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight
Sex + El Nino	5	117.90	0.00	0.55
Sex × El Nino	7	119.58	1.68	0.24
Sex + Year	1	119.91	2.01	0.20
Sex + SOI	5	126.90	9.00	0.01
Sex	4	128.15	10.25	0.00
Sex × SOI	7	129.33	11.44	0.00
Sex + Rain	5	130.26	12.36	0.00
Sex × Rain	7	133.63	15.73	0.00
Sex × Year	19	134.62	16.72	0.00

Sex, males versus females; *El Nino*, the effect of El Nino years versus other years; *SOI*, time trend of annual summed SOI; *Rain*, time trend of total annual rainfall.

brought about by reduced emigration rather than reduced mortality. A concurrent radio-tracking study carried out on the trapping grid during survey periods from 2005 to 2008 revealed that the emigration rate of male civets was high: 44% ($n = 9$) of collared adult males permanently emigrated from the study site during survey periods. In contrast, emigration rates in radio-collared females were low, and none ($n = 8$) were observed to emigrate from the study site in the same period (A. Seymour & M. Tarrant, unpublished data). Emigration is therefore a likely cause of disappearance of male civets between surveys. One explanation for a reduction in emigration rate in the year after El Niños could be that El Niño events skew age distributions (e.g. fewer dispersing young), though we found no consistent biases in the age structure of male civets captured in El Niño years. Another possible explanation is that male civets change mating tactics and dispersal behaviour in response to changing food availability (Sandell & Liberg, 1992).

Using spatially explicit capture–mark–recapture models, we were unable to detect any effect of climate on density, nor indeed any significant difference in density between years, suggesting no net loss or gain of civets during the study. However, it is important to bear in mind the caveat of small sample sizes and correspondingly wide confidence limits, and it is possible that considerable annual changes in density remained undetected. The SCR density estimate (1.36 ± 0.14 [SE] civets per km^2) was lower than the closed population model density estimates (2.55 ± 0.56 to 3.10 ± 0.35 civets km^{-2}). In a dipterocarp forest on Borneo, Colón (2002) recorded a density of 2.17 Malay civets per km^2 in unlogged forest. Although this density estimate is not directly comparable with those reported here (calculated from the combined home range area of a sample of six radio-collared civets; Colón, 2002), it is broadly similar lying in between our SCR and closed population model density estimates. Colón's (2002) study was conducted during a period of peak fruit abundance on Borneo (Sakai, 2002). In addition, the body masses recorded by Colón during this period were not significantly different from those recorded at our study site following the moderate 2002–2003 El Niño event (Jennings *et al.*, 2006) which might suggest similar resource abundance during the two studies. However, there are no estimates of civet density during periods of low fruit abundance on Borneo.

Our estimates of annual apparent survival and capture probability, the number of individuals captured and mean adult body mass showed much stronger relationships with a climate index (SOI) than local weather (rainfall). This paradoxical observation is common in studies on the effect of climate on animal populations (Hallett *et al.*, 2004), and can occur because indices encapsulate a number of weather variables and tend to average conditions over a period of time and over large areas. The weather station from which rainfall data were obtained in this study was separated from the trapping grid by a small mountain range (max elevation c. 800 m), which may result in locally distinct patterns of rainfall (Whitten *et al.*, 2002), and thus contribute to the observed lack of correlation between rainfall and ecological measurements.

This study is the first to show an effect of El Niño on the demography and body condition of a vertebrate population east of the Wallace line, adding to the growing evidence that interannual variation in climate can have significant effects on the demography of rainforest vertebrates even in locations where large-scale general flowering and synchronizing masting events do not occur. The effects we detected are likely to be quite strong given the limited statistical power with only 8 years of data, and given that only weak to moderate ENSO events occurred during our study. However, many questions remain unanswered, including exactly how El Niños affect tree phenology east of the Wallace line, what causes the increase in apparent survival in male civets the year after El Niño events and how El Niño affects the fecundity of females and recruitment.

Acknowledgements

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Graphical Abstract

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The effect of climate on the population dynamics of rainforest vertebrates is known only for a limited subset of species and study locations. To extend this knowledge, Malay civets *Viverra tangalunga* on Buton Island (Sulawesi) were trapped annually from 2003 to 2010, during which there were four weak to moderate El Niño events and one moderate La Niña event. Adult civet body mass was significantly higher in El Niño years. There was also support for a 1-year time lagged effect of El Niño on the apparent survival of male (but not female) civets, which was approximately 50% higher in the year following El Niño events.