# Temporal and spatial dynamics of insular Rusa deer and wild pig populations in Komodo National Park

Achmad Ariefiandy, David M. Forsyth,* Deni Purwandana, Jeri Imansyah, Claudio Ciofi, Heru Rudiharto, Aganto Seno, and Tim S. Jessop

*Komodo Survival Program, Jl. TegalWangi 2, Gg. Kubusaba No. 11, Denpasar, Bali 80223, Indonesia (AA, DP, JI)*
*School of BioSciences, The University of Melbourne, Parkville, Victoria 3010, Australia (DMF, TSJ)*
*Vertebrate Pest Research Unit, Department of Primary Industries, 1447 Forest Road, Orange, New South Wales 2800, Australia (DMF)*
*Department of Biology, University of Florence, Via Madonna del Piano 6, Sesto Fiorentino 50019, Italy (CC)*
*Komodo National Park, Labuan Bajo, Flores 86554, Indonesia (HR, AS)*
*Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Victoria 3220, Australia (TSJ)*

* Correspondent: dave.forsyth@dpi.nsw.gov.au

The roles of density-dependent and density-independent factors in the dynamics of tropical large herbivore populations are poorly understood. Understanding these dynamics is particularly important if the herbivore is prey for an apex predator of conservation concern because a decline in the prey could cause the predator to decline. We tested hypotheses about the roles of density-dependent and density-independent factors in the dynamics of 2 tropical ungulates, Rusa deer (*Rusa timorensis*) and wild pigs (*Sus scrofa*), in Komodo National Park, eastern Indonesia. We counted the dung of Rusa deer and wild pigs (a validated index of abundance for these 2 species) along permanently marked transects at 10 sites over 4 islands annually during 2003–2014 to estimate ungulate abundance. Ungulates were much more abundant on the 2 larger islands compared with the 2 smaller islands, with wild pig dung completely absent from the latter. During our 12-year study, Rusa deer abundance declined slightly on Nusa Kode and Rinca islands, did not change on Komodo Island, and increased on Gili Motang Island. There was a decline in abundance of wild pigs on Komodo Island and an increase on Rinca Island. Annual variation in population growth rate was strongly density-dependent and island-specific for both species, with annual rainfall and vegetation composition being relatively unimportant. Population growth rates of Rusa deer exhibited spatial synchrony, with synchrony declining with increasing intersite distance. Our findings confirm the importance of density dependence in the dynamics of tropical large herbivore populations. However, the strength of density dependence varied between species and spatially. Declines of Rusa deer and wild pigs on the larger 2 islands, which are strongholds of the Komodo dragon, are cause for concern. Continued monitoring of ungulate populations is critical for the conservation of Komodo dragon populations in Komodo National Park.

Peran faktor-faktor yang terpengaruh kepadatan (*density-dependent*) dan faktor-faktor yang tidak terpengaruh kepadatan (*density-independent*) dalam dinamika populasi herbivora besar di daerah tropis masih sangat kurang dipahami. Pemahaman terhadap dinamika populasi satwa herbivora sangatlah penting ketika satwa tersebut merupakan satwa mangsa dari predator puncak terutama bagi kelangsungan upaya konservasi satwa predator tersebut. Penurunan populasi mangsa dapat menyebabkan penurunan populasi satwa predatornya. Kami menguji hipotesis mengenai peranan faktor-faktor yang terpengaruh kepadatan dan faktor-faktor yang tidak terpengaruh kepadatan pada dinamika populasi dua satwa mangsa ungulata tropis, yaitu rusa (*Rusa timorensis*) dan babi hutan (*Sus scrofa*) di dalam kawasan Taman Nasional Komodo, Indonesia bagian timur. Estimasi kelimpahan ungulata ini dilakukan dengan cara menghitung kotoran rusa dan babi hutan (indeks kelimpahan yang telah divalidasi pada kedua spesies tersebut) di sepanjang transek permanen pada 10 lokasi penelitian di empat pulau setiap tahunnya dalam kurun waktu tahun 2003–2014. Kelimpahan kedua satwa ungulata tersebut jauh lebih tinggi di dua pulau besar dibandingkan di dua pulau kecil lainnya, di mana pada kedua pulau kecil, kotoran babi hutan bahkan sama

sekali tidak dijumpai. Dalam kurun waktu 12 tahun penelitian ini, kelimpahan rusa sedikit menurun di Pulau Nusa Kode dan Pulau Rinca, namun stabil di Pulau Komodo dan meningkat di Pulau Gili Motang. Penurunan kelimpahan babi hutan terpantau di Pulau Komodo, sebaliknya di Pulau Rinca populasinya meningkat. Variasi tahunan laju pertambahan jumlah populasi satwa ungulata tersebut sangat dipengaruhi oleh faktor kepadatannya meskipun untuk kedua spesies ungulata ini sangat spesifik pada setiap pulau, di mana curah hujan tahunan dan komposisi vegetasi relatif tidak memberikan pengaruh. Laju pertumbuhan populasi rusa menunjukkan adanya perbedaan berdasarkan lokasi, dengan kecenderungan penurunan seiring dengan bertambahnya jarak antar lokasi penelitian. Hasil penelitian membuktikan pentingnya faktor yang tergantung kepadatan dalam dinamika populasi herbivora besar di daerah tropis, meskipun terdapat variasi antar spesies dan lokasi. Penurunan populasi ungulata di kedua pulau besar yang menjadi habitat utama biawak komodo ini menjadi hal penting untuk diperhatikan. Pemantauan secara kontinyu terhadap populasi satwa ungulata sangatlah penting bagi kelangsungan kegiatan konservasi biawak Komodo di Taman Nasional Komodo.

Ungulates are keystone species in many ecosystems, and changes in their abundance can affect adjacent trophic levels (Hobbs 1996; Sinclair et al. 2003; Karanth et al. 2004). For example, overharvesting and habitat loss can reduce ungulate prey populations such that apex predators decline (Ramakrishnan et al. 1999; Winterbach et al. 2013). Conversely, overabundant ungulate populations can alter vegetation composition and soil properties (Hobbs 1996; Côté et al. 2004). The dynamics of ungulate populations can, therefore, alter the status of threatened species and ecosystems (Ramakrishnan et al. 1999).

Density-dependent (or "intrinsic") processes affect the survival and reproduction of individuals and are common in ungulate populations (Fowler 1981; McCullough 1999; Coulson et al. 2000; Bonenfant et al. 2009). There is debate, however, about the relative importance of density-dependent and density-independent processes (Bonenfant et al. 2009). Rainfall, through its effects on vegetation, can be an important density-independent factor for ungulate populations (Choquenot 1998; Ogutu and Owen-Smith 2003; Dunham et al. 2004; Shaw et al. 2012).

The dynamics of a population also can be influenced by surrounding populations of the same species (Royama 1992; Koenig 1999). Populations may be linked directly by dispersal (Ranta et al. 1995) or indirectly by environmental factors synchronizing their dynamics (Grenfell et al. 1998). Whereas synchronous dynamics have commonly been observed in small mammal populations (e.g., Bjørnstad et al. 1999), the only demonstration in ungulates is in 2 populations of Soay sheep (*Ovis aries*) in the St Kilda Archipelago (Grenfell et al. 1998).

Evaluating ungulate population dynamics requires long-term data (Grenfell et al. 1998; Forsyth and Caley 2006). Most long-term studies of ungulate populations have been conducted in the temperate zone (Gaillard et al. 1998, 2000; Bonenfant et al. 2009). Knowledge of the dynamics of ungulate populations in tropical environments is, therefore, limited, particularly near the equator. The paucity of studies evaluating synchrony among ungulate populations likely reflects the logistical challenges of simultaneously monitoring populations at appropriate spatial scales. Here, we use long-term data to evaluate support for hypotheses explaining temporal and spatial patterns of population abundance, growth, and synchrony in 2 widespread tropical ungulate species, Rusa deer (*Rusa timorensis*) and wild pigs (*Sus scrofa*), at 10 sites on 4 islands in Komodo National Park, eastern Indonesia (8°35′22″S, 119°36′52″E). Komodo National Park is a World Heritage Site that is critical for the conservation of ungulates and the iconic and threatened Komodo dragon (*Varanus komodoensis*). Ungulates are primary prey for the Komodo dragon (Auffenberg 1981), and we have previously shown that spatial variation in the density of Rusa deer (hereafter "Rusa"), wild pigs ("pig"), and water buffalo (*Bubalus bubalis*) can have prodigious effects on the phenotypic and demographic processes of Komodo dragons (Jessop et al. 2006, 2007; Purwandana et al. 2014, 2015). We first tested the hypothesis that Rusa and pig population growth rates would increase with decreasing density in the preceding year(s) (i.e., exhibit density dependence; $H_1$, hypothesis 1). We also expected Rusa and pig abundances to vary with 2 density-independent factors—rainfall and vegetation composition ($H_2$, hypothesis 2). Finally, we tested the prediction that Rusa populations and pig populations would exhibit synchronous dynamics ($H_3$, hypothesis 3).

## METHODS

*Study areas.*—Nusa Tengarra Timor in eastern Indonesia comprises the major islands of Sumbawa, Flores, Timor, and Sumba, and hundreds of smaller isles (Monk et al. 1997). A highly seasonal wet–dry cycle is dominant in the region, and there is considerable annual rainfall variation during the short summer monsoon season, which is followed by a long and hot dry season (Monk et al. 1997; Supplementary Data SD1). This climate promotes relatively dry vegetation communities, including open deciduous forest and savannah grassland (Monk et al. 1997).

We performed our study at 10 sites distributed over 4 islands within Komodo National Park (Fig. 1): Komodo (343 km²; 4 sites), Rinca (232 km²; 4 sites), Gili Motang (13.4 km²; 1 site), and Nusa Kode (11.0 km²; 1 site). Study site selection was informed primarily by the need to establish long-term monitoring sites to permit detailed and representative ecological studies
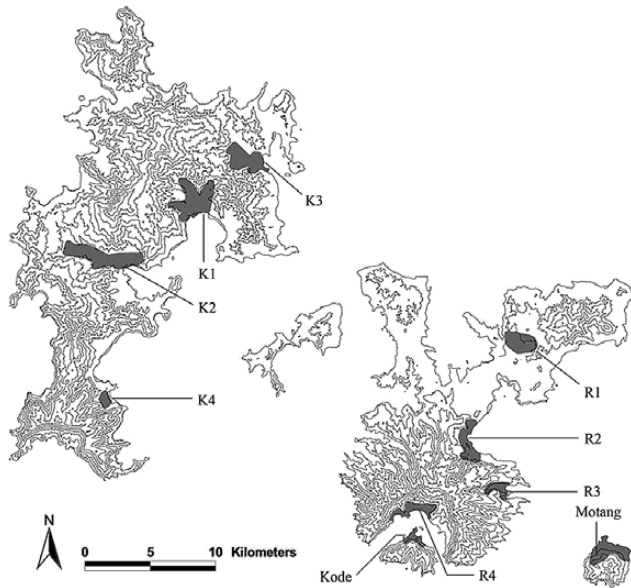
**Fig. 1.**—Location of the 10 study sites on 4 islands in Komodo National Park, eastern Indonesia. The shaded areas indicate the study sites in which field work was conducted. The Komodo Island sites are K1 (Loh Liang), K2 (Loh Lawi), K3 (Loh Sebita), and K4 (Loh Wau); the Rinca Island sites are R1 (Loh Buaya), R2 (Loh Baru), R3 (Loh Tonkir), and R4 (Loh Dasami); the 2 small islands are Nusa Kode and Gili Motang.

of Komodo dragons and ungulates across different island populations in Komodo National Park (Jessop et al. 2004, 2006). For this reason, we chose sites that possessed a landscape mosaic of different vegetation communities to ensure high ecological resource diversity. This was deemed necessary to ensure that all sites had sufficient densities of Komodo dragons and ungulates to permit evaluation (via direct and indirect methods) of their population dynamics. On the 2 large islands (Komodo Island and Rinca Island), we selected 8 sites that comprised low-elevation valleys (including adjacent valley slopes; Fig. 1). The 2 small islands (Gili Motang and Nusa Kode) comprised low-lying vegetated sea mounts that lacked valleys. Here, we chose study sites (~10% of total each island's area) that extended from the fore dune up into hilltop forest (< 200 m above sea level) on each island. For further information about the sites, see Jessop et al. (2007) and Purwandana et al. (2014, 2015).

*Dung count methodology.*—We used dung counts to index Rusa and pig abundance at each of the 10 study sites. Compared with direct estimation methods, dung counts are affected less by the tendencies of Rusa and pigs to avoid people or by the low abundances at some sites (Thompson et al. 1998; Marques et al. 2001). Counts of the standing crop of dung have been used widely to estimate the relative abundance of many ungulate taxa, including deer (Mayle et al. 1999; Forsyth et al. 2009, 2012) and pigs (Hone 2002). Using data collected at our 10 sites, we have shown previously that Rusa and pig dung counts are positively correlated with absolute Rusa and pig abundances estimated using line-transect distance sampling (Ariefiandy et al. 2013). The dung counts were not corrected for potential variation in dung deposition (Rogers 1987) or

decay rates (Laing et al. 2003). Whereas there was a linear (i.e., proportional) relationship between pig dung density and pig density, the relationship between Rusa pellet group density and Rusa density became saturated (i.e., curvilinear) at high Rusa densities (Ariefiandy et al. 2013). Since only 1 site (K4) had high Rusa densities (Ariefiandy et al. 2013), we assumed that changes in dung abundance were proportional to changes in abundance for both pigs and Rusa, and hereinafter use "ungulate population growth rate," rather than "ungulate dung population growth rate."

We used a table of random numbers to generate start points across grid-referenced digital maps for between 20 and 48 dung count transects in each of the 10 sites. We also used a table of random numbers to generate a compass bearing for each transect. The 150-m transects consisted of 30 circular plots measuring 3.14 m$^2$ (i.e., radius = 1 m) at 5-m intervals. We used a small plot size so that the entire plot could be searched easily in all habitats, ensuring that all dung was detected (Ariefiandy et al. 2013). We navigated to the start point of each transect using a GPS (Garmin Etrex, Olathe, Kansas). A 150-m nylon cord (with flagging tape at 5-m intervals) delineated each transect. We pushed a plastic peg into the ground at the plot center and used a 1-m string to delineate the perimeter of the plot. We removed and parted leaf litter and grass, respectively, to enable all dung to be counted. We searched each plot thoroughly and recorded the numbers of Rusa dung groups and pig dung.

The authors, with additional support from trained Komodo National Park rangers, performed all ungulate dung counts and associated fieldwork. We conducted monitoring surveys in September and October (i.e., late dry season; Supplementary Data SD1) annually during 2003–2014 (except for 2007 and 2008, due to budget restrictions). For further information on the field methods, see Forsyth (2005) and Ariefiandy et al. (2013).

*Predictors of Rusa and pig abundances.*—We quantified 4 variables that might explain temporal or spatial variation in ungulate abundance based on 1) our team's combined research experience within the study area accumulated over 16 years (e.g., Ciofi and Bruford 1999; Jessop et al. 2006; Purwandana et al. 2015); 2) consultation with park authorities (i.e., rangers who have manned posts in Komodo National Park for the last 35 years); and 3) a review of the literature pertaining to ecological and environmental determinants of population dynamics of tropical ungulates (Dunham et al. 2004; Shaw et al. 2012) and principles of island biogeography (MacArthur and Wilson 1967). The 4 variables we considered were:

1) Time: Rusa and pig abundances could increase or decrease annually, independent of the other variables described below; long-term declines in the abundance of either species would be particularly concerning because of the importance of these ungulates as prey for Komodo dragons.

2) Rainfall: total annual rainfall measured in the previous 1 and 2 years before each annual survey period could influence Rusa and pig dynamics. We used rainfall data collected at Labuan Bajo, the nearest meteorological station and approximately 30 km from the midpoint of our 10 study sites

(see Supplementary Data SD1). We considered mean multiyear rainfall because the effect of precipitation on primary productivity can have a lag of 1–2 years in semiarid systems (Oesterheld et al. 2001; Yahdjian and Sala 2006).

3) Island: differences in island area and elevation could drive ecosystem complexity and productivity (Wardle et al. 1997). We therefore considered island as a fixed effect. The 4 islands in our study consist of 2 large-area, high-elevation (i.e., > 200 km² and > 700 m above sea level) islands and 2 small-area, low-elevation (i.e., < 15 km² and < 200 m above sea level) islands (Fig. 1).

4) Vegetation composition: vegetation can vary significantly from island to island, and within islands (Auffenberg 1981; Monk et al. 1997). Hence, ungulate populations can be exposed to contrasting vegetation communities that could directly or indirectly affect survival and reproductive rates and hence, abundances. The ungulates use 4 vegetation communities within our study areas (Auffenberg 1981; Purwandana et al. 2016). Quasi-cloud forest grew only on hilltops (> 500 m above sea level) and along some permanent watercourses. The canopy of quasi-cloud forest is closed and dominated by trees not typically found at lower elevations, primarily *Terminalia zollingeri*, *Podocarpus neriifolia*, and *Ficus orupacea* (Auffenberg 1981). Deciduous monsoon forest grew only on coastal valley floors abutting elevated hills, which receive precipitation, providing runoff to the valley floors. Monsoon forest consists of deciduous fire-resistant trees, primarily *Tamarindus indica*, *Sterculia foetida*, *Jatropha curcas*, and *Cladogynos orientalis*. The canopy of monsoon forest is partially closed, and the understory is either open or dominated by perennial shrubs. In areas that receive little runoff or precipitation, savannah woodland or savannah grassland displaces monsoon forest. The canopy of savannah woodland is open, and the dominant trees are *Borassus flabellifer*, *Zizyphus jujube*, and *T. indica* (Auffenberg 1981). Savannah grassland and the understory of savannah woodland are both composed of medium and tall grasses. We used the percentages of each area that were classified as the 2 densest vegetation community types (i.e., open deciduous forest and closed riparian forest) at each site as an index of vegetation structure. We assessed the areas using digital vegetation maps and validated the assessments with on-ground surveys.

Komodo dragons, as the sole predator of ungulates, could be considered an additional determinant of spatial and temporal regulation of ungulate population dynamics in Komodo National Park. However, our unpublished data indicate that interaction between dragons and ungulates is a bottom-up process. We therefore did not include Komodo dragon density (i.e., a proxy of predation pressure) as a predictor variable.

*Statistical analyses.*—The total number of Rusa dung groups and pig dung counted along transect $j$ at time $t$ was the variable of interest and was termed dung abundance ($\lambda$—Forsyth et al. 2007). To estimate the population status of Rusa and pig populations in Komodo National Park, we constrained variation in dung abundance to be a linear function of annual sampling events (i.e., a year effect) using a generalized linear mixed effect model (GLMM—Crawley 2012). We used this procedure to assess each of the island populations individually, and we fitted these models with transect, nested in site, as random effects to account for potential spatial autocorrelation.

We considered 12 a priori GLMMs of spatial and temporal variation in ungulate dung abundance (Table 1). These models assumed that dung abundance could vary in response to different combinations of the 6 predictor variables. Predictor variables could have interactive effects on dung; hence, we fitted models with additive (+) and multiplicative (×) covariate combinations. We also evaluated null and global models.

We evaluated the relative parsimony of each model with Akaike's Information Criterion (AIC) and considered models with small AIC values to be more parsimonious descriptions of the data relative to models with larger AIC values. We computed Akaike model weights ($w_i$), which can be interpreted as the probability that the model is the "best" among the candidate set of models, following Burnham and Anderson (2002).

We evaluated the distribution of Rusa and pig dung counts so that any overdispersion could be properly modeled in our GLMMs. We compared the Rusa and pig global models fitted sequentially with negative binomial, Poisson, and Gaussian distributions (Zuur et al. 2009). AIC revealed that negative binomial and Gaussian distributions best fitted Rusa and pig dung counts, respectively.

To analyze determinants of variation in Rusa and pig population growth rates, we first calculated annual $r$ using the natural

**Table 1.**—Description of the parameters used in 12 GLMMs fitted to assess temporal and spatial variation in Rusa deer and wild pig dung abundance ($\lambda$) in Komodo National Park.

| Model | Description |
|---|---|
| $\lambda\{.\}$ | Dung abundance varies randomly (i.e., null model) |
| $\lambda\{yr\}$ | Dung abundance varies linearly with year ($yr$) |
| $\lambda\{i\}$ | Dung abundance varies among the 4 islands ($i$) |
| $\lambda\{ia\}$ | Dung abundance varies linearly with island area ($ia$) |
| $\lambda\{yr + ia\}$ | Dung abundance varies additively with year ($yr$) and island area ($ia$) |
| $\lambda\{yr + i\}$ | Dung abundance varies additively with year ($yr$) and island ($i$) |
| $\lambda\{y \times i\}$ | Dung abundance varies due to an interaction between year ($yr$) and island ($i$) |
| $\lambda\{yr \times ia\}$ | Dung abundance varies due to an interaction between year ($yr$) and island area ($ia$) |
| $\lambda\{RF_{t-1}\}$ | Dung abundance varies linearly with annual rainfall ($RF$) in the previous year |
| $\lambda\{RF_{\bar{x}(t-1+t-2)}\}$ | Dung abundance varies linearly with mean annual rainfall ($RF$) in the previous 2 years |
| $\lambda\{veg\}$ | Dung abundance varies with site-level vegetation composition ($veg$) |
| $\lambda\{global\}$ | Dung abundance varies additively with all predictor variables |

log of ($N_{t+1}/N_t$) (Sibly and Hone 2002). This provided 8 estimates of *r* for each of the 10 study sites. Dung density was presented per hectare (i.e., we multiplied the search area of each transect [94.45 m²] by 106). We evaluated the relative support for 9 candidate GLMMs explaining variation in Rusa and pig population growth rates. The 9 models evaluated the effects of density, year, and island as independent, additive, or interactive effects on population growth rates. All models included site as a random effect.

To analyze population synchrony in annual estimates of ungulate population growth rates between sites, we obtained all pairwise Pearson correlation coefficients (Koenig 1999). We then used Mantel tests (Manly 1997) to evaluate correlations between annual change in ungulate dung abundance and corresponding intersite distances. We ran all Mantel tests for 10,000 permutations.

## RESULTS

*Rusa and pig population status.*—We counted a total of 58,453 Rusa dung groups and 1,426 pig dung along 462 km of transect within the 10 sites during 10 annual sampling occasions. Rusa dung was present at all 10 sites. In contrast, pig dung was found at all 8 sites on the 2 larger islands (Komodo and Rinca) but was absent from the 2 smaller island sites (Gili Motang and Nusa Kode).

Mean abundances of deer dung were much higher on the larger Komodo (26.8±1.1 dung groups ± standard error of the mean (*SE*)/transect; range = 20.5–34.5 dung groups/transect) and Rinca islands (18.8±1.2 dung groups/transect; range = 13.5–34.5 dung groups/transect) compared with the small islands of Nusa Kode (7.0±0.5 dung groups/transect; range = 4.1–9.9 dung groups/transect) and Gili Motang (6.4±0.7 dung groups/transect; range = 3.0–10.5 dung groups/transect; Fig. 2). There was an annual decline in Rusa dung abundance (Fig. 2) on Nusa Kode (β = −0.03±0.012 dung groups/year) and Rinca (β = −0.025±0.001 dung groups/year). In contrast, there was little annual change in Rusa dung abundance on Komodo (β = −0.002±0.003 dung groups/year), and Rusa dung abundance increased on Gili Motang (β = 0.023±0.011 dung groups/year; Fig. 2).

Mean abundances of pig dung were higher on Komodo (0.7±0.1 dung/transect; range = 0.4–0.7 dung groups/transect) than on Rinca (0.5±0.1 dung/transect; range = 0.2–0.5 dung groups/transect). Pig dung declined on Komodo (β = −0.023±0.001 dung/year) and increased on Rinca (β = 0.019±0.007 dung/year) during the 10-year monitoring period (Fig. 3).

*Predictors of Rusa and pig population variation.*—For both ungulate species, variation in dung abundance was overwhelmingly best explained by a model that considered the interaction between temporal trend (i.e., year) and island
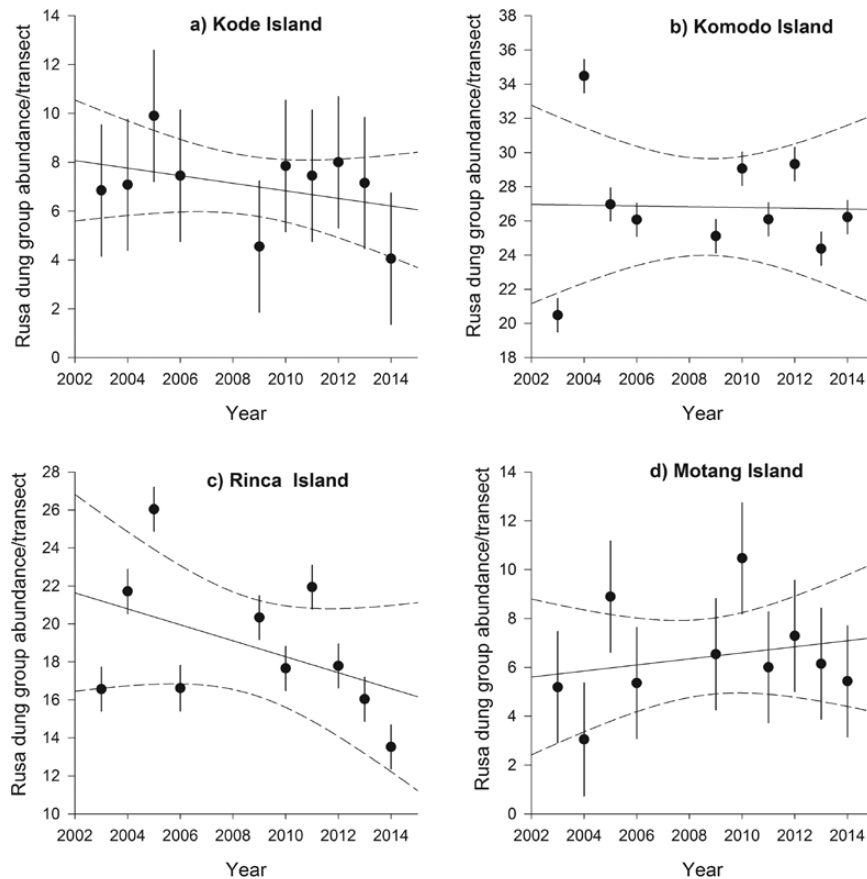


**Fig. 2.**—Plots of annual mean variation and trends (i.e., generalized linear mixed effect model regression with 95% *CI*s) in Rusa deer dung abundances on 4 islands in Komodo National Park, Indonesia.
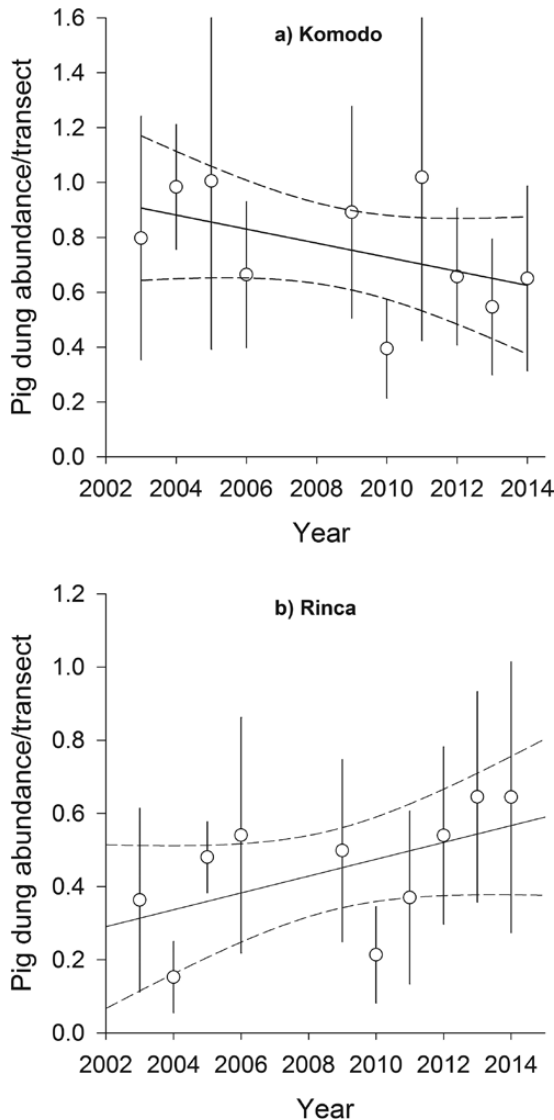
**Fig. 3.**—Plots of annual mean variation and trends (i.e., generalized linear mixed effect model regression with 95% *CI*s) in wild pig dung abundances on Komodo and Rinca islands in Komodo National Park, Indonesia.

area ($w_i = 0.96$ for deer and 0.73 for pigs; Table 2). Models accounted for 26% and 6% of the variation (i.e., adjusted $R^2$) in abundance of Rusa and pig dung, respectively. However, the year × island effect for Rusa dung was better explained by a nonlinear parameterization of year. In contrast, variation in abundance of pig dung was best explained by a linear parameterization of year.

*Density dependence in Rusa and pig population growth rates.*—For both Rusa and pigs, annual variation in $r$ was overwhelmingly best explained by a model that included additive effects of dung density in the previous year and island ($w_i = 1.00$ for Rusa and 0.76 for pigs; Table 3; Fig. 4). These models accounted for 28% and 41% of the variation (i.e., adjusted $R^2$) in Rusa and pig population growth rates, respectively. Across all islands, the population growth rates of both species decreased as dung densities in the previous year increased.

**Table 2.**—Model selection summary depicting models testing effects of year (*yr*), island (*i*), island area (*ia*), rainfall (*RF*), and vegetation (*veg*) on Rusa deer and wild pig dung abundance on 4 islands in Komodo National Park, 2003–2014. AIC = Akaike's Information Criterion; $\Delta$AIC = difference between model AIC and the lowest AIC in the model set, $w_i$ = Akaike model weight, $k$ = number of estimated parameters, *logLik* = log likelihood of model.

| Model[a] | $\Delta$AIC | $w_i$ | $k$ | *logLik* |
|---|---|---|---|---|
| **Rusa deer** | | | | |
| $\lambda\{yr \times i\}$ | 0.00 | 0.96 | 13 | −2,682.86 |
| $\lambda\{yr + ia\}$ | 8.37 | 0.01 | 9 | −2,691.04 |
| $\lambda\{global\}$ | 9.00 | 0.01 | 20 | −2,691.42 |
| $\lambda\{RF_{\bar{x}(t-1+t-2)}\}$ | 9.47 | 0.01 | 7 | −2,693.59 |
| $\lambda\{yr + i\}$ | 10.09 | 0.01 | 8 | −2,690.90 |
| $\lambda\{yr \times ia\}$ | 24.67 | 0.00 | 8 | −2,700.19 |
| $\lambda\{yr\}$ | 25.32 | 0.00 | 7 | −2,701.52 |
| $\lambda\{ia\}$ | 58.94 | 0.00 | 7 | −2,718.12 |
| $\lambda\{i\}$ | 60.51 | 0.00 | 7 | −2,718.33 |
| $\lambda\{.\}$ | 75.51 | 0.00 | 5 | −2,726.03 |
| $\lambda\{RF_{t-1}\}$ | 78.85 | 0.00 | 7 | −2,726.95 |
| $\lambda\{veg\}$ | 78.85 | 0.00 | 7 | −2,728.28 |
| **Wild pigs** | | | | |
| $\lambda\{yr \times i\}$ | 0.00 | 0.73 | 12 | −4,692.47 |
| $\lambda\{yr \times ia\}$ | 3.50 | 0.13 | 8 | −4,698.22 |
| $\lambda\{ia\}$ | 5.70 | 0.04 | 7 | −4,700.32 |
| $\lambda\{RF_{t-1}\}$ | 6.17 | 0.03 | 7 | −4,700.56 |
| $\lambda\{global\}$ | 6.41 | 0.03 | 18 | −4,689.68 |
| $\lambda\{i\}$ | 6.83 | 0.02 | 8 | −4,699.89 |
| $\lambda\{yr + ia\}$ | 8.94 | 0.01 | 9 | −4,699.94 |
| $\lambda\{yr + i\}$ | 10.07 | 0.00 | 10 | −4,699.51 |
| $\lambda\{.\}$ | 15.65 | 0.00 | 5 | −4,704.31 |
| $\lambda\{veg\}$ | 16.60 | 0.00 | 6 | −4,707.30 |
| $\lambda\{RF_{\bar{x}(t-1+t-2)}\}$ | 17.54 | 0.00 | 7 | −4,706.77 |
| $\lambda\{yr\}$ | 18.89 | 0.00 | 7 | −4,706.24 |

[a]The 12 models are defined in Table 1.

*Spatial synchrony in ungulate population growth rates.*— The mean (± *SE*) Pearson correlation coefficient derived from annual changes in Rusa dung at the 10 sites was $0.166 \pm 0.111$. Rusa population growth rates were most synchronous between nearest neighboring sites, with synchrony declining significantly with increasing distance (Mantel test: $Rm = -0.45$, $P = 0.004$; Fig. 5a). The mean Pearson correlation coefficient at the 8 sites at which pigs were present was $0.078 \pm 0.061$. There was no significant relationship between distance and pig population growth rates (Mantel test: $Rm = -0.21$, $P = 0.4$; Fig. 5b).

## DISCUSSION

Our 12-year study of Rusa and pigs at 10 sites on 4 islands in Komodo National Park generated important insights into the dynamics of these tropical ungulates. As predicted, both Rusa and pig population growth rates exhibited density dependence ($H_1$), with a lag of 1 year. There was no support, however, for the prediction that population growth rates would vary with annual rainfall or vegetation composition ($H_2$). For both Rusa and pigs, density-independent factors were, therefore, unimportant relative to density-dependent factors. Finally, there was evidence of synchronous dynamics in Rusa—but not pig—populations ($H_3$).

**Table 3.**—Model selection summary for models testing effects of population density, year, and island on Rusa deer and wild pig population growth rates ($r$) on 4 islands in Komodo National Park, 2003–2014. AIC = Akaike's Information Criterion; ΔAIC = difference between model AIC and the lowest AIC in the model set, $w_i$ = Akaike model weight, $k$ = number of estimated parameters, $logLik$ = log likelihood of model.

| Model[a] | ΔAIC | $w_i$ | $k$ | $logLik$ |
|---|---|---|---|---|
| Rusa deer | | | | |
| $r\{D_{t-1}{}^{b} + i\}$ | 0.00 | 0.93 | 9 | −7.72 |
| $r\{D_{t-1} \times yr\}$ | 6.85 | 0.03 | 7 | −17.46 |
| $r\{yr\}$ | 6.87 | 0.03 | 7 | −17.47 |
| $r\{D_{t-1} + yr\}$ | 10.47 | 0.00 | 6 | −20.26 |
| $r\{D_{t-1}\}$ | 12.48 | 0.00 | 6 | −21.26 |
| $r\{.\}$ | 14.48 | 0.00 | 4 | −22.07 |
| $r\{D_{t-1} \times i\}$ | 15.37 | 0.00 | 12 | −22.79 |
| $r\{i\}$ | 19.24 | 0.00 | 7 | −23.64 |
| $r\{yr \times i\}$ | 22.06 | 0.00 | 12 | −24.26 |
| Wild pigs | | | | |
| $r\{D_{t-1} + i\}$ | 0.00 | 0.75 | 7 | −60.59 |
| $r\{D_{t-1} \times yr\}$ | 3.89 | 0.11 | 8 | −60.70 |
| $r\{D_{t-1}\}$ | 4.69 | 0.07 | 6 | −62.94 |
| $r\{D_{t-1} \times i\}$ | 5.39 | 0.05 | 7 | −63.24 |
| $r\{D_{t-1} + yr\}$ | 6.69 | 0.03 | 7 | −64.14 |
| $r\{.\}$ | 25.80 | 0.00 | 4 | −75.50 |
| $r\{i\}$ | 27.37 | 0.00 | 5 | −75.29 |
| $r\{yr\}$ | 29.80 | 0.00 | 6 | −75.50 |
| $r\{yr \times i\}$ | 33.80 | 0.00 | 8 | −75.28 |

[a]The models are defined in Table 1.
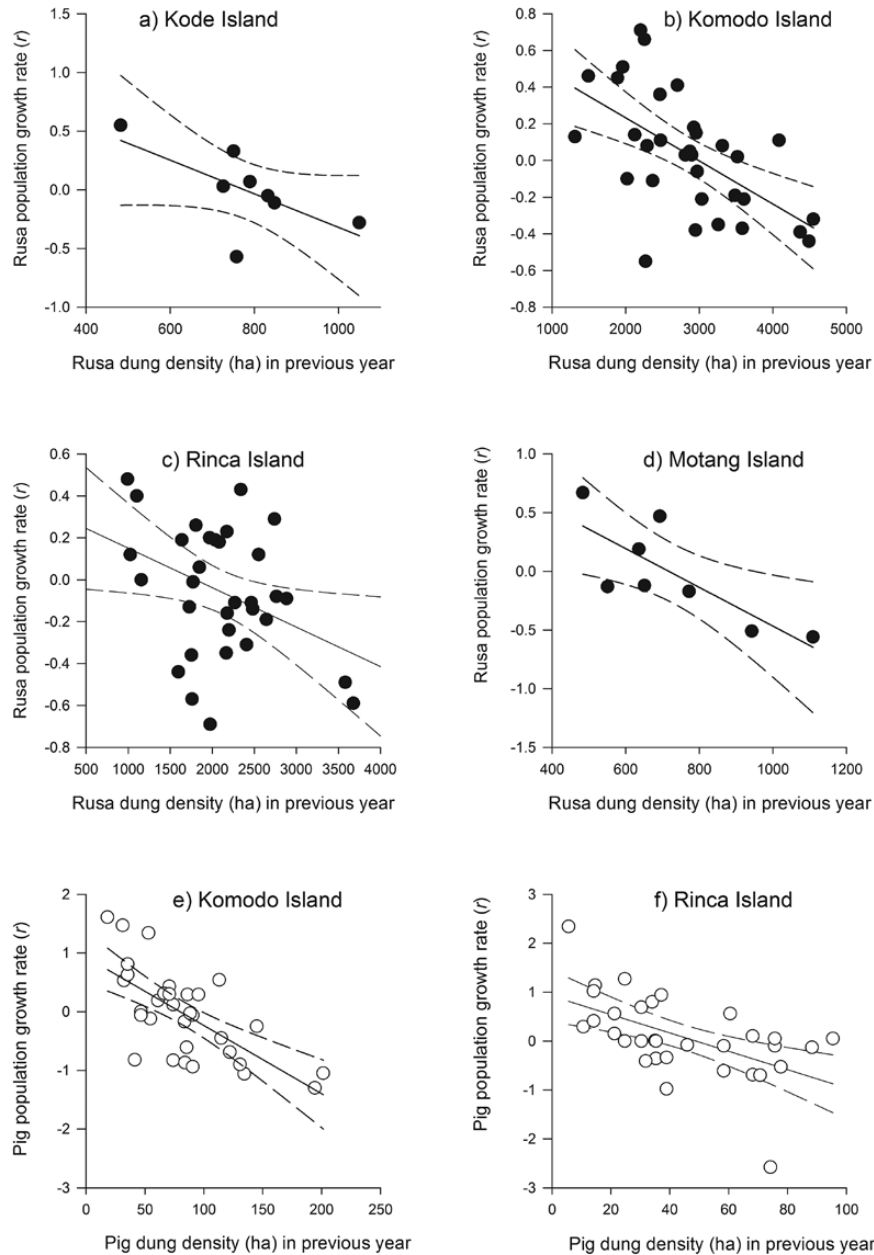[b]$D_{t-1}$ is dung density in the previous year.

Population growth rates of both Rusa and pigs in Komodo National Park were influenced by population density in the previous year. Negative density dependence is commonly observed in mammalian population growth rates (reviews in Sibly et al. 2005; Brook and Bradshaw 2006), including ungulates (Coulson et al. 2000), and is strongest when a population fluctuates around its carrying capacity, which is often determined by food availability and may change from year to year (Mduma et al. 1999). Pigs have a much higher maximum population growth rate (intrinsic rate of increase, $r_m$) than Rusa (Choquenot et al. 1996; Choquenot 1998; Hone et al. 2010). Population growth rates ≥ 1 for pigs were observed on both islands on which they occurred, whereas population growth rates of Rusa were ≤ 0.8 on all 4 islands on which they occurred. These results confirm that pigs can recover from large reductions in density, or respond to increased carrying capacity, faster than can Rusa.

Rainfall can be a major determinant of ungulate population dynamics because of its effects on vegetation composition (Choquenot 1998; Ogutu and Owen-Smith 2003), but there was little support for either variable influencing Rusa or pig dynamics in Komodo National Park. This may have been because rainfall data were available from only 1 meteorological station and did not reflect the true underlying spatial heterogeneity in rainfall (Monk et al. 1997). Large spatial variation in rainfall is possible because the 4 islands have different topographies and elevations and vary in their proximity to the weather station on Flores. Rainfall also can affect the decay and disappearance rates of ungulate dung (Jung and Kukka 2016). The effects of variable rainfall during the wet season on Rusa and pig distribution, and also on dung decay and disappearance rates, would nevertheless have been minimized because we conducted our dung surveys late in the dry season.

Rusa population growth rates were most synchronous between nearest neighboring sites. Synchronous population dynamics are caused by dispersal or by environmental factors (Ranta et al. 1995; Grenfell et al. 1998). The only previous demonstration of synchronous dynamics in ungulate populations is for 2 insular Soay sheep populations (Grenfell et al. 1998). Those populations were synchronized by spring gales reducing survival rates (Grenfell et al. 1998). It is unclear which environmental variables might be synchronizing Rusa dynamics in Komodo National Park, but 1 possibility is small-scale variation in rainfall affecting Rusa carrying capacity through its effects on food quality and quantity. Dispersal of Rusa between sites and islands is likely to be limited, the former because of the steep terrain surrounding the valleys on Komodo and Rinca islands (Fig. 1) and the latter because of inter-island distance (Fig. 1) and strong tidal currents (Auffenberg 1981). Studies of marked animals are required to quantify Rusa and pig dispersal within Komodo National Park, but the inter-island distances exceed the known maximum swimming distances of both species (Choquenot et al. 1996; Fraser 2005).

There were substantial differences in the abundance of Rusa and pig dung on the 2 large islands compared with the 2 small islands, which is consistent with meta-analytical studies reporting positive correlations between animal population densities and patch or island area (Connor et al. 2000). The mechanism generating this pattern in Komodo National Park is unclear, but habitat resources and, hence, island productivity are often greater in larger patches than in smaller patches, leading to higher population densities on large islands that are more buffered against stochasticity compared with the lower population densities on small islands (MacArthur and Wilson 1967). The larger Komodo and Rinca islands have many low-elevation valleys, which contained high deer densities. In contrast, the smaller Nusa Kode and Gili Motang islands do not have low-elevation valleys (Fig. 1). The low-elevation valleys on Komodo and Rinca islands have permanent fresh water and a mix of vegetation, both of which are important for Rusa and pigs (Auffenberg 1981). The absence of pigs from the 2 small islands could arise from physiological, demographic, or biogeographic factors. Because pigs lack sweat glands or other physiological cooling mechanisms (Heitman and Hughes 1949; Mount 1968), they will have a lower threshold of thermal stress than Rusa. Pigs, therefore, require access to shade and free water during hot weather (Choquenot and Ruscoe 2003). Both small islands lack permanent standing water and, hence, may be unsuitable habitat for pigs. If pigs ever established populations on the smaller islands, then they may be more likely to go extinct because of their smaller maximum population sizes. Across the archipelagos of Southeast Asia, pigs are thought to have spread from continental Asia as a consequence of human-assisted colonization, commencing about 7,000 years before present, and thus their current distribution to some extent likely reflects concordance

**Fig. 4.**—Plots of annual site variation and trends (i.e., generalized linear mixed effect model regression with 95% *CI*s) in Rusa deer a)–d) and wild pig e) and f) population growth rates in response to the previous year of dung density on 4 islands in Komodo National Park, Indonesia.

with the human settlements needed to establish wild populations (Morwood et al. 2004). Pigs may be absent from Gili Motang and Nusa Kode because these small islands have not been inhabited, due to an absence of water and arable land, since at least 1800 (Verheijen 1982). Finally, diseases such as classical swine fever, which is present in eastern Indonesia (Leslie 2012), may affect pig distributions and abundances. However, there was no evidence to suggest that infectious disease played a role in pig population dynamics at our study sites.

Declines in the abundance of Rusa and pigs are of particular conservation concern in Komodo National Park because these 2 species are key prey for adult Komodo dragons (Auffenberg 1981; Jessop et al. 2006). Our long-term monitoring program revealed significant declines of Rusa on Rinca and Nusa Kode islands, and of pigs on Komodo Island. The observed rates of

decline in these populations were small compared with those observed elsewhere for deer and pigs (Young 1994; Steinmetz et al. 2010; Forsyth et al. 2012). Hunting is illegal within Komodo National Park and rangers commonly conduct anti-poaching patrols. During the period of our study, neither the authors nor rangers encountered poachers or other evidence of illegal hunting (e.g., Rusa or pig carcasses). We, therefore, do not believe that hunting had a significant impact on the abundances of Rusa or pigs during our study. In the absence of strong declines in ungulate populations in Komodo National Park, the most important result of our study was the much lower ungulate abundance and the presence of only Rusa (but not pigs) on the small Nusa Kode and Gili Motang islands. The 2 smaller islands support much lower densities of Komodo dragons, at least partly because of the low abundance of ungulates there
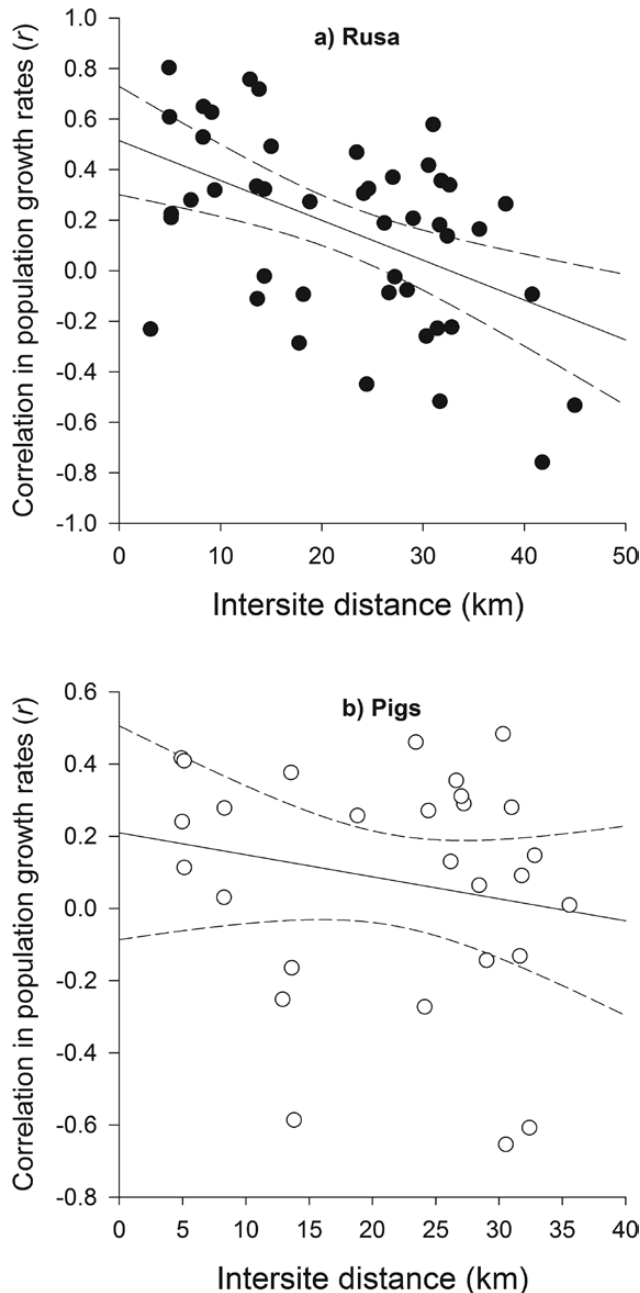
**Fig. 5.**—Corellograms describing the relationship between annual variation in the dung densities of a) Rusa deer and b) wild pigs, and intersite distances at 10 sites on 4 islands in Komodo National Park, Indonesia.

(Purwandana et al. 2015). Since this finding is likely a consequence of island area, little can be done to increase Rusa abundances other than to ensure that they are protected from illegal harvesting. Continued monitoring of Rusa and pigs in Komodo National Park will further increase our understanding of the population dynamics of these tropical species and also help prevent extirpation of Komodo dragon populations.

## SUPPLEMENTARY DATA

**Supplementary Data SD1.**—Monthly and annual rainfall at Labuan Bajo during our study.

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