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The influence of tropical seasonality on breeding phenology, growth, survival and movement of a large reptile (*Varanus komodoensis*)

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Terrestrial animals in global wet-dry tropical ecosystems experience year-round high temperatures but concentrated summer rainfall. This highly seasonal precipitation is expected to have major evolutionary and ecological consequences for animals. We considered how strong seasonal patterns of rainfall might influence the environment and biological attributes of the world's largest predatory lizard, the Komodo dragon (*Varanus komodoensis*). We predicted that annual variation in rainfall or temperature may influence the seasonal phenology of vegetation, and in turn, the phenology of Komodo dragon reproduction and hatchling emergence. Similarly, seasonal environmental differences may affect Komodo dragon rates of somatic growth, body condition, survival and daily movement. Our results indicated evidence of strong seasonal variation in mean monthly rainfall and leaf area index for open deciduous forest and closed dense forest. These environmental variables were significantly correlated with female Komodo dragon nesting activity and hatchling emergence. Neither Komodo dragon somatic growth rate nor body condition exhibited seasonal differences. There was, however, increased daily movement rates of Komodo dragons during the dry season. This suggests dry season associated life-history activities or thermoregulatory efficiency might explain increased daily movement. Ultimately, the Komodo dragon showed differential sensitivities in its biology to seasonal environmental variation.

ADDITIONAL KEYWORDS: breeding phenology – growth rates – movement – reptile – survival – tropical environmental variation – *Varanus*.

INTRODUCTION

Warm year-round, the world's tropics vary considerably in their seasonal rainfall patterns (Bailey, 1983). Variation in the volume and timing of tropical rainfall patterns produces diverse ecosystems, including tropical rainforests, tropical woodlands and tropical savannahs (Bullock *et al.*, 1995). Where annual rainfall is lower in volume and concentrated over the summer (i.e. the wet-dry tropics), woodlands and savannahs are the dominant tropical ecological vegetation communities (Taylor & Tulloch, 1985; Shine & Brown, 2007). There is compelling evidence

that organisms inhabiting wet-dry tropics exhibit conspicuous biological and ecological responses in these distinct ecosystems (Monk *et al.*, 1997; Shine & Madsen, 1997; Madsen & Shine 2000a).

The highly seasonal rainfall patterns of the wet-dry tropics produce multiple direct and indirect effects that influence environmental and ecological processes faced by organisms (Shine & Madsen, 1997; Madsen & Shine, 2000a; Brown & Shine, 2006). Noticeably, organisms experience a reduction in standing water, soil moisture and humidity as the seasons transition from wet to dry (Kearney *et al.*, 2018). Reduction in water can place physiological constraints on the water and energy balance of both plants and animals (Prawiradilaga & Soedjito, 2013; Kearney *et al.*, 2018).

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When water is scarce, animals can avoid water loss by reducing periods of daily activity (e.g. aestivation) during thermally suitable times (Nagy, 1972; Christian & Conley, 1994). Similarly, seasonal reduction in water can arrest plant development and thus decrease the availability of leaves, seeds or fruit available to herbivores (Guan *et al.*, 2015). Seasonal constraints can also influence biomass and interactions of species at multiple trophic levels. Thus, transitions between the wet and dry seasons can bring about immense change in hydric and thermal microhabitats alongside biotic resource availability available to tropical animals (Brown *et al.*, 2002).

Animals inhabiting the wet-dry tropics are expected to show adaptive strategies, through phenology or phenotypic plasticity (Shine & Brown, 2007). For example, reproduction in tropical breeding species may be highly seasonal (Brown *et al.*, 2002). Seasonal reproduction can allow the emergence/birth of offspring to coincide with environmental conditions that most benefit survival. However, the dry season may pose multiple abiotic and biotic challenges that can affect animal behaviour and fitness. For example, if vegetative biomass and quality are subject to seasonal fluctuations, then animals could be expected to respond by migrating elsewhere. As if they remain resident, they could experience limited access to resources that could affect phenotypic processes (e.g. movement, growth, body condition) and fitness (e.g. survival). Similarly, because of water constraints, animals may reduce activity to limit water loss and refuge in microclimatic refugia to conserve body water and energy (Christian *et al.*, 1995)

We evaluated correlations between seasonal climatic and vegetation variation and the biology and ecology of the world's largest lizard, the Komodo dragon (*Varanus komodoensis*) (Jessop *et al.*, 2006, 2007; Purwandana *et al.*, 2016) (Fig. 1A). The Komodo dragon is an apex predator that inhabits tropical low lying coastal habitats on five islands in eastern Indonesia (Auffenberg, 1981; Sastrawan & Ciofi, 2002; Bull *et al.*, 2010; Ciofi & De Boer, 2004; Jessop et al., 2019). These islands fall under the influence of a wet-dry tropical climate that exhibits a marked environmental transition between the wet (November to April) and dry seasons (May to October) (Monk *et al.*, 1997) (Fig. 1B, C).

In this study, our first aim assessed seasonality in annual patterns of air temperature, precipitation and leaf area index (LAI) of the two key vegetation types in our study area. Knowledge of seasonal variation in the parameters would be expected to influence the phenology and ecology of Komodo dragons. Consistent with the study area's latitude, we would expect to see limited mean monthly thermal variation across the year. However, monthly rainfall would be predicted to be concentrated over the November to April period with little precipitation falling outside these months (Monk *et al.*, 1997). With the expectation that seasonal precipitation affects standing water, run-off and soil moisture availability, we would assume to see a large annual variation in the LAI, a dimensionless index related to plant biomass production, in key vegetation communities in Komodo National Park. In particular, we would expect the LAI of open deciduous forest (e.g. tree species that arrest growth and drop foliage) to vary considerably in response to seasonal water availability (Doughty & Goulden, 2008).

Second, we examined the relationships between seasonal variation in climatic and vegetation variables with annual variation in the patterns of Komodo dragon nesting behaviour and hatchling emergence. Although tropical reptiles can experience low annual variation in monthly temperatures, reproductive seasonality is nevertheless commonly reported in a diverse number of tropical taxa (Brown *et al.*, 2002; Brown & Shine, 2002b; Shine & Brown, 2007). This is because seasonal environmental variation, outside of temperature-related effects, can promote selection on the timing of reproduction and the subsequent emergence of offspring. For example, because we expect annual variation in rainfall to influence vegetation biomass (i.e. LAI) in Komodo National Park, it might influence shade and food (e.g. insects) availability and hence selection on the timing of emergence for hatchling Komodo dragons (Auffenberg, 1981). Then we might predict, given the long development period of Komodo dragon eggs (9 months), that Komodo dragons would need to commence nesting activities in the early to mid dry season to ensure that offspring emerge in the wet season when vegetation biomass is high to improve survival (Auffenberg, 1981; Jessop *et al.*, 2004a).

Third, we considered if phenotypic and fitness-related attributes of Komodo dragons were associated with seasonal environmental variation. We investigated if Komodo dragons exhibited seasonal differences in somatic growth rate, body condition, survival and capture probability. If, for example, ecological resources varied appreciably between the wet and dry seasons, then one or more life stages of Komodo dragons could exhibit differences in somatic growth, body condition and survival between the dry and wet seasons.

Fourth, we evaluated what influence seasonal variation has on the daily activity of Komodo dragons. Again, the amount of daily movement in tropical animals also appears to be strongly governed by seasonal variation in climate or resource availability (Brown *et al.*, 2002). Different movement-related strategies are used by tropical animals and can involve seasonal migration in dispersive species. In contrast, less mobile species may decrease activity (e.g. dormancy) and use microrefugia if environmental
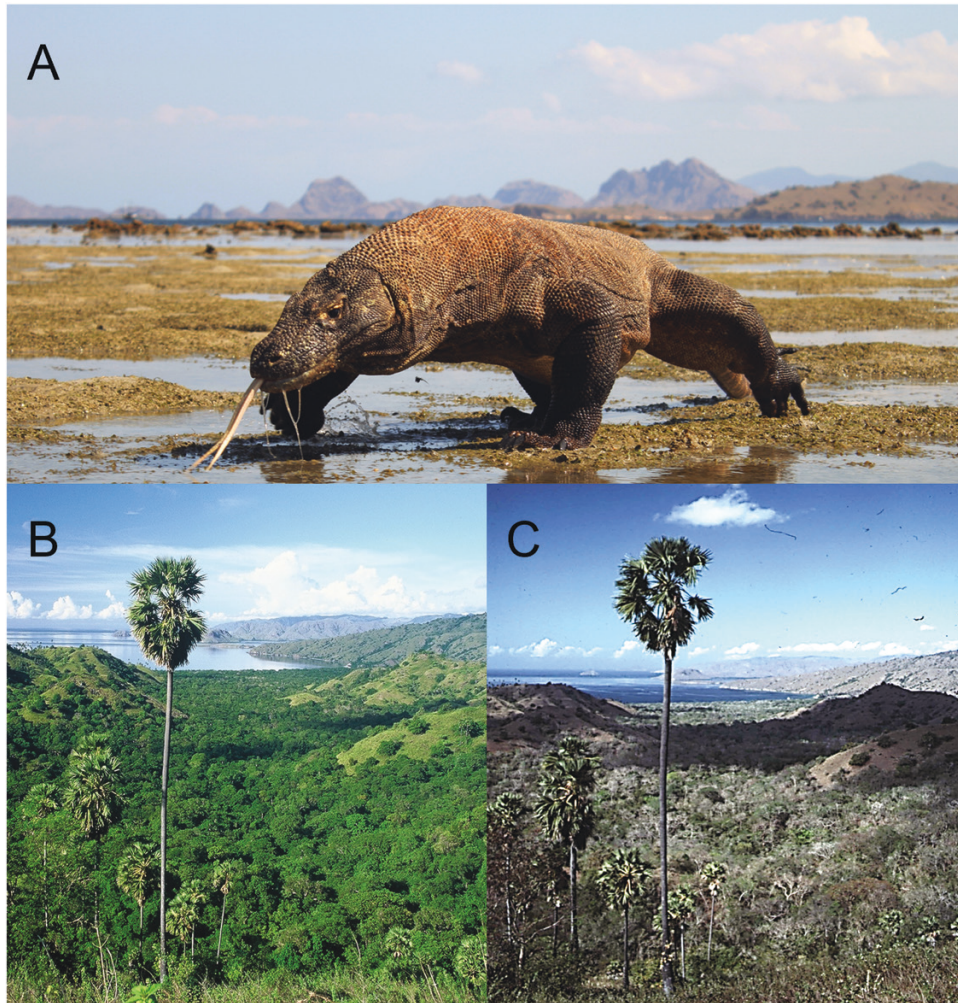
Figure 1. The Komodo dragon (*Varanus komodoensis*), the focal species of this study (A), inhabits tropical island habitats that, because of distinct seasonal patterns in annual rainfall, produce strong intra-annual environmental variation between the wet (B) and dry seasons (C).

conditions become adverse (Fleming & Hooker, 1975; Bodmer, 1990; Madsen & Shine, 1996; Brown & Shine, 2002a). To ascertain if Komodo dragons adjusted their movement behaviour in response to seasonal environmental variation, we used telemetry to measure seasonal differences in the daily movement rate of Komodo dragons between the wet and dry seasons. This approach allowed us to consider both broad and fine scale seasonal adjustments to Komodo dragon movement behaviour.

MATERIAL AND METHODS

STUDY AREA

Our study was conducted in Komodo National Park (8°35'22"S, 119°36'52"E) in eastern Indonesia. Here we utilized multiple sites located on Komodo and Rinca islands, the two largest islands that maintain the largest extant Komodo dragon populations (Purwandana *et al.*, 2014) (Supporting Information, Fig. S1). All sites were similar concerning elevation and comprised open deciduous monsoon forest interspersed with woodland or savannah grassland.

We collated monthly data for four environmental variables that represented both the area (i.e. Komodo National Park) and the duration of our study (i.e. 2002 to 2006). Monthly mean air temperature and precipitation data concordant with the study duration were obtained from the closest national weather monitoring station (Labuan Bajo Airport ~35 km from centre of study area; https://www.bmkg.go.id) and the leaf area index (LAI) was obtained from the MOD13Q1 product of the MODIS 16-Day Terra Vegetation Indices data set (Didan, 2019) via the MODISTools R package (Tuck *et al.*, 2014). LAI is a dimensionless index

related to plant biomass production and is directly proportional to gross photosynthesis; it is ultimately useful for monitoring vegetation condition. LAI has been extensively used to measure the phenology of vegetation in response to climatic variation over time and space. We obtained LAI data for two vegetation types, closed dense forest (CDF) and open deciduous forest (ODF), the two vegetation communities most widely used by Komodo dragons.

We first used generalized additive mixed models to evaluate the relationships between variation in temperature, precipitation, LAI (CDF), LAI (ODF) and the effect of month. We selected a general additive mixed-effect model (GAMM) for testing seasonal effects from these environmental parameters because of the expectation of the non-linear association between months of the year and environmental variables (Zuur, 2012). These models were fitted with a Gaussian distribution and an identity canonical link, with year fitted as a random effect. In addition, because data may be temporally dependant we added an autocorrelation regressive function (AR1) to our model to account for any potential lack of independence in the model residuals (Simpson, 2018). All models were run using the mgcv package (Wood & Wood, 2015) in the program R (R Core Team, 2016).

To further assess seasonal relationships between the month and variation in temperature, precipitation, LAI (CDF) and LAI (ODF) we used a Pearson correlation coefficient and then a cross-correlation function (CCF) to identify the strength of correlation and the extent of monthly time lags or leads between each pair of data. Both analyses were conducted in the program R.

SURVEYS TO ASSESS THE TIMING OF REPRODUCTION AND HATCHLING EMERGENCE

Between 2002 and 2006, we conducted monthly surveys from January to December to record annual patterns in female reproductive and hatchling emergence activities. These monthly surveys were repeated across eight valleys. Seven valleys were located on Komodo Island: (K1) Loh Bo, (K2) Loh Boko, (K3) Loh Lawi, (K4) Loh Liang, (K5) Loh Pinda, (K6) Loh Sebita, (K7) Loh Wenci; and the eighth valley was located at Loh Buaya (R1) on Rinca Island (Supporting Information, Fig. S1). Field methods used to identify and annually monitor Komodo dragon nesting sites are described elsewhere (Jessop *et al.*, 2004b; Purwandana *et al.*, 2020). However, briefly, in 2002, a sample of potential Komodo dragon nesting sites were located using intensive foot-based focal sampling surveys conducted across transects (Jessop *et al.*, 2004b). This method involved multiple observers (5–8) walking at intervals of approximately 25 m apart along a series of parallel transects marked with projected GPS waypoints. The length and number of transects in each valley were defined by the general topography of the valley. The purpose of these comprehensive transects was to allow us to identify a 'reference set' of 45 Komodo dragon nesting sites. Then in each year of the study, we re-checked these nesting sites in monthly surveys to describe, through repeated observations, in which month breeding females arrived at these nesting sites to prepare their nest, lay their eggs, exhibit nest guarding, and finally depart their nests to resume other activities.

Because hatchling Komodo dragons are very difficult to observe and hence estimate their emergence time, we encircled seven active Komodo dragon nests with 1 m-high aluminium fencing (~ 10 m in diameter) and covered these enclosures with netting to prevent escape. Nests were fenced between February and April in 2004 and 2005 and monitored daily to check for the emergence of hatchlings at three localities in Komodo National Park.

A general additive mixed-effect model (GAMM) with a binomial distribution and an associated logit canonical link was used to evaluate the effects of monthly precipitation, monthly mean temperature and month on the probability of occurrence for Komodo dragon nesting activities. Nest identity was included as a random effect in the model. We also used a GAMM with a Poisson distribution to test the effects of monthly precipitation, monthly mean temperature and month on the number of Komodo dragon hatchling nest emergences.

ESTIMATING GROWTH, BODY CONDITION AND SURVIVAL

From November 2002 to April 2006, we conducted eight capture-mark-recapture fieldwork events. We conducted fieldwork in the late dry season (mid-November, $N = 4$) and the late wet season (mid-April, $N = 4$). Komodo dragons were captured using either traps or a noose pole at 22 fixed trapping locations within the R1 site on Rinca Island. This number of trapping locations within this study site was determined by the total area of habitat types (e.g. open deciduous forest and savannah woodland) commonly used by Komodo dragons. These trapping methods permit the capture of individuals from small juveniles (but not hatchlings) to the largest adults (Jessop *et al.*, 2006; Imansyah *et al.*, 2008). Each Komodo dragon captured was permanently identified using a passive integrated transponder (i.e. PIT tag) (Microchips Australia Pty Ltd, Australia). A sterile needle and applicator were used to insert the PIT tag laterally between the dermis and the muscle of the upper left hind leg of each individual. The PIT tag insertion site was sealed with surgical glue (Vetbond Tissue Adhesive, 3M, USA).

To evaluate seasonality in Komodo dragon growth patterns, we measured individual growth histories from uniquely marked individuals (i.e. via PIT tag identity) (Laver *et al.*, 2012). Growth measurements (*N* = 348) were obtained from 123 (48 females: 75 males) individual Komodo dragons captured between 2002 and 2006 in the R1 valley on Rinca Island. Male and female individuals comprised a random sample drawn from all size classes present within this local population. Data recorded for each individual included head length defined as the straight line distance measured between the frontal maxilla and the occipital condyle recorded to the nearest millimetre using callipers. Snout-to-vent length (SVL) was also measured from each individual and is defined as the distance between the ventral tip of the snout to the most posterior opening of the cloacal slit. Head length was used as the metric for growth measurement as the solid structure of the head provides well-defined and consistent landmarks to improve growth measurement accuracy. As an individual's annual growth increments in head length and SVL were significantly correlated (R = 0.73, *P* < 0.001, Supporting Information, Fig. S2), we expect that head length and SVL exhibit similar growth patterns across ontogeny. To calculate seasonal effects on an individual's growth rate, we compared differences in individual growth rates recorded over the wet season (the period between November and April) with that recorded during the dry season (the period between April and November). Here an individual's growth rate for each season was estimated as the amount of head growth between consecutive wet and dry season trapping periods and then corrected for the number of days between each consecutive trapping event. A linear mixed-effect model with a Gaussian distribution and an associated identity link was used to evaluate the effects of season on Komodo dragon somatic growth rates. Individual identity was included as a random effect in the model. We also included the fixed effect of body size (i.e. the corresponding individual's SVL measurement taken at the same time as a measurement of head growth was recorded) as a covariate in our model. As it was necessary to account for the fact that somatic growth rates of Komodo dragons decrease with body size, and hence the inclusion of SVL in our model allowed us to make standardized comparisons of any seasonal differences in Komodo dragon growth rates (Laver *et al.*, 2012).

We estimated Komodo dragon body condition values using measurements (*N* = 348) again obtained from 123 individual Komodo dragons captured between 2002 and 2006 in the R1 valley on Rinca Island. Here an individual's body condition using an individual based index was estimated as the residual value derived from the ordinary least squares regression of ln-transformed mass on ln-transformed SVL. To obtain Komodo dragon body mass we measured the weight of each individual using a digital scale. The use of log-log calculated residuals reduced the underlying allometry associated with the exponential increase in reptile body mass with body length (Jessop *et al.*, 2004a). Here Komodo dragons with a positive residual are considered to have a heavier than average body mass (i.e. good condition) for their body length, and conversely, individuals with negative residuals have a less than average or poorer body condition (Madsen & Shine, 2000b; Jessop *et al.*, 2007). Log transformed residual-based based body condition indices can exhibit similar performance in inferring physical state change in animals as found in other methods including the 'scaled mass index' (Peig & Green, 2009).

A linear mixed-effect model with a Gaussian distribution and an associated identity link was used to evaluate the effects of season on Komodo dragon body condition. Individual identity was included as a random effect in the model.

Multi-state models in the program MARK were used to quantify seasonal effects on Komodo dragon survival and the probability of capture between the wet and dry seasons (Brownie *et al.*, 1993; Nichols & Kendall, 1995). Multi-state models simultaneously estimate apparent survival (Φ), resighting (P) and dispersal (ψ) for marked individuals (White & Burnham, 1999). A candidate set of nine models was assessed to evaluate survival, capture probability and state transition estimates in Komodo dragons. These models considered variation in parameter combinations influencing Φ and ψ. Multi-state models were ranked using the AIC_c value (AIC_c). We used UCARE to assess goodness-of-fit and estimate $\hat{c}$ (the overdispersion parameter) (Choquet *et al.*, 2009). Individual model weights (w_i), a measure of relative support for a model, were estimated (Burnham & Anderson, 2003). Results were adjusted for overdispersion in the program MARK using QAICc based on a $\hat{c}$ value of 1.7. We present site-specific model parameter estimates for survival and site fidelity, using the top-ranked model because it had substantial support (i.e. model weight = 0.76; Table 1) among candidate models.

SEASONAL DIFFERENCES IN DAILY MOVEMENT

We used telemetry to ascertain the effects of seasonal variation on Komodo dragon daily movement behaviour. To record the daily movement rate (m/h), we first attached very high frequency (VHF) and GPS transmitters to 22 Komodo dragons. These individuals comprised 12 immature (seven males: five females) and ten adult (six males: four females) Komodo dragons all captured from within the (K4) Loh Liang Valley on Komodo Island. We monitored Komodo dragons for a mean (± SEM) period

Table 1. Multi-state mark-recapture models of apparent survival and capture probability for Komodo dragons. Models are ranked from most to least supported, with the best model in bold. Table terms are QAIC$_c$, Quasi Akaike Information Criterion corrected for small sample size and overdispersion; ΔQAIC, the difference in value between QAIC of this model and the most parsimonious model; QAIC weights (w_i) ranking models by relative support; K, number of estimated parameters; QDEV, deviance. Model covariates included *svl* (snout-to-vent length) which is the mean body size of individuals. Φ = survival probability; P = recapture probability; Ψ = probability of transition; $_{(.)}$ = constant; (t) = time dependence; (s) = seasonal dependence

Model	QAIC$_c$	ΔQAIC	w_i	K	QDEV
Φ$_{(s)}$P$_{(s)}$Ψ$_{(.)}$	**400.06**	**0.00**	**0.76**	**5**	**389.82**
Φ$_{(.)}$PsΨ$_{(.)}$	402.57	2.52	0.21	4	394.42
Φ$_{(.)}$P$_{(t)}$Ψ$_{(.)}$	407.59	7.54	0.02	9	388.86
Φ$_{(s)}$P$_{(.)}$Ψ$_{(.)}$	409.37	9.32	0.00	4	401.21
Φ$_{(.)}$P$_{(.)}$Ψ$_{(.)}$	420.04	19.98	0.00	3	413.94
Φ$_{(.)}$P$_{(t*s)}$Ψ$_{(.)}$	423.13	23.07	0.00	16	388.86

The asterisk denotes an interaction between time and season.

of 151.7 ± 31.9 days across the year. Movement data were collected either automatically (GPS collars, Televilt, Sweden) or manually (VHF collars, AVM Instruments, USA), the latter by using Yagi antennas and VHF receivers (AVM) to locate dragons visually. We collected five fixes per dragon per day at ~3-h intervals between 06:00 and 18:00 to estimate an index of daily movement rate (i.e. minimum straight line distance). To estimate a measure of daily movement rate per hour, we divided the straight line distance calculated from total distances moved among the five daily fixes by the daily monitoring duration of 12 h. A linear mixed-effect model with a Gaussian distribution and identity link was used to evaluate the effects of season on Komodo dragon daily movement rates. Individual identity was included as a random effect in the model.

RESULTS

EVIDENCE OF SEASONAL ENVIRONMENTAL VARIATION IN THE STUDY AREA

The annual trend in air temperature (monthly mean: 25.48 °C, range: 23.60–27.40 °C) was defined by a small but significant amount of variation in the mean monthly temperature [GAMM: estimated degrees of freedom (EDF) = 7.73, F = 37.15, $P < 0.0001$; Fig. 2A]. Monthly temperatures were consistently warm during the first quarter of the year, then decreased slightly during winter (June-August) before increasing to yearly maximums in October and November. The annual trend in precipitation (monthly mean: 175.42 mm, range: 0.80–657.90 mm) was defined by significant seasonal variation with most rain falling between November and April (i.e. the wet season) and very low levels recorded between May and October (i.e. the dry season) (GAMM: EDF = 4.25, F = 9.10, $P < 0.0001$; Fig. 2B).

There was significant annual variation in the leaf area index for both open deciduous forest (ODF) (GAMM: EDF = 5.40, F = 11.34, $P < 0.0001$; Fig. 2C) and closed dense forest (CDF) (GAMM: EDF = 4.52, F = 6.91, $P < 0.0001$; Fig. 2D). Both vegetation types increased their LAI values across the wet season and peaked in April indicating strong seasonal variation in vegetation biomass and productivity across the study area.

Concerning correlations among climatic and vegetation variables, there was a significant positive correlation between monthly temperature and rainfall values (Pearson's correlation: $R^2 = 0.41$, $P < 0.01$). Neither monthly variation in temperature nor precipitation were significantly correlated with monthly LAI values for open deciduous forest and closed dense forest (all Pearson's correlations: $R^2 = < \pm 0.15$, all $P > 0.05$) (Supporting Information, Fig. S3). However, there was strong evidence that the seasonal peak in open deciduous forest LAI was most correlated with a 3-month lag ($R^2 = 0.62$; Supporting Information, Fig. S4) after peak monthly rainfall and a 5-month lag after peak monthly temperature ($R^2 = 0.62$; Supporting Information, Fig. S4). Similarly, there was strong evidence that the seasonal peak in closed dense forest LAI was most correlated with a 2-month lag ($R^2 = 0.59$; Supporting Information, Fig. S5) after peak monthly rainfall and a 4-month lag after peak monthly temperature ($R^2 = 0.52$; Supporting Information, Fig. S6).

SEASONAL EFFECTS ON REPRODUCTION AND HATCHLING EMERGENCE

Through repeated foot-based and multi-annual surveys, we routinely visited 42 reference nesting sites between 2002 and 2006. At each nest site, we made direct monthly observations of adult female Komodo dragons and noted their behavioural activities. There was evidence of a strong seasonal pattern and associated environmental
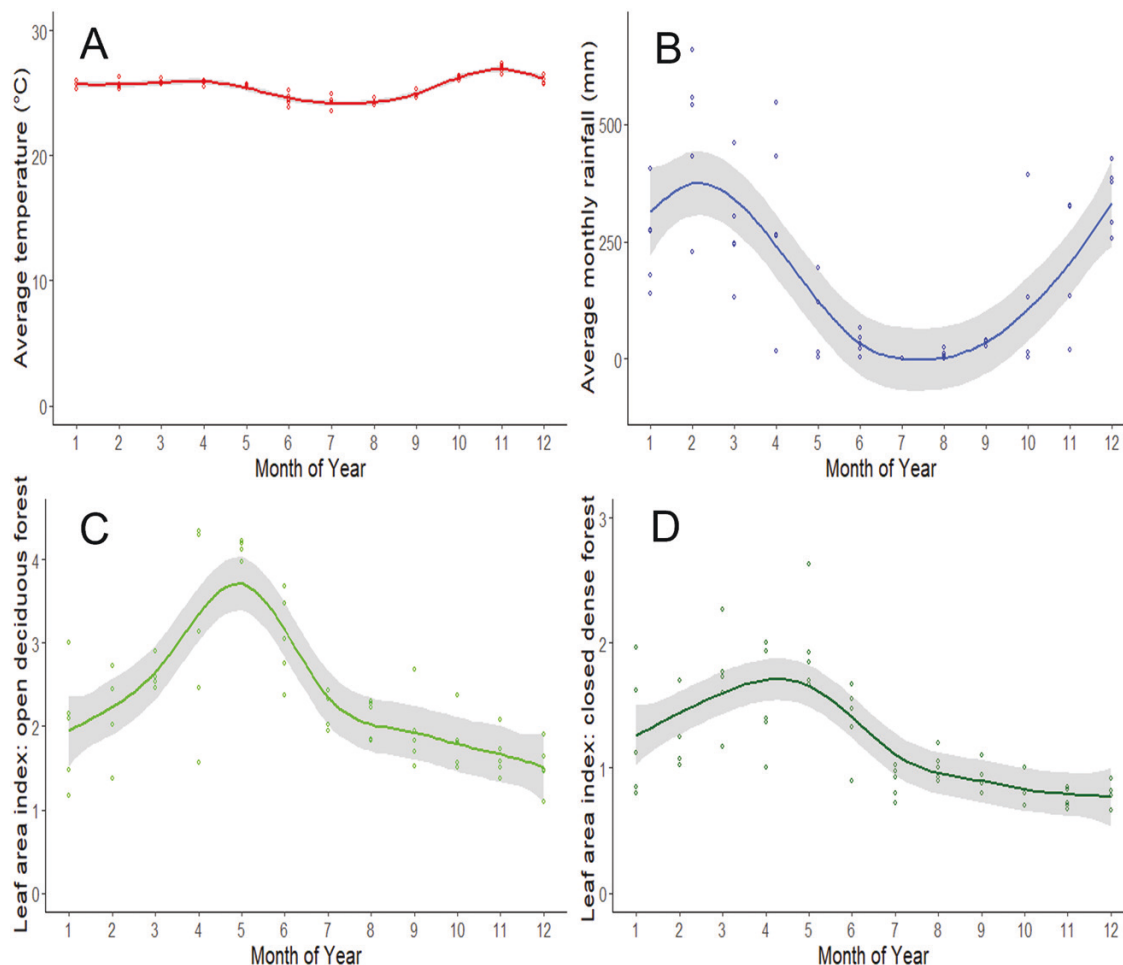
Figure 2. Annual variation in the monthly mean temperatures (A), rainfall (B), leaf area index for open deciduous forest (C) and leaf area index for closed dense forest (D) recorded in the Komodo National Park study area between 2002 and 2006.

correlations in annual nesting activities. Specifically, the probability of Komodo dragon nesting activity was significantly influenced by month (binomial GAMM, EDF = 1.99, χ^2 = 38.38, P < 0.001; Fig. 3A), by mean monthly temperature (binomial GAMM, EDF = 1.88, χ^2 = 7.353, P = 0.03; Fig. 3B), but not by monthly variation in precipitation (GAMM, EDF = 1.00, χ^2 = 0.25, P = 0.62; Fig. 3C). Here it was evident that breeding females arrived at nesting sites in late July through to August (i.e. mid-dry season). Females then began nest preparation over an ~ 2-week period in August that culminated in oviposition of their eggs into deep chambers. Females were observed to remain at the nests after oviposition and exhibited nest guarding from September until December, after which time females departed their nests to resume non-reproductive activities.

Through the fencing of a small sample of active nests, we were also able to observe the date of the emergence of seven clutches of Komodo dragon hatchlings. All hatchling emergences took place over

an approximately 4-week duration from mid-February (e.g. 14 February, 18 February) to mid-March (4 March, 12 March, 15 March, 19 March). The number of hatchling nest emergences was significantly correlated with the month of the year (GAMM, EDF = 6.36, F = 10.40, P < 0.001; Fig. 4A), monthly variation in precipitation (GAMM, EDF = 2.42, F = 2.75, P < 0.001; Fig. 4B), monthly variation in the mean combined ODF/CDF leaf area index (GAMM, EDF = 2.42, F = 2.75, P < 0.001; Fig. 4C), but not mean monthly temperature (GAMM, EDF = 2.09, χ^2 = 7.353, P = 0.005; Fig. 4D).

SEASONAL EFFECTS ON SOMATIC GROWTH

Komodo dragon somatic growth rates declined with increasing body size (GLMM, F = 12.57, d.f. = 117, P = 0.001, natural log-scale beta coefficient β = -0.004 ± 0.002; Fig. 5A). However, there was no effect of season (GLMM, F = 0.93, d.f. = 117, P = 0.337) or an interaction between season and body size (GLMM,
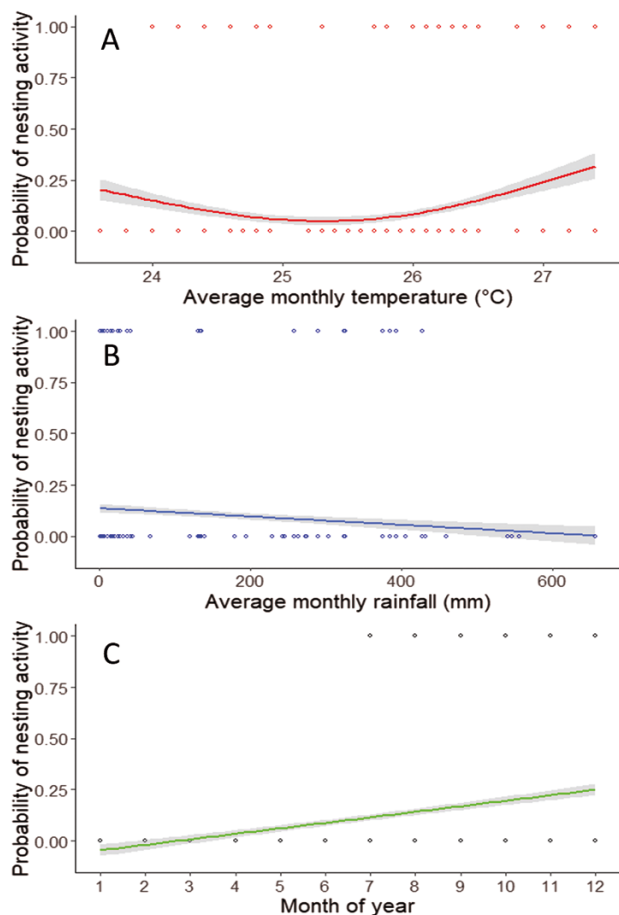
Figure 3. Relationships between annual variation in the monthly mean temperatures (A), rainfall (B) and month (C) and the occurrence of Komodo dragon nesting activities.

F = 0.924, d.f. = 117, P = 0.338) on growth rates. This result suggested that Komodo dragons were capable of growing at similar rates between the wet and dry seasons (Fig. 5B).

SEASONAL EFFECTS ON BODY CONDITION

The body condition of Komodo dragons was significantly influenced by the effect of the season (GLMM, F = 0.15, d.f. = 357, P = 0.90), body size (GLMM, F = 0.19, d.f. = 357, P = 0.89) or their interaction (GLMM, F = 0.002, d.f. = 357, P = 0.96). This result suggested that Komodo dragons maintained similar body condition across the year independent of seasonal variation in their environment.

SEASONAL EFFECTS ON APPARENT SURVIVAL AND CAPTURE PROBABILITY

The top ranked model indicated that there were significant seasonal effects on Komodo dragon survival

and probability of detection but not site fidelity (Table 1). Mean estimates of survival appeared higher during the dry than the wet season, but this was associated with more uncertainty (i.e. 95% confidence intervals) than the lower mean wet season survival estimate (Fig. 6). There were also substantial seasonal differences in capture probability, with the capacity to recapture animals during the dry season lower than the wet season.

SEASONAL EFFECTS ON MOVEMENT RATE

There was evidence for significant effects of season, body size and their interaction on hourly movement rates of Komodo dragons (Fig. 7). Komodo dragons moved significantly more during the dry season (188.96 ± 6.22 m/h) than the wet season (143.76 ± 11.20 m/h) (GLMM; F = 10.542; P = 0.001). Body size had a significant negative effect on Komodo dragon movement rates [β = -3.13 ± 0.59 (natural log-scale beta coefficient); GLMM, F = 130.81; P < 0.001]. Similarly, the significant interaction between season and body size indicated that the effect of body size on the daily movement rate was greater in the dry season than compared to the wet season decreased (β = -1.32 ± 0.66; GLMM, F = 3.96; P = 0.047).

There was evidence for strong seasonality in female reproductive cycles with nesting activities beginning in late July to early August and concluding in December. This pattern is consistent with some reptiles, including varanid lizards (e.g. *Varanus glauerti* and *Varanus glebopalma*), in northern Australia that occur in a similar wet-dry tropical environment (James & Shine, 1985; Brown & Shine, 2002b; Brown *et al.*, 2002). For example, Thompson *et al.* (1999) reported that female *Varanus tristis* laid their eggs in mid to late October. This timing of oviposition is similar to Komodo dragons, which lay eggs in late August or early September. However, because of the longer developmental period (9 months) of Komodo dragon eggs, their reproductive activities must begin earlier (Murphy *et al.*, 2015).

Strong seasonality in reptile reproductive activities could arise because it favours optimal incubation and egg survival or because it allows for the emergence of offspring at a specific time of the year that again improves survival (Whittier & Crews, 1987; Brown & Shine, 2006). Like some other wet-dry tropical varanids, Komodo dragons also oviposit eggs into deep chambers (> 1.5 m below the ground) (Jessop *et al.*, 2004b; Doody *et al.*, 2014, 2017). At such depths, Komodo dragon eggs are likely to experience an environment that is thermally benign and maintains high soil moisture and thus favour conditions for successful offspring development and survival (Doody *et al.*, 2014). Similarly, as explained below, females are unlikely to suffer substantial seasonal variation
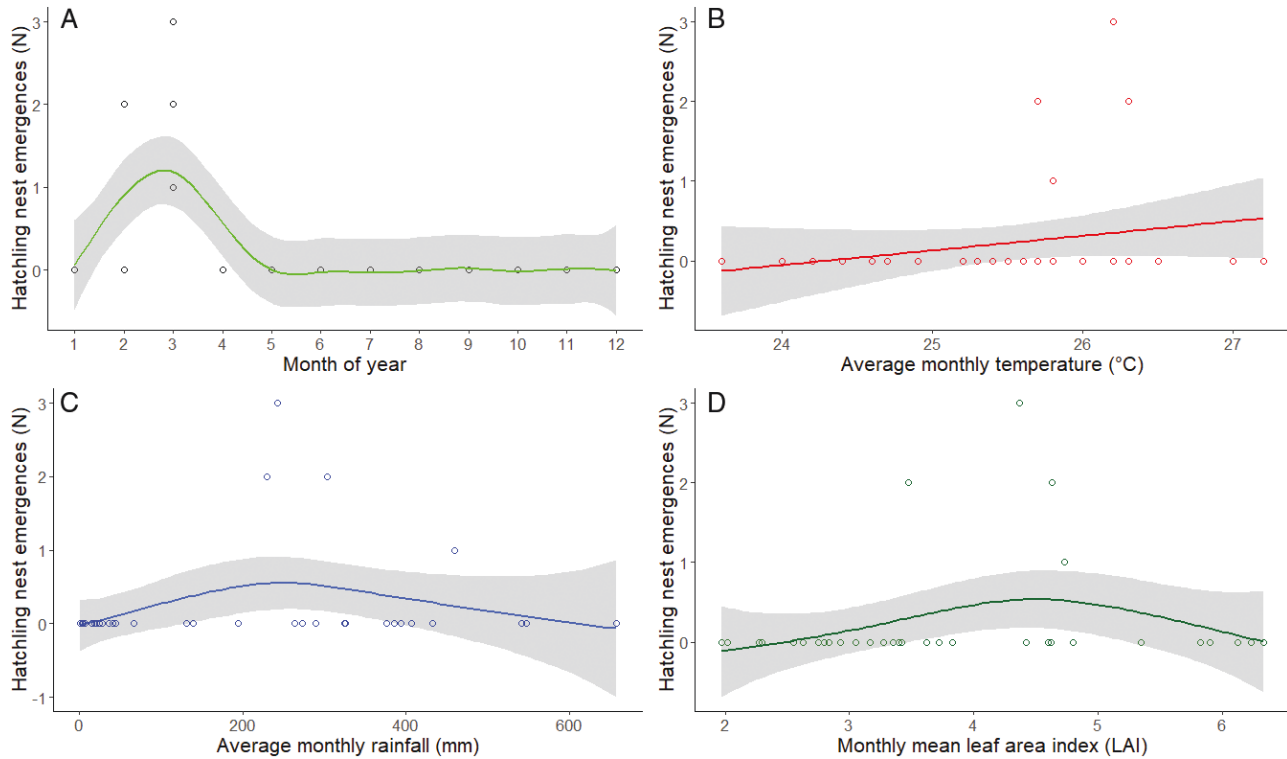
Figure 4. Relationships between annual variation in the month (A), monthly mean rainfall (B), leaf area index (C), monthly mean temperature (D) and Komodo dragon hatchling nest emergences.

in food quantity or quality and thus incur seasonal energetic constraints, which in other reptiles can strongly influence the timing of seasonal reproductive activities (Whittier & Crews, 1987; Rubenstein & Wikelski, 2003). Therefore seasonal environmental variation may impose less selection on egg development and survival, but instead, require females to ensure synchronization between the timing of hatchling emergence and specific environmental conditions to increase offspring survival (Brown & Shine, 2006; Shine & Brown, 2007; DeNardo et al., 2018).

Komodo dragon hatchlings, albeit a small sample size, emerged towards the end of the wet season in March and April. Several hypotheses are potentially relevant in explaining seasonality in hatchling emergence (Brown & Shine, 2006). For example, highly synchronized hatchling emergence in both time and space can occur to reduce predation risk (i.e. predator swamping) (Janzen, 1967; Furey et al., 2016). We discount predation risk as a significant selective force on seasonal hatchling emergence because of the absence of communal or high-density nesting activities displayed by female komodo dragons (Jessop et al., 2004b). Instead, we propose that hatchling emergence during the late wet season coincides with a distinct resource pulse driven by substantive vegetative growth and productivity that would increase the invertebrate prey biomass consumed by hatchling

Komodo dragons (Auffenberg, 1981; Imansyah et al., 2008). Across taxa, the phenology of offspring emergence is commonly synchronized by seasonal resource pulses to improve survival (Van Noordwijk et al., 1995; Møller et al., 2006; Lehikoinen et al., 2011).

Temporal and spatial variation in abiotic and biotic resources, alongside population density, can significantly affect somatic growth rates and body condition of animals (Dunham, 1978; Ballinger & Congdon, 1980; Andrews, 1982; Madsen & Shine, 2000b; Laver et al., 2012). However, our study did not detect a seasonal effect on the growth rates or body condition of Komodo dragons. This result may suggest that vertebrate prey availability is not subject to strong seasonal variation because spatial variation in prey availability is correlated with differences in Komodo dragon growth rate and survival (Laver et al., 2012; Purwandana et al., 2016). However, we lack specific information to support this claim as most reports on trends in Komodo dragon prey abundance have been investigated at annual intervals (Ariefiandy et al., 2013, 2016). Nevertheless, patterns of yearly variation in prey abundance are also relatively weak, supporting the notion that temporal, unlike spatial, sources of environmental variation may have little influence over Komodo dragon growth and body condition (Laver et al., 2012). However, because growth rates represent
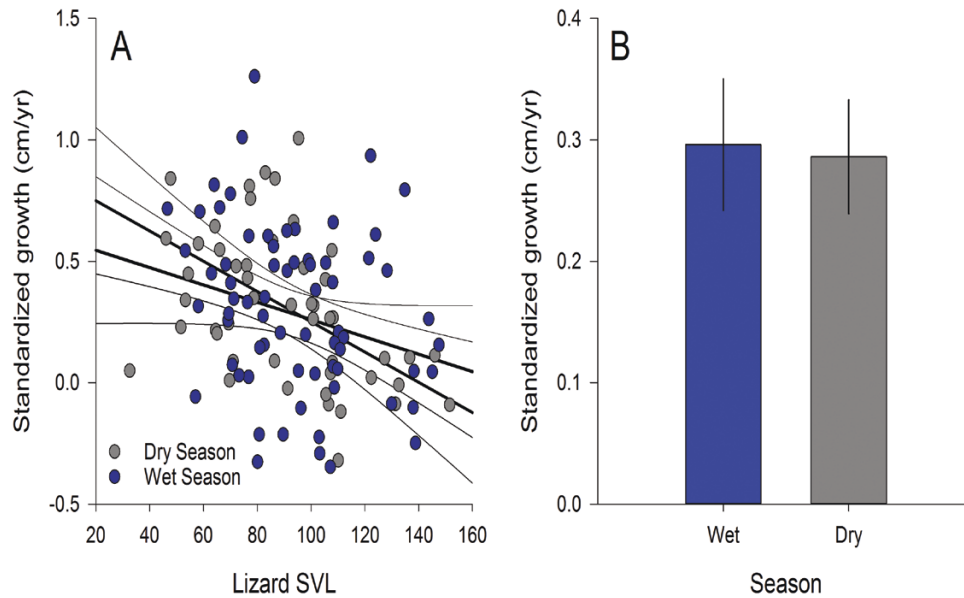
Figure 5. The relationships between body size and seasonal effects on Komodo dragon standardized somatic growth rates. The scatter plot (A) depicts the relationship between the Komodo dragon body length (SVL) and individual growth rates in the wet and dry season, respectively. The mean predicted seasonal relationships between Komodo dragon body size and growth are represented by the linear regression lines and associated standard errors. The bar graph (B) indicates the mean growth rate and the error bars report the standard error of the mean for somatic growth rates in each season.
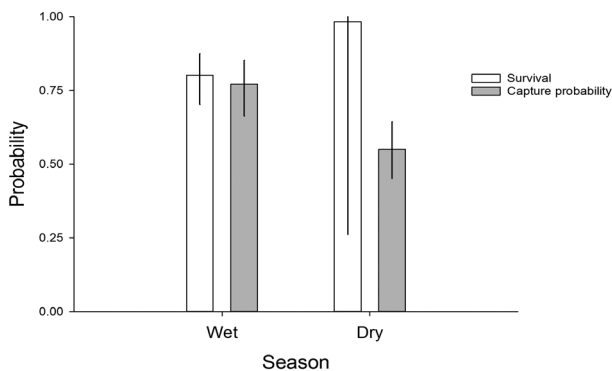

Figure 6. The relationships between seasonal effects on Komodo dragon apparent survival and capture probability. The bar graph indicates the mean estimate and the error bars report the standard error of the mean.

Figure 7. The relationships between seasonal effects on Komodo dragon hourly movement rate. The bar graph indicates the mean estimate and the error bars report the standard error of the mean.

complex organismal trade-offs reflecting energy allocation partitioned among growth, maintenance, reproduction and associated daily activities, we cannot discount that other processes further contribute to reduced seasonal variation in either measure (Stearns, 1989). For example, seasonal differences in daily activity or the efficiency of thermoregulation could alter reptile energy budgets that influence energy allocated to the maintenance of growth and body condition across the year (Christian & Bedford, 1995; Christian *et al.*, 1995; Sears & Angilletta Jr, 2015).
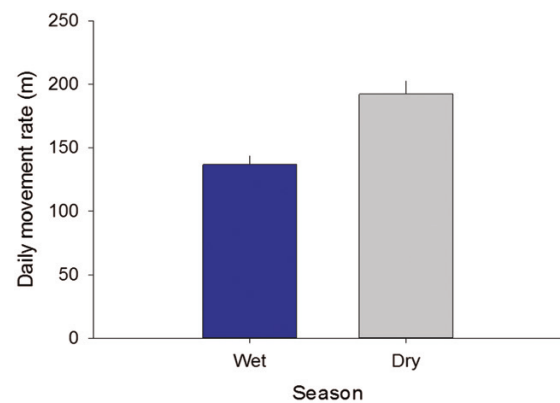
Seasonally dependent processes may influence the survival of animals, including variation in climate, life-history and ecological interactions (e.g. disease) (Gaillard *et al.*, 2000; Sæther & Bakke, 2000; Lok *et al.*, 2013; Hoye *et al.*, 2016). In this study, there was some evidence that Komodo dragon survival was higher during the dry season. Komodo dragons are known to exhibit substantial spatial variation in survival rates. However, we are cautious about the significance of any seasonal effect on Komodo dragon survival for multiple

reasons. First, the dry season survival estimate was associated with high variance, indicating a lot of uncertainty in this estimate (Nichols *et al.*, 1984; Williams *et al.*, 2002). However, the absence of seasonal effects on growth rates and body condition, which are important phenotypic signatures of animal health and wellbeing, further indicates that any seasonal impact on survival is not due to seasonal resource constraints. Nevertheless, further research should be conducted to assess if other seasonal processes (e.g. disease) could explain the lower wet season survival. For example, malaria can induce seasonal mortality in some lizard populations (Schall, 1990), but the potential mortality of this and other pathogens currently remains unknown for Komodo dragons.

Robust estimates of seasonal differences in capture probability indicated that in the dry season, Komodo dragons had a reduced recapture rate compared to the wet season. Such responses could arise for many reasons (Willson *et al.*, 2011). For example, if Komodo dragons seasonally migrated out of the study area during the dry season, we would expect recapture rates to decrease. Indeed, such responses have been observed in other tropical reptiles, including water pythons (*Liasis fuscus*) (Madsen & Shine, 1996). However, Komodo dragons appear to exhibit extraordinary levels of site fidelity with little evidence of movement out of natal areas (Jessop *et al.*, 2018). Instead, it is possible that seasonal differences in daily movement rates or other activities (e.g. behavioural thermoregulation) could reduce dry season recapture rates (Willson *et al.*, 2011).

Daily movement rates of Komodo dragons significantly increased during the dry season compared to the wet season. Seasonal differences in the daily movement rates are also reported for several varanid species (e.g. *Varanus gouldii* and *Varanus panoptes*) inhabiting wet-dry tropical and sub-tropical regions (Christian *et al.*, 1995; Phillips, 1995; Thompson *et al.*, 1999). Varanids can both increase or decrease daily movement rates during the dry season to satisfy life-history or climatic influences. For example, in some varanids, adult males increase daily movement rates to facilitate dry season reproductive activities (e.g. mate searching) (Phillips, 1995). Adult male Komodo dragons also appear to increase daily movements during the early dry season, a period known to coincide with their mate-searching and mating activities (Auffenberg, 1981). Reduced cloud cover during the dry season may allow Komodo dragons to more effectively thermoregulate (i.e. reduced basking time) and increase daily activity and movement relative to the overcast and rainy wet season (Harlow *et al.*, 2010a, b). This increased dry season daily movement rate contrasts with some varanid species in Australia's non-coastal wet-dry tropics, including *V. gouldii* and *V. panoptes*,

that substantially reduce their daily activity to avoid the harsh dry season conditions (Christian *et al.*, 1995).

We recognize that several of our measures (e.g. growth, body condition, movement and survival) were sourced from individuals within a single site from within the larger study area. Thus, this study design may limit our capacity to generalize or consider how site-related effects interact with seasonal environmental influences to affect Komodo dragon biology and ecology. However, our previously published work on Komodo dragon somatic growth rates, population growth and annual survival measured at eight sites on the two largest islands in Komodo National Park indicates little evidence of strong site-specific effects (Laver *et al.*, 2012; Purwandana *et al.*, 2014; Purwandana *et al.*, 2015).

Our results indicate that seasonality in their wet-dry tropical environment is associated with variable effects on key aspects of Komodo dragon biology and ecology. Reproduction, hatchling emergence, recapture probability and daily movement rates appeared to be influenced by seasonal environmental variation. In contrast, growth, body condition and most-likely survival were not. These differences indicate the complexity of interactions between the environment and Komodo dragon biology and ecology. Importantly, given that seasonal variation in environmental conditions is likely to be influenced by climate change, we advocate that understanding the consequences for key fitness-related attributes, including reproduction and hatchling emergence, now be investigated to aid the conservation of this iconic species.

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DATA AVAILABILITY

The data underlying this work are available on request to the corresponding author.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. The study was conducted at eight sites on Komodo (K prefixed sites) and Rinca islands (R prefixed sites) located in Komodo National Park in eastern Indonesia. Our study conducted research in seven valleys on Komodo Island: (K1) Loh Bo, (K2) Loh Boko, (K3) Loh Lawi, (K4) Loh Liang, (K5) Loh Pinda, (K6) Loh Sebita, (K7) Loh Wenci; and at an eighth valley comprising Loh Buaya (R1) on Rinca Island

Figure S2. The relationship between annual growth increment measurements for snout-to-vent length (SVL) and head length obtained from Komodo dragons (N = 676 measurements obtained from 372 individuals) of all size classes from eight localities in Komodo National Park. The black line represents the predicted relationship between SVL and head length annual growth increments, and the blues lines are the associated upper and lower 95% confidence interval lines. The relationship between annual SVL increment and the head length was highly significant (GLMM: $F_{1,674}$ = 69.7, P < 0.001, R = 0.73).

Figure S3. Pairwise correlation plots and summary statistics for comparisons between mean monthly variation in daily temperature (avg.mth.Temp), precipitation (avg.mth.Precip) and the leaf area index for closed dense forest (avg.mth.LAI.CDF) and open deciduous forest (avg.mth.LAI.ODF). The numbers report the pairwise correlation coefficients and the asterisks denote the level of significance (no asterisks = P > 0.05, * = P < 0.05, ** = P < 0.01 and *** = P < 0.001) arising from two-tailed Pearson correlation tests.

Figure S4. Lagged correlation plots depicting the strength of cross-correlation between sequential monthly lags in daily temperature (avgmthtemp) and open deciduous forest (avg.mth.LAI.ODF) leaf area index. The numbers report the pairwise cross-correlation coefficients and the lines are the predicted LOESS regression between each variable.

Figure S5. Lagged correlation plots depicting the strength of correlation between sequential monthly lags in precipitation (avg.mth.Precip) and closed dense forest (avg.mth.LAI.CDF) leaf area index. The numbers report the pairwise cross-correlation coefficients and the lines are the predicted LOESS regression between each variable.

Figure S6. Lagged correlation plots depicting the strength of correlation between sequential monthly lags in daily temperature (avg.mth.Temp) and closed dense forest (avg.mth.LAI.CDF) leaf area index. The numbers report the pairwise cross-correlation coefficients and the lines are the predicted LOESS regression between each variable.