Demographic status of Komodo dragons populations in Komodo National Park

Deni Purwandana [a], Achmad Ariefiandy [a], M. Jeri Imansyah [a], Heru Rudiharto [b], Aganto Seno [b], Claudio Ciofi [c], Damien A. Fordham [d], Tim S. Jessop [e,*]

[a] *Komodo Survival Program, Denpasar, Bali, Indonesia*
[b] *Komodo National Park, Labuan Bajo, Flores, Indonesia*
[c] *Department of Biology, University of Florence, 50019 Sesto Fiorentino, FI, Italy*
[d] *Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, North Terrace, SA 5005, Australia*
[e] *Department of Zoology, University of Melbourne, Parkville, Vic 3010, Australia*

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ABSTRACT

The Komodo dragon (*Varanus komodoensis*) is the world's largest lizard and endemic to five islands in Eastern Indonesia. The current management of this species is limited by a paucity of demographic information needed to determine key threats to population persistence. Here we conducted a large scale trapping study to estimate demographic parameters including population growth rates, survival and abundance for four Komodo dragon island populations in Komodo National Park. A combined capture mark recapture framework was used to estimate demographic parameters from 925 marked individuals monitored between 2003 and 2012. Island specific estimates of population growth, survival and abundance, were estimated using open population capture–recapture analyses. Large island populations are characterised by near or stable population growth (i.e. $\lambda \sim 1$), whilst one small island population (Gili Motang) appeared to be in decline ($\lambda = 0.68 \pm 0.09$). Population differences were evident in apparent survival, with estimates being higher for populations on the two large islands compared to the two small islands. We extrapolated island specific population abundance estimates (considerate of species habitat use) to produce a total population abundance estimate of 2448 (95% CI: 2067–2922) Komodo dragons in Komodo National Park. Our results suggest that park managers must consider island specific population dynamics for managing and recovering current populations. Moreover understanding what demographic, environmental or genetic processes act independently, or in combination, to cause variation in current population dynamics is the next key step necessary to better conserve this iconic species.

1. Introduction

The Indonesian archipelago possesses extraordinary species diversity and endemism (McKinnon, 1996; Mittermeier et al., 1998; Whitten, 2000). However, rapid and wide spread habitat loss, variable capacity in natural reserve management, alongside the looming challenges of climate change pose considerable risk to the nation's biodiversity (Sodhi et al., 2004; Fordham and Brook, 2010). Establishing the threat human impacts pose to biodiversity in Indonesia is made difficult by the absence of important demographic data needed to assess conservation status (Harris et al., 2011). For example, even for the iconic Komodo dragon (*Varanus komodoensis*), the world's largest lizard lacks estimates of rates of population growth or abundance (Jessop et al., 2007). The Komodo

dragon is an apex predator and has an isolated island distribution making it particularly sensitive to global change (Cardillo et al., 2004).

Komodo dragons inhabit five islands in eastern Indonesia, with four island populations located within Komodo National Park (KNP) and several fragmented populations persisting on the larger island of Flores (Ciofi and De Boer, 2004; Jessop et al., 2004, 2007). Komodo dragon range area is thus small, with isolated populations. Its distribution is suspected to have decreased substantially in recent decades (Ciofi, 2002) as a consequence of prey removal by humans (e.g. Timor deer) and habitat loss (forest conversion to agriculture) (Ciofi, 2002; Jessop et al., 2007), especially outside protected areas. The Komodo dragon is classified by the International Union for the Conservation of Nature (IUCN) as 'vulnerable' due to demographic decline and limited distribution (IUCN, 2012).

We undertook a large-scale field study to estimate island specific demographic parameters in Komodo National Park in Eastern Indonesia. Komodo National Parks remains the largest and best

* Corresponding author. Address: Department of Zoology, University of Melbourne, Parkville, Vic 3052, Australia. Tel.: +61 83440206.
E-mail address: tjessop@unimelb.edu.au (T.S. Jessop).

resourced of the protected areas existing within the distribution of Komodo dragons. Intuitively, given the large difference in island area and proximity among the park's extant Komodo dragon populations, we hypothesised that demographic parameters could vary among populations due to different evolutionary histories and contemporary variation in habitat quality or demographic and genetic processes (Frankham, 1998; Whittaker and Fernandez-Palacios, 2007; Laver et al., 2012). Our aims were three fold. The first was to assess the status of the four island populations by evaluating averaged population growth rates to summarise population trajectories as exhibiting positive, stable or negative population growth. Our second aim was to estimate mean survival for each Komodo dragon populations to ascertain further potential island differences in population demography. Our final aim estimated population abundance at ten sites on four islands and extrapolated these island estimates to produce a total Komodo dragon population abundance for Komodo National Park. These demographic estimates represent a long-standing goal of our field monitoring activities and a key request of the Indonesian National Park Authority. Ultimately having access to this important demographic information enabled us to discuss the ensuing implications for current management and prioritization of conservation activities for Komodo dragons within Komodo National Park.

2. Materials and methods

2.1. Study area

Fieldwork for this study was conducted from April 2003–November 2006 and again from April 2009–April 2012 in Komodo National Park, Eastern Indonesia (8°35′40″S, 119°25′51″E). The total area of Komodo National Park is 1817 km^2 of which 603 km^2 is land and 1214 km^2 is sea (Fig. 1). Komodo National Park consists of the two large islands of Komodo and Rinca (311.5 km^2 and 204.8 km^2, respectively) and three smaller islands (Padar, 14.1 km^2; Gili Motang, 9.5 km^2; and Nusa Kode, 7.8 km^2). There are four main vegetation communities in Komodo National Park. Tropical monsoon forest dominates areas above 500–700 m. At lower elevations deciduous monsoon forest (primarily *Tamarindus indica*) occurs in valley floors holding permanent and ephemeral water courses. Savannah woodland and savannah grassland occupy drier areas distal from water courses. The climate is highly seasonal and dominated by a long dry season (March–November) and a short summer wet season (December–February). The annual rainfall is less than 1000 mm. The mean monthly maximum and minimum temperature ranges from 31–38 °C and 19.5–25.6 °C, respectively.

2.2. Trapping protocols

We captured Komodo dragons at 273 fixed trapping locations established at ten study sites on the four islands (Komodo, Rinca, Nusa Kode and Gili Motang) that have extant lizard populations (Figs. 1 and 2a). The Komodo Island sites: Loh Liang (K1), Loh Lawi (K2), Loh Sebita (K3) and Loh Wau (K4) consisted of 32, 32, 21 and 9 trapping locations respectively. The Rinca Island sites: Loh Buaya (R1), Loh Baru (R2), Loh Tongker (R3) and Loh Dasami (R4) consisted of 22, 22, 13 and 24 trapping locations respectively. Gili Motang (GM) and Nusa Kode (NK) sites consisted of 16 and 12 trapping locations. The variation in sampling effort reflected differences in the area of the study sites (that often consisted of discrete valleys). Trapping locations within each study site were located in landscapes dominated by deciduous monsoon forest that is considered high quality habitat for Komodo dragons (Fig. 2b).

Within each study site, we used purpose built traps set at different trapping locations to capture Komodo dragons (Fig. 2c). Traps
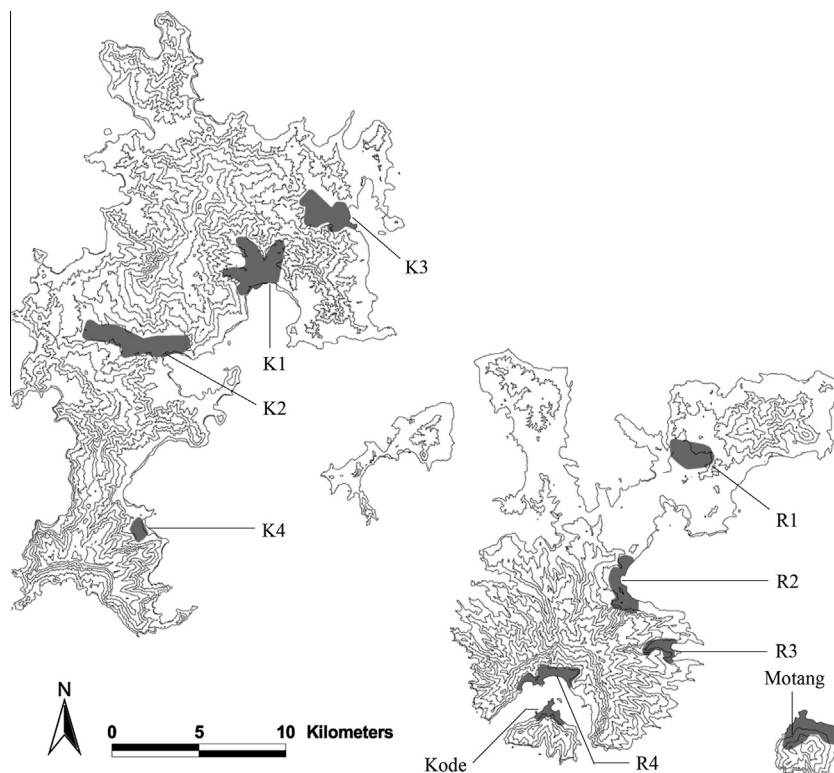

Fig. 1. Map of Komodo National Park and the location of the 10 trapping sites used in this study. Four sites were each located on the large islands of Komodo (sites denoted as K1, K2, K3, K4); and Rinca (R1, R2, R3, R4). A single trapping site was located each on the small islands of Gili Motang and Nusa Kode. The shaded area constitutes the effective trapping area within each site.
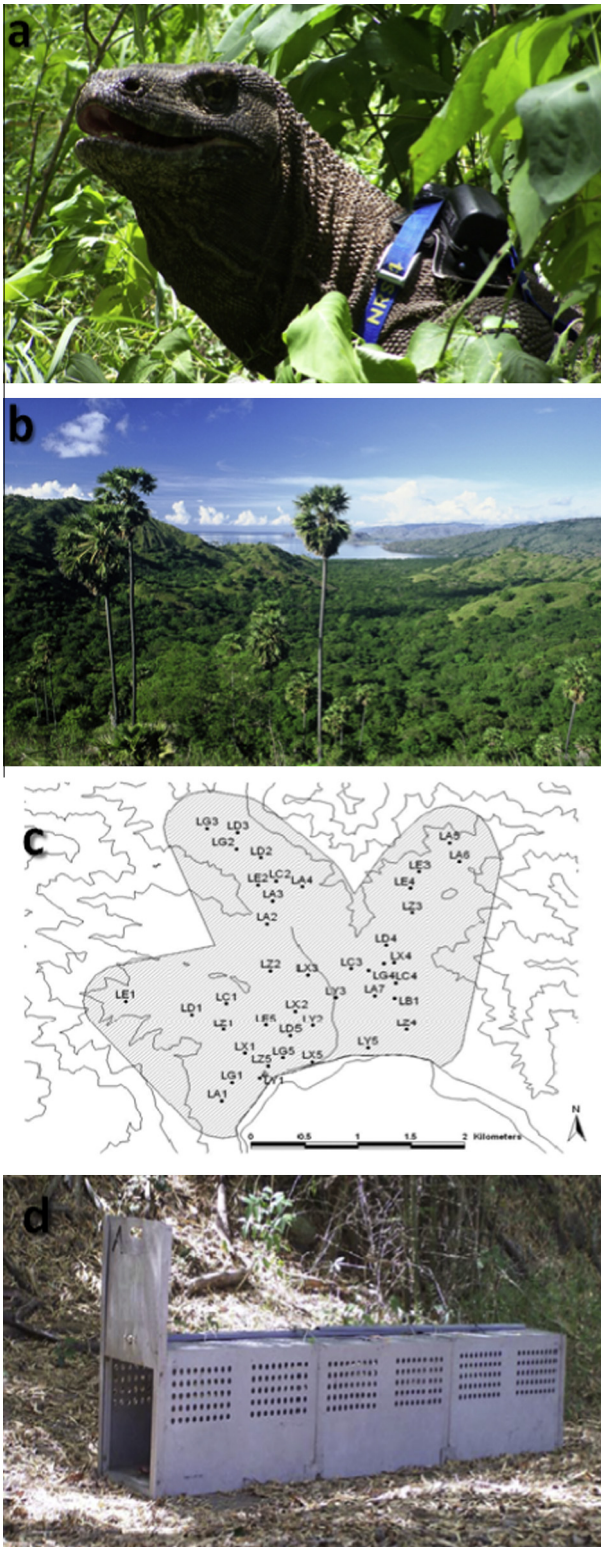
Fig. 2. Depicts (a) Komodo dragon, the target species of this study; (b) typical site specific habitat used to conduct trapping in Komodo National Park; (c) an example of a trapping grid design used to conduct mark recapture analyses; (d) and a purpose built trap (3 m length) used to capture lizards in this study.

comprised aluminium boxes (300 cm L × 50 cm H × 50 cm W) fitted with a wire activated front door (Fig. 2d). The distance between trap locations was set at approximately 500 m in order to maintain independence among traps (based on telemetry data; e.g.

Imansyah et al., 2008). Traps were positioned in shaded areas to avoid the potential overheating of trapped individuals. Fresh goat meat (≈ 0.5 kg) was used as bait to lure lizards into traps.

Field work durations varied between 8 and 14 days per site (in each year) to enable coverage of all trapping locations within each site. Field work was conducted during the dry season with each study site monitored sequentially at the same time each year. Within sites, at each trapping location, trapping occurred for three consecutive days, with each trap checked twice daily (8:00–11:00 and 14:00–17:00). The time interval between the morning and afternoon daily check for each trap was ~6 h. We also attempted to directly capture, via noose pole, any Komodo dragon that was located within a 50 m radius of each trap to increase sample size at each trapping location. Both traps and noose pole permitted capture of all Komodo dragon size classes, with the exception of hatchling and small juvenile lizards (<1.5 kg) that exhibit an arboreal life phase before exploiting terrestrial habitat use (Imansyah et al., 2008).

2.3. Lizard handling and restraint protocols

Following capture, dragons were restrained with rope and their mouths taped closed. Snout to vent length (SVL) was measured using a flexible plastic tape between the tip of the snout (i.e. juncture between upper and lower jaw) and the cloaca. The SVL recorded for each individual represented the average of two measurements that were within 0.5 cm of each other. Body mass was obtained using digital scales. Each dragon was permanently identified using a passive integrated transponder (Trovan ID100a, Microchips Australia Pty Ltd., Australia) inserted between the dermis and muscle of the upper right hind leg. In addition we painted each lizard's back with a unique paint code (using non-toxic fabric marker) to increase our ability to recognise individual lizards and make general observations of their behaviour whilst conducting our study. Processing time was usually less than 20 min before lizards were released at their point of capture.

2.4. Demographic analyses

We collated captures of individually marked lizards to develop capture histories. All analyses were conducted in Program Mark (White and Burnham, 1999). Analyses were performed on a single combined data set in which each island population was coded as an individual group.

For estimates of population growth, survival and abundance, we developed a set of candidate models for analysis, evaluated goodness-of-fit, and estimated an overdispersion parameter ($\hat{c}$) for the data set. We used an information theoretic approach to select the most parsimonious model, based on the AICc model selection criterion (lower AICc values represented better fitting models) (Burnham and Anderson, 2002). Models were then ranked using the quasi-likelihood AIC$_c$ value (QAICc) to account for the any overdispersion and their respective model weights (w) estimated to evaluate their strength of model support (Anderson et al., 1994). We used the model-averaging approach (conducted in program Mark) that incorporated model selection uncertainty for all models with substantial model support (ΔAIC < 2 from the top ranked model).

We calculated rates of finite population growth (λ) time-averaged across the study for each Komodo dragon population. Population growth rate ($\lambda = N_{t1}/N_t$) describes the per capita rate of growth of population, either as the factor by which population size increases ($\lambda > 1.0$), decreases ($\lambda < 1.0$), or is stable ($\lambda = 1.0$) per unit time (Sibly and Hone, 2002). Using the combined mark recapture data with each island identified as a group we applied the Pradel Survival and Lambda analysis (Pradel, 1996) to estimate time averaged population specific growth rates and survival estimates.

A candidate set of 18 models were assessed to evaluate average population specific growth rates and survival estimates. Here models varied in parameter combinations with survival (Φ) and recapture (p), parameters considering all combinations of time constant (.) or variable (t) time and group (i.e. island) effects. The population growth (λ) parameter was modelled as function of group (i.e. λ_g). Additionally null and global models were estimated in model comparisons. We assessed goodness-of-fit of the global model and estimated overdispersion ($\hat{c} = \chi^2/df$ using combined χ^2 values and degrees of freedom from tests 2 and 3) in Program RELEASE (Burnham et al., 1987).

Population abundance estimates were derived using the POPAN formulation of the Jolly–Seber (JS) method (Arnason and Schwarz, 1995; Schwarz and Arnason, 1996). The following parameters could be estimated from POPAN JS models: Φ (apparent survival), p (recapture probability), PENT (probability of entry into the population at each occasion) and N (size of super-population, i.e. the total number of individuals present within the population during the entire study period). This JS model is assumed to be 'open', and allows additions (births and immigration) and losses (deaths and emigration) between successive sampling occasions (Schwarz and Arnason, 1996).

A set of candidate 32 Jolly–Seber models were tested on the total data set (with each island coded as a individual group) of all captured lizards where survival (Φ), recapture (p), parameters were estimated by considering all combinations of time constant (.) or variable (t) time and group (i.e. island) effects (models). The PENT parameter was modelled as time variable or group by time combination. The N parameter was modelled as function of group (i.e. N_g). Popan produces two different estimates of population abundance the super population estimate (N) and the derived annual abundance parameter ($N_{g,t}$) for each island (g) at each annual sampling period (t). In this study we refer to the latter as we only wanted to use the final annual sampling estimate of abundance to calculate total abundance for the four islands. We assessed goodness-of-fit of the global model and estimated overdispersion using the median ($\hat{c} = 3.4$) implemented in program Mark.

Total island and Komodo National Park Komodo dragon population abundances were then estimated for each island using only the 2011/2012 (i.e. final sampling period) derived estimate of annual population abundance (plus SEM; upper and lower 95% CI). To extrapolate to island-wide abundances we divided the 2011/2012 estimates by the proportion of habitat sampled (i.e. the ratio of the effective trapping area to the total dragon specific habitat on each island). To estimate the effective trapping area for each island we summed each site's trapping grid area and inflated this with a boundary layer to consider capture of individuals moving into the trapping grid area from external habitat. The area of the boundary layer was estimated as half the radius of the mean linear distance between all individual recapture locations within a site's trapping grid (Krebs, 1999).

Next we estimated the total dragon specific habitat on each island. We felt it prudent to produce an estimate that considered variation in lizard habitat use. This was deemed necessary as our published telemetry studies (e.g. Imansyah et al., 2008; Harlow et al., 2010a,b) have clearly indicated that Komodo dragons do not occupy all island habitats equally (i.e. density is not uniform across habitats). To estimate the dragon specific habitat for each island, we first calculated the area of each of the 5 major vegetation communities using satellite imagery. We then adjusted (a penalty between 0 [absence of dragons in habitat] and 1 [maximum preferred habitat] for each vegetation community area in accordance to their respective lizard occupancy and use. The degree of habitat penalisation was based on percentage frequency of respective habitat obtained by radio telemetry of lizards (~2300 observations from 53 individuals) and visual recordings of lizard-habitat use

associations collected during routine visual surveys conducted between 2002–2013 (e.g. Imansyah et al., 2008). Poorly utilised habitat types included savannah grassland/savannah woodland, mangrove forests, and quasi cloud forest. These habitats permit some lizards to forage or transition through them, but are otherwise not considered good quality resident habitat compared to open deciduous forest and closed low altitude dense canopy forest (<300 m elevation). As a consequence, by penalising unfavourable habitats there was a considerable reduction in the total island area (uncorrected = 533.6 km^2 versus corrected = 300.3 km^2).

Finally we divided the abundance estimates by the proportion of habitat sampled on each island and calculated an island-wide Komodo dragon population abundance estimate; and by summing four islands together we produced a total estimate for Komodo dragons inhabiting Komodo National Park in 2011/2012.

3. Results

3.1. Island specific population growth rate and survival estimates

From 2003–2012, we encountered 925 individual lizards during 2002 capture events. This data was analysed using a candidate set of 16 Pradel lambda and survival models that were ranked by model fit criteria to estimate average population and survival for each island across all sampling periods (Appendix A). Several models received high model support and hence the derived estimates were calculated using weighted model averaging techniques. We adjusted our population growth and survival parameter estimates to accommodate overdispersion in the data set ($\hat{c} = 3.4$).

Time averaged population growth rates (λ) derived from model averaged estimates indicated clear differences among the four island populations (Table 1). The two large populations on Komodo ($\lambda = 0.97 \pm 0.02$; 95% CI = 0.84–1.00) and Rinca Island ($\lambda = 1.00 \pm 0.03$; 95% CI = 0.93–1.06) exhibited near-stable or stable time averaged growth rates. The estimates of population growth on the small island of Motang ($\lambda = 0.68 \pm 0.09$; 95% CI = 0.47–0.83) indicated that this population was in decline. The estimate for Kode ($\lambda = 0.97 \pm 0.15$; 95% CI = 0.16–1.00) was associated with a large margin of error making it difficult to infer the status of population growth for this island population.

Differences in average apparent survival (Φ) derived from model averaged Pradel models were also evident among the four island populations. Survival estimates were much higher for the Komodo and Rinca Komodo dragon populations compared to the small island Kode and Motang populations (Table 1).

3.2. Estimates of Komodo dragon population abundance

Abundance estimates were obtained from a candidate set of 32 open population Jolly–Seber models (POPAN) that were ranked by model fit criteria to estimate a derived population abundance for each island at each annual sampling period (Appendix B). Several models received high model support and hence the derived 2011/2012 abundance estimates were calculated using weighted

Table 1
Time averaged estimates of population growth rate (λ) and survival (Φ) for the four extant Komodo dragon populations inhabiting Komodo National Park. Standard error of the mean (SEM) and the lower and upper 95% confidence intervals (CI) are presented as measures of error.

Island	$\bar{x}\lambda \pm$ SEM	95% CI	$\bar{x}\Phi \pm$ SEM	95% CI
Komodo	1.00 ± 0.03	0.94–1.06	0.72 ± 0.05	0.61–0.80
Rinca	0.96 ± 0.03	(0.83–0.99)	0.75 ± 0.05	0.64–0.84
Motang	0.68 ± 0.1	(0.46–0.84)	0.54 ± 0.18	0.22–0.83
Kode	0.97 ± 0.16	(0.01–1)	0.52 ± 0.23	0.16–0.87

Table 2
Total island population abundance estimates for Komodo dragons in Komodo National Park in 2011–2012. Table reports data necessary to estimate total population abundance drawn from island specific population abundances within island trapping areas then corrected to total island area after considering the availability of suitable lizard habitat.

Island (area km^2)	$\bar{X}N \pm$ SEM Island (95% CI)	Island trapping area (km^2)	Corrected island area for lizard habitat (km^2)	% trapped area/ corrected island area	Extrapolated island (corrected) $N \pm$ SEM (95% CI)
Komodo (311.5)	166.8 ± 13.5 (132–179)	23.61	164.48	14.3	1166 ± 94.4 (923–1252)
Rinca (204.8)	168.2 ± 13.5 (159–212)	17.16	120.93	14.2	1185 ± 95.1 (1119–1493)
Motang (9.5)	18.7 ± 6.0 (5–34)	3.6	8.45	42.3	44 ± 14.1 (12–80)
Kode (7.8)	12.1 ± 5.8 (3–22)	1.47	6.47	22.7	53 ± 25.6 (13–97)
				Total National Park Abundance	2448 ± 229 (2067–2922)

model averaging techniques. Derived annual abundance estimates indicated clear differences among islands over the duration of the study (Appendix C). The estimates of median ($\hat{c} = 3.4$) was 1.39 ± 0.04 suggesting limited overdispersion, but nevertheless, model output was adjusted to accommodate this value.

Site specific population abundances were then used to produce extrapolated estimates of total island and National Park population abundance. These estimates were considerate of habitat suitability and hence only considered vegetation communities known to harbour resident Komodo dragons. These estimates indicated that the total island population abundances were much greater on the large islands compared to small islands due to higher densities as well as their considerably larger habitat areas (Table 2). Summing the four island population abundances produced a total population estimate for Komodo National Park of 2448 ± 229 (95% CI: 2067–2922) Komodo dragons (Table 2).

4. Discussion

Using a large scale mark recapture study; we provide the first spatiotemporal estimates of demographic rates for the Komodo dragon sampled over 10 years. Our results indicated obvious demographic differences between lizard populations on the two large islands (i.e. Komodo and Rinca) and those on the two small islands (i.e. Kode and Motang). Key differences included higher and more stable population growth for the large island populations. These differences culminated in large islands having stable population growth and higher survival. In contrast, the population on the small Motang Island appeared to be experiencing a substantial decline and lower survival relative to the large island populations. The other small island population inhabiting Kode Island was also associated with broad confidence intervals around the population growth and survival estimates making it less easy to determine the status of this population. Such findings provide important insights into the population status, prioritization and ultimately how managers could better conserve Komodo dragons in Komodo National Park.

A major challenge to management of often small island populations, especially those in decline, is to understand what processes influence demography (Caughley, 1994). For example, the apparent decline in the Motang population could be conceivably triggered by one or more processes that arise due to its geographic isolation, small island area and presumably historically small population size (Jessop et al., 2007). For example, spatial or temporal variation in food availability can induce dramatic population fluctuations on islands as a result of altered survival, fecundity and recruitment (Laurie and Brown, 1990; Grant et al., 2000). Demographic responses to food availability are often more pronounced in island systems given relatively depauperate food webs limiting forage choice. Similarly it is conceivable that inbreeding depression could negatively influence survival of Komodo dragons particularly on small isolated island populations (Frankham, 1998, 2005; Eldridge et al., 1999). For example, inbreeding could decrease population survival via higher rates of abnormal offspring or reduced clutch

sizes as observed in other small isolated populations (including reptiles) (Madsen et al., 1996; Saccheri et al., 1998; Keller and Weller, 2002). Inbreeding could also covary with other ecological pressures to exacerbate mortality (Lande, 1988; O'grady et al., 2004, 2006). Additionally an Allee effect may arise and contribute to demographic stochasticity and inbreeding again increasing extinction risk in small and especially declining island populations (Courchamp et al., 2008).

Hence limited dispersal, simple trophic dynamics, inbreeding and Allee effects could independently or additively decrease survival in small island Komodo dragon populations. Thus managers may well need to identify and then rank these different processes to best determine their relative threat and hence choose one or more courses of action to best promote population recovery. This could be done using a population viability analysis framework (e.g. Beissinger, 2002). For example, if there was clear evidence that low prey availability was responsible for poor survival then prey supplementation would seem warranted. However if evidence for inbreeding depression was found it would require translocation of individuals from genetically appropriate populations to increase genetic diversity and effective population size.

Importantly, given the apparent strength of decline in the Motang population, we encourage conservation managers to rapidly consider options for recovery of this population if this in fact deemed necessary (e.g. under legislation). However, we also acknowledge that consideration of recovery options for this population might also be influenced by the relative impact of this population's extirpation on the Park's total Komodo dragon population size which appears minimal (i.e. extirpation of the Motang population represents ~2% of the park's total population size); and that costs of management actions to conserve this small population could inadvertently compete for resources needed for other important conservation activities including ranger patrolling that ensures high quality habitat is maintained across the park.

However, even if this were true, a "do nothing" rational would be inappropriate if there was clear evidence for functional evolutionary novelty in this population for which we currently do not know. Examples of functional evolutionary novelty could include identification of novel genes (e.g. conferring immune tolerance); or evolution of different life-history attributes that could underpin large body size variation observed among different island populations (Jessop et al., 2006). If present such attributes would be worth conserving as they could maintain functional diversity important to larger populations that will need to contend with dramatic climate change consequences over the next century (Moritz, 2002).

We extrapolated site specific abundance to produce a total population abundance estimate for each island and by summing these for Komodo National Park. We estimated that 2448 ± 229 (95% CI: 2067–2922) Komodo dragons were present in Komodo National Park. This estimate is ecologically plausible, as it considers that all islands possess varying areas of poorly utilised habitat due to absence of prey (e.g. coastal mangrove forest or elevated quasi-cloud forest) or adequate shade (e.g. savannah grassland) to permit efficient thermoregulation (Harlow et al., 2010a,b).

This extrapolated abundance estimate is encouraging from a population viability perspective because species population sizes that exceed several thousand individuals are thought to confer substantially greater evolutionary resilience to extinction (Reed, 2005; Traill et al., 2010). However, it is important to remember for Komodo dragons, and indeed for many non-volant terrestrial island species, that there is a strong likelihood that different island populations do not function as metapopulations due to infrequent dispersal and gene flow (Whittaker and Fernandez-Palacios, 2007; Ciofi, 2002; Jessop et al., 2008). This means that in the advent that all island are closed to dispersal and gene flow, mangers must consider each island as independent demographic management units. Equally important is that there now consideration for how to prioritize conservation investment into these different island populations (Wilson et al., 2006). In the absence that either small island population lacks unique functional attributes that could confer broader evolutionary potential, then it would seem straightforward to prioritize the two largest islands that possess substantially larger populations as a demographic based prioritization strategy to ensure evolutionary resilience (Traill et al., 2010).

How do our results interact with current park management? At present the park management focuses its conservation activities via regular ranger patrols conducted primarily across the two large islands of Komodo and Rinca. These patrols provide habitat security and should be maintained indefinitely to help promote stable lizard populations on large islands. However, as discussed above, it will now be necessary for park managers to consider additional strategies for how to manage small island populations. A central tenant of future park managers will thus be contingent on determining the demographic and evolutionary value of small island populations to the population viability of Komodo National Park populations as a whole. This is far from a trivial task and will require the park to enhance technical capacity and collaborate with other national and international research organisations to help acquire the evidence necessary to make a well informed decision on the management value of small island populations.

5. Conclusions

This is the first comprehensive and rigorous attempt to estimate the demographic status of extant Komodo dragon populations across the species' distribution. These demographic estimates provided for Komodo National Parks are clearly essential for prioritising conservation actions within the largest protected area afforded to extant lizard populations. Our results indicate clear differences in the population demography of Komodo dragons within Komodo National Park. Currently, Komodo National Park does not differentiate among island populations from a management perspective, but in doing so increases the risk of failing to recognise inherent island specific differences necessary to optimise conservation and management of Komodo dragons. Needless to say, given the increased potential for genetic and demographic processes underpinning small population extinctions on islands, managers of Komodo National Park should consider ongoing annual demographic and genetic monitoring of all island populations (Lande, 1988; Frankham, 1998; Eldridge et al., 1999). Such information is essential to guide what strategies may be best suited to attempt to reduce population declines across the range of this species.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.01.017.

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