

Maximum body size among insular Komodo dragon populations covaries with large prey density

Tim S. Jessop, Thomas Madsen, Joanna Sumner, Heru Rudiharto, John A. Phillips and Claudio Ciofi

Jessop, T. S., Madsen, T., Sumner, J., Rudiharto, H., Phillips, J. A. and Ciofi, C. 2006. Maximum body size among insular Komodo dragon populations covaries with large prey density. – *Oikos* 112: 422–429.

This study documents variation in maximum body size of Komodo dragons (*Varanus komodoensis*) among the four extant island populations in Komodo National Park and compares an indirect measure of deer density, the major prey item for large dragons, to differences in maximum body size among islands. The largest 15% of dragons from the large islands of Komodo and Rinca were significantly longer and heavier than the largest 15% of dragons on the small islands of Gili Motang and Nusa Kode. There was a 33% difference in snout vent length (SVL) between dragons found on Komodo and those found on Gili Motang, with mass varying by more than four-fold. Density of deer pellet groups between islands ranged from 5.86 ± 0.75 groups per transect on Gili Motang to 20.73 ± 1.02 groups per transect on Komodo Island. Maximal dragon SVL and mass was highly positively correlated with this index of deer density. Low prey density on the two small islands could constrain body size via energetic constraints. At present we can not deduce if insular body size variation has arisen through genotypic or phenotypic mechanisms.

T. S. Jessop and J. A. Phillips, Beckman Center for Conservation and Research of Endangered Species, Zool. Soc. of San Diego, Escondido, CA 92112, USA. – T.S.J., J. Sumner and T. Madsen, School of Biological Sciences, Univ. of Wollongong, NSW 2522, Australia (timj@uow.edu.au). – H. Rudiharto, Komodo National Park, Labuan Bajo, Flores, Indonesia. – C. Ciofi, Dept of Ecology and Evolutionary Biology, Yale Univ., 165 Prospect Street, New Haven, CT 06520, USA. Present address: Dept of Animal Biology and Genetics, Univ. of Florence, Via Romana 17, IT-50125 Florence, Italy.

Across an island archipelago, body size within a single species may span from dwarf to gigantic. A number of hypotheses have been postulated for this variation in body size among islands, including interspecific competition (Grant 1968, Lomolino 1985, Roth 1992, McNab 1994, Petren and Case 1997), size specific predation pressure, sexual selection (Wikelski and Trillmich 1997) and resource availability and its interplays (Case 1978, Heaney 1978, Wikelski et al. 1997, Anderson and Handley 2002, Boback 2003). Lomolino (1985) suggested ‘competitive release’ as a mechanism to explain why in insular mammals, small species become larger (Roth 1992, McNab 1994) and “resource limitation” for why large mammals, which are often resource limited on

islands, tend to decrease in size (Anderson and Handley 2002). In addition it has been proposed that island area determines which factor drives selection: competitive release on large islands and resource limitation on small ones (Heaney 1978). Body size variation in island populations may thus evolve in response to the availability and quality of resources among islands or by differences in biotic interactions among island habitats. Such intraspecific variation reflects local adaptive strategies for dealing with contrasting island environments (Leips et al. 2000, Reznick and Travis 2001, Sultan 2001). Intraspecific variation in body size between island populations can arise through interactions between natural and sexual selection. Selection for increased

Accepted 8 July 2005

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ISSN 0030-1299

body size appears to be related to an increase in reproductive fitness manifested through fighting ability (Parker 1974) and increased fecundity. However an increased body size, despite having lower metabolic requirements per gram of body weight (Dobson and Headrick 1995) requires more food in absolute terms than smaller bodied animals and is thus harder to maintain (Wikelski and Trillmich 1997).

While all vertebrate taxa can exhibit a body size response to island dwelling, reptiles in particular demonstrate considerable variation in body size and may vary over an order of magnitude in mass among the biggest individuals from different populations (Schwaner and Sarre 1988, 1990, Petren and Case 1997, Wikelski and Trillmich 1997). Morphological shifts in island populations can occur extremely rapidly, repeatedly, and in a predictable fashion, as demonstrated by field experiments in *Anolis* lizards (Losos et al. 1997, 1998). Similar observations of gigantism have been described in Chuckwalla lizards (*Sauromalus*) from two islands (Petren and Case 1997). Behavioral comparison to mainland conspecifics suggests relaxation of predation as the selective force responsible. The density of prey, particularly in solitary predators (i.e. most reptiles), appears to be a major selective pressure shaping their body size (Schoener 1969). Case (1978) inventoried body size data for snakes and found a tendency for dwarfism on islands. He proposed that reduction in food availability on islands could explain these decreases in size. A more recent review of size in island dwelling snakes by Boback (2003) found that physiographic variables such as island area, island age, distance to mainland, and latitude were not determinants of evolution of body size, nor was phylogenetic history. Rather, change in body size was bimodal, and snake body size was found to increase if snakes encountered larger prey, or decreased if they encountered smaller prey compared with those on the mainland (Madsen and Shine 1992, Boback 2003). The magnitude of size change in insular giant populations of varanid lizards in Australia was also found to be positively correlated with prey abundance and these size changes were reported as occurring within 100 years (Case and Schwaner 1993).

The Komodo dragon (*Varanus komodoensis*) is a large carnivorous monitor, currently endemic to five islands in the Lesser Sunda region of south eastern Indonesia (Ciofi and De Boer 2004). Four of these islands occur within the boundaries of Komodo National Park. They differ in area by more than a magnitude and fall naturally into two size categories, with two small and two large islands. The key factor determining community assembly and dynamics of species in archipelagoes is island area, and its interactions with physiogeographic variables (e.g. topographic relief and rainfall; MacArthur and Wilson 1967, Whittaker 1998). Thus for an apex predator, such as the Komodo dragon, insular

variation in prey attributes (size, diversity and abundance), driven by island area and physiogeographic variables, could influence the ecology of this species. Throughout ontogeny, Komodo dragons change dietary niche breadth (Auffenberg 1981). Adults have a more narrow diet relative to the other size classes due to high selectivity for large ungulate prey, including Timor deer (*Cervus timorensis*), wild pigs (*Sus scrofa*) and to some extent water buffalo (*Bubalis bubalis*; Auffenberg 1981). Thus, if there is considerable inter-island variation in ungulate prey diversity and availability, different life stages of Komodo dragons, and adults especially, may respond with differences in ecological and life-history processes.

Here we study one interaction between large prey and the ecology of the adult Komodo dragon. Specifically, we examined if differences in maximal body size of adult Komodo dragons across four islands could covary with density differences in ungulate prey, the Timor deer. Moreover, we predict that maximal body size would scale positively with the density of ungulate deer and that small-island populations of Komodo dragons would be smaller than large-island dragons due to a reduction in the density of Timor deer.

Examining the basis to intraspecific variation in body size of animals can be confounded by interactions between different selection forces and mechanisms that influence body size, including predation pressure and interspecific competition for food (Dunham et al. 1978, Wikelski et al. 1997). Fortunately, Komodo dragons are exempt from some of these key factors, as direct predation on adults is very low (Auffenberg 1981). Additionally, interspecific competition for large prey is negligible due to the absence of other large predators on these islands (Auffenberg 1981).

Material and methods

Study sites

Komodo dragon populations on four islands in the Lesser Sunda region of south eastern Indonesia were studied (Fig. 1). These islands encompass the extant distribution of this species within Komodo National Park and include populations from Komodo (393.4 km²), Rinca (278.0 km²), Gili Motang (10.3 km²) and Nusa Kode (also referred to as Gili Dasami; 9.6 km²). The only other island, not included in the national park, on which there are extant populations, is the large island of Flores. Within Komodo and Rinca, four sites per island were selected to assess among island body size variation, and included the valleys of Loh Liang, Loh Sebita, Loh Lawi and Loh Wau on Komodo, and Loh Buaya, Loh Baru, Loh Tongker and Loh Dasami on Rinca (Fig. 1). On the small mountainous islands of Gili Motang and Nusa Kode, studies were confined to the

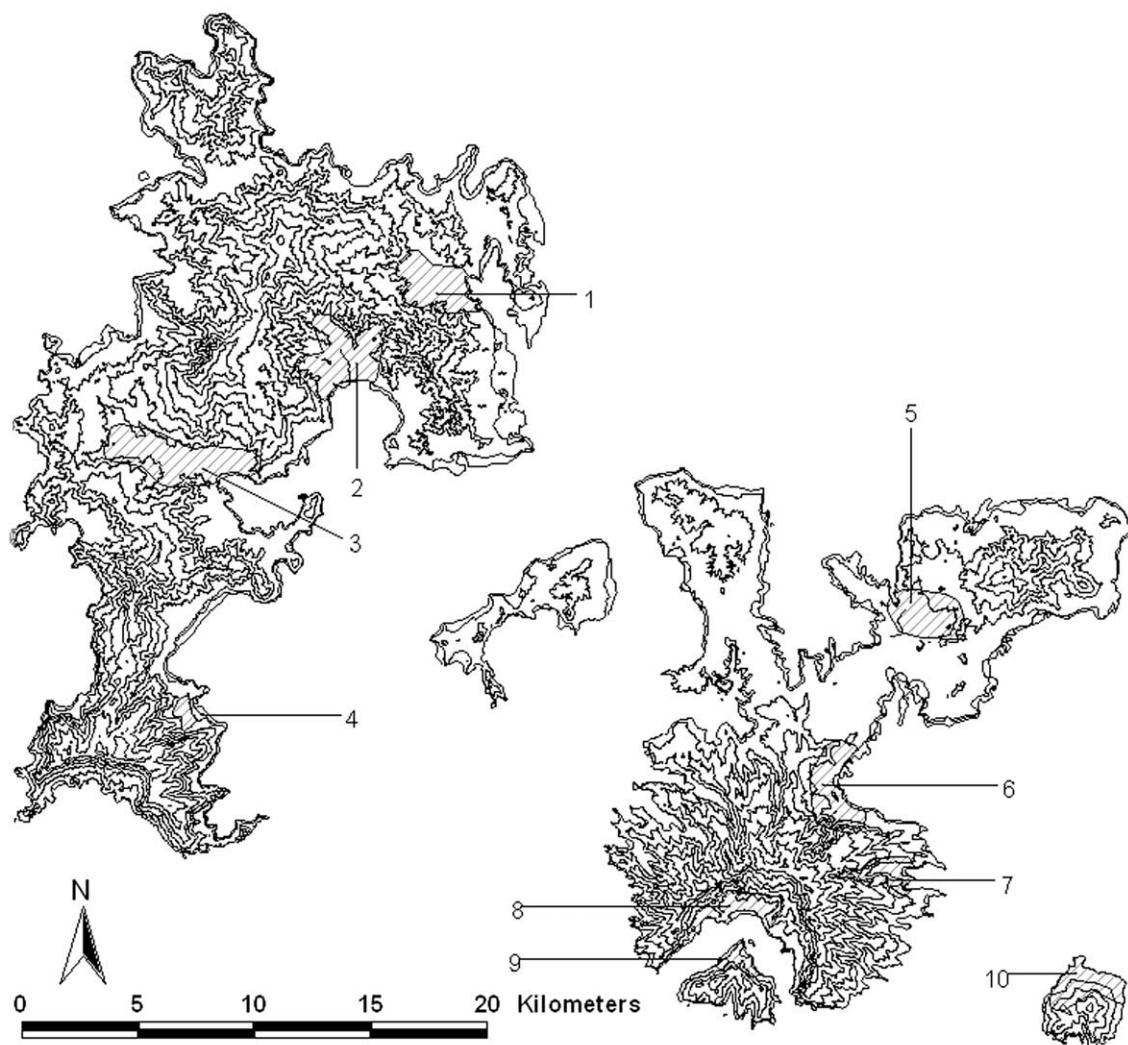


Fig. 1. The distribution of Komodo dragon populations across islands in Komodo National Park Indonesia. Sampling sites are marked numerically and were situated across four islands and include Komodo Island sites: 1) Loh Sebita 2) Loh Liang, 3) Loh Lawi, 4), Loh Wau, 5); Rinca Island sites: Loh Buaya, 6) Loh Baru, 7) Loh Tonker, 8) Loh Dasami, and the two small islands of 9) Nusa Kode and 10) Gili Motang. Stippled areas represent the effective trapping area of each study site.

coastal flats and adjacent hills representing approximately 20% of available island habitat.

An annual mark-recapture census was conducted in 2003 and again in 2004 at each of the 10 sites, on the four islands, within Komodo National Park. Data from each site collected over the two consecutive years was pooled. On Nusa Kode, only a small sample size ($N=9$) was collected over two years because of this island's apparently low population abundance, coupled with the difficulty of trapping dragons due to the steep topography that limited trap coverage and the unusual wariness of the dragons in entering traps. To increase the overall sample size for Nusa Kode we used additional samples ($N=11$) collected in 1998 (Ciofi et al. 2002). There were no statistical differences among samples collected

from Nusa Kode in 1998 and samples collected in 2003 and 2004 with respect to mass (T-test, $t_{1,18}=1.20$, $P=0.25$) and snout-vent length (T-test, $t_{1,18}=0.78$, $P=0.86$).

Sampling

Komodo dragons ($N=515$) within Komodo National Park were captured using baited traps, noose or by hand (restricted to smaller size classes only). Combined, these methods are extremely effective for capturing all size classes of monitor above yearlings, which are largely arboreal and rarely susceptible to these capture techniques. Following capture, dragons were restrained with

rope and their mouths taped. 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 was the average of two measurements that were within 0.5 cm of each other. Body mass was obtained using digital scales. Dragons that had obvious distension of the stomach region due to recently ingested prey were not included in analysis as this can increase the mass of large animals by more than 20 kg (T. S. Jessop, unpubl.). Dragons were permanently marked using passive integrated transponders (Trovan ID100a). Processing time was usually less than 20 min and dragons were released at their point of capture.

Calculating adult dragon maximum body size

To determine maximum body size differences between islands, truncated samples representing the largest 15% of all individuals captured within each island were used for analysis, and an average of these individuals was calculated. The whole data set was not used as results could be skewed by differences in population size structure among islands (Case and Schwaner 1993). At present, no quantitative information is available on the sex of the individuals measured. Other than the largest dragons usually being male, Komodo monitors have no obvious external morphological differences between sexes. Probing the cloaca for presence or absence of inverted hemipenes is troublesome since females have hemilitoreal sacs at approximately the same position as males' hemipenes, so gender can often be confused.

Calculating an index of deer density

Direct surveying methods for estimating the abundance of Timor deer were not possible across study sites due to likely biases arising from observational differences among forest types. For example, some sites consisted of more open, dryer habitats including savannah woodland which enable easy observation of deer. Other study sites consist of closed dense forest, which reduce deer detection. In addition, deer are typically wary and avoid people, so direct methods (e.g. distance sampling) would likely generate gross underestimates of abundance. We therefore chose to use indirect survey techniques (reviewed by Thompson et al. 1998) based on faecal counts; estimates from these techniques should be less influenced by the tendencies of deer to avoid people or be missed in dense forest. Counts of the standing crop of faecal pellets or faecal pellet groups have been widely used to estimate the relative or absolute abundance of many deer species (Bennett et al. 1940, White 1992, Thompson et al. 1998).

An indirect index of ungulate density was calculated using pellet counts on linear transects. Within each site

between 20 and 49 transects were randomly positioned and orientated. Pellet groups were tallied from 30 sample plots placed across each 150 m long transect. Each plot was a circle with a radius of 1 m and an area of 3.14 m², and all faecal matter within the plot was recorded. A group was standardized as a dense aggregation of pellets exceeding 40 pellets; groups below 40 were counted as individuals then divided by the mean pellet count (taken from counting 60 intact pellet groups). Pellet groups that were greater than 50% inside the plot area were counted as an entire group. To standardize seasonal differences in pellet density we conducted all surveys across the 10 sites in late September and early October of 2003. We did not estimate the density of wild pig and water buffalo as they are only found on the two large islands of Komodo and Rinca.

Statistics

Body size data are first presented as frequency distributions and then as the mean and the standard error of the mean (SEM) of the largest 15% of the population. Pellet data is presented as the mean and the SEM. Parametric tests including ANOVA were used to assess differences between means. Data that failed to meet the assumptions of normality and equal variance were log transformed. Regression and ANOVA was used to test for a significant correlation between two factors.

Results

Inter-island variation in body size

There were obvious differences between island populations with respect to distribution and frequency of body sizes, with the largest two islands (Komodo and Rinca) displaying a greater range and abundance of snout-vent lengths and body masses compared to the two small islands (Gili Motang and Nusa Kode; Fig. 2, Table 1) located within Komodo National Park. Even between Komodo and Rinca Island, there were large differences in the relative frequencies of particular body sizes. For example on Komodo Island, the population was comprised of a greater proportion (28.31%) of large individuals (>120 cm SVL) compared to Rinca (15.35%). In contrast, on Rinca the population was comprised of a greater proportion of small (<60 cm SVL = 37.65%) and medium sized lizards (60–120 cm SVL = 57.00%) compared to the Komodo population that contained 26.12% and 45.57% of small and medium sized lizards, respectively. These frequency differences in population size structure between Komodo and Rinca Island were significant (Kolmogorov–Smirnov test: $D=0.144$; $P=0.016$). With respect to the largest individuals captured in our study, a specimen measuring 154.05 cm SVL (304

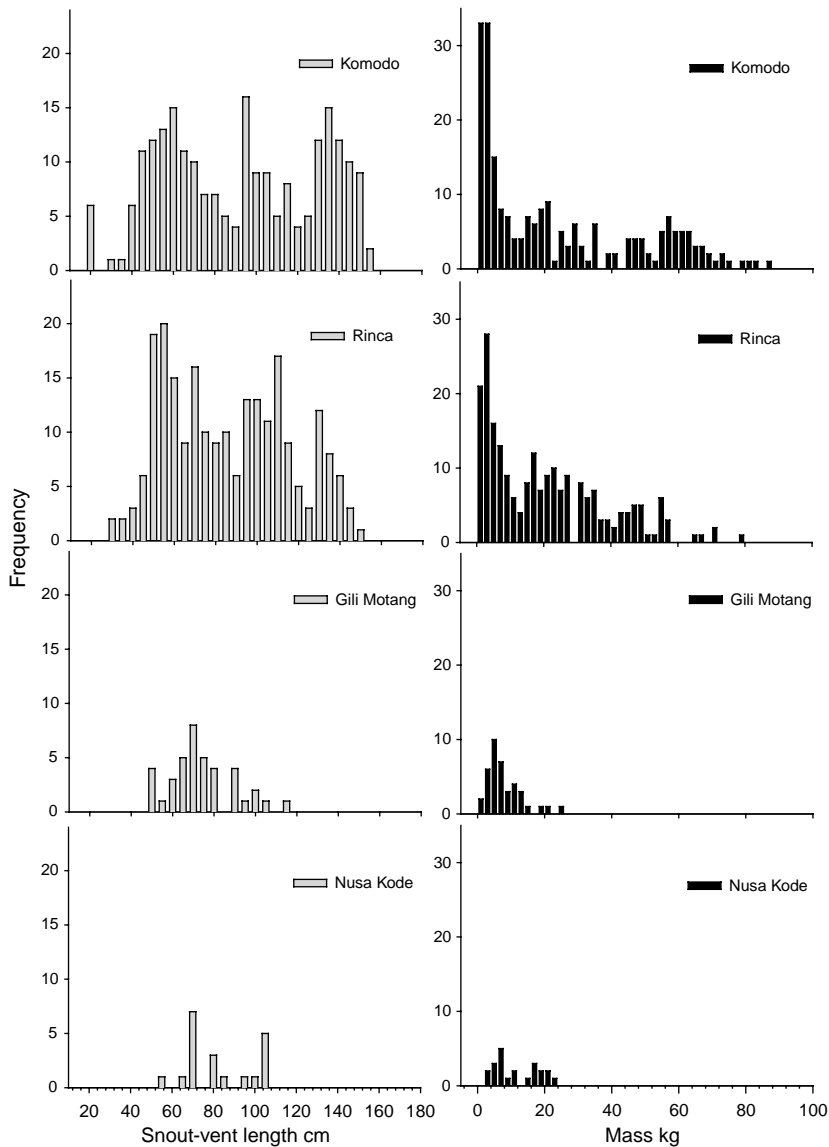


Fig. 2. Frequency distribution of snout-vent length (grey bars) and body mass (black bars) of four island populations of Komodo dragons within Komodo National Park.

cm total body length) was captured in Loh Liang on Komodo Island and weighed 81.5 kg. There were two animals heavier than this individual, albeit shorter: the heaviest individual captured weighed 87.4 kg, a mass we considered unduly influenced by recent ingestion of prey. Large male dragons with recently ingested ungulate prey can increase their body mass in excess of 20 kg and thus can exceed 100 kg (T. S. Jessop, unpubl.).

With respect to maximum body size, the largest 15% of dragons on the four islands varied from a SVL length of 96.91 ± 1.19 cm and a mass of 13.5 ± 1.06 kg on Gili Motang to a SVL of 145.61 ± 0.83 cm and a mass of 66.39 ± 3.06 kg on Komodo Island (Fig. 3). This is a 33% difference in maximum SVL between Komodo and Gili Motang, with maximum mass varying by 439%. There were significant differences among island populations in

Table 1. Summary statistics of body size attributes for four Komodo dragon populations inhabiting islands within Komodo National Park.

Island population	Mean SVL \pm SEM (cm)	Mean mass \pm SEM (kg)	(N)
Komodo	92.14 ± 2.4545	23.47 ± 1.5690	226
Rinca	86.29 ± 1.9721	20.94 ± 1.1765	228
Nusa Kode	83.14 ± 3.6973	10.83 ± 1.4031	20
Gili Motang	74.76 ± 2.4686	7.89 ± 0.8514	39

SVL (ANOVA: $F_{3,75} = 104.51$, $P < 0.001$) and body mass (ANOVA: $F_{3,75} = 34.71$, $P < 0.001$). Post hoc tests demonstrated that populations from the large islands of Komodo and Rinca were significantly longer and heavier than populations on the small islands of Gili Motang and Nusa Kode.

Deer density and Komodo dragon body size

Density of deer pellet groups varied significantly among islands from 5.86 ± 0.75 groups per transect on Gili Motang to 20.73 ± 1.02 groups per transect on Komodo (Fig. 4). This index of deer density was highly correlated with the insular differences in SVL ($R^2 = 0.99$, $F_{1,3} = 595.7550$, $P = 0.029$) and body mass ($R^2 = 0.99$, $F_{1,3} = 17408.943$, $P = 0.005$). The relationships between body size and deer density were non-linear and best explained by three parameter sigmoidal curve models (SVL = $164.04 / (1 + \exp(-(deer\ density - 8.55) / 2.87))$; mass = $72.31 / (1 + \exp(-(deer\ density - 11.46) / 3.85))$).

Discussion

Island-dwelling vertebrates can exhibit differences in body size relative to mainland or other insular populations (Grant 1968, Case 1978, Lomolino 1985). Amongst vertebrates, reptiles can demonstrate some of the most extreme differences in body size and may vary over a magnitude in mass among the largest individuals from different populations (Schwaner and Sarre 1988, 1990, Petren and Case 1997, Wikelski and Trillmich 1997, Boback 2003). We found that Komodo dragons exhibited significant variation in maximal body size across the four islands within Komodo National Park. There was a 33% difference in snout vent length between the largest

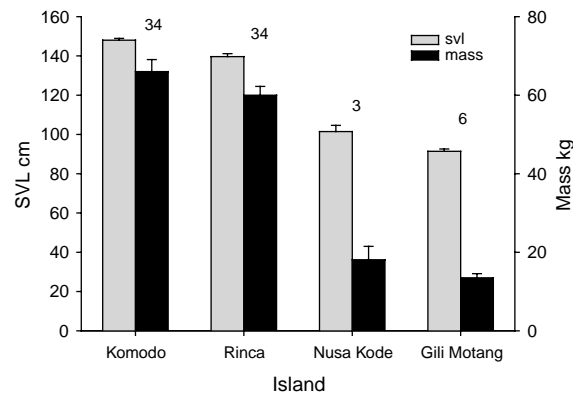


Fig. 3. Komodo dragon mass and snout to vent length (SVL) for four islands in Komodo National Park, calculated using the largest 15% of individuals in each population. Sample sizes for each island are presented above the bars. All data was collected in 2003–2004.

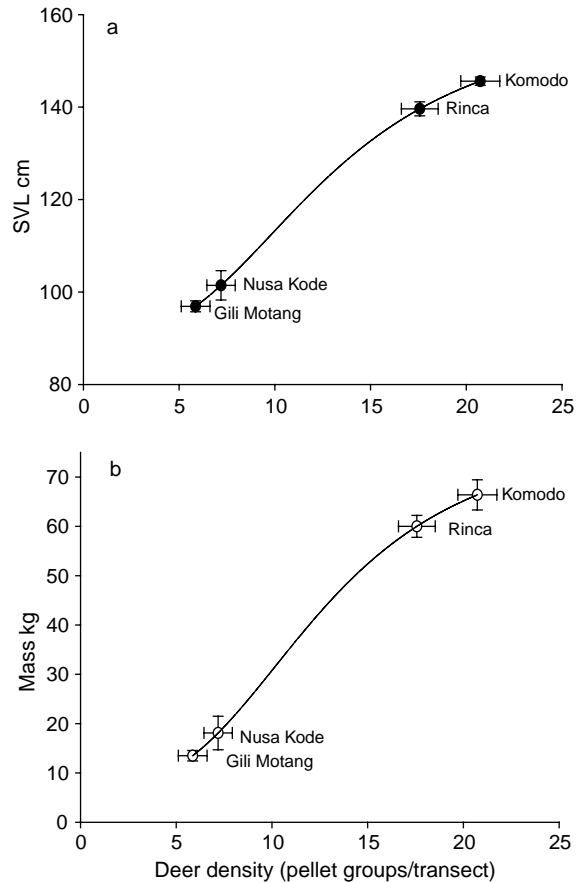


Fig. 4. The relationships between island specific mean deer density (based on the average number of deer fecal pellet groups per transect) and the largest 15% of individuals for SVL (a) and body mass (b) calculated for each island population. Bidirectional error bars are presented as the standard error of the mean (SEM, horizontal bars = deer density SEM; vertical bars = body size SEM).

15% of dragons found on Komodo Island compared to the largest 15% of dragons found on Gili Motang, with mass varying by more than four fold. Of the extant populations persisting within Komodo National Park, the two small islands of Gili Motang and Nusa Kode possessed the lowest maximal body sizes, whilst Komodo and Rinca, the largest and second largest islands, possessed individuals with the largest maximal body size.

These extremes in Komodo dragon maximal body size amongst islands appear to covary with the corresponding island density of the key large prey species, the Timor deer. It was evident that the two smallest islands containing the smallest dragons in Komodo National Park also coincided with a 3–4 fold lower density of Timor deer and also lacked the presence of the other two ungulate prey species. Thus maximal body size in Komodo dragons appear to be strongly associated with the density of large prey; lizards reached greater body

size on the large islands with the highest densities of deer, pigs and buffalo, compared to dragons inhabiting the small islands which contained the lowest-densities of deer and no pigs or buffalo. In other island dwelling reptiles, large differences in body size has been attributed to density differences in prey or forage availability and, equally importantly, the size of prey (Case and Schwaner 1993, Boback 2003, Wikelski and Romero 2003).

How could deer density influence maximal body size in adult Komodo dragons among the four islands? In general, populations on small islands are thought to be more prone to the effects of resource limitation, resulting in a decrease in maximal body size (Heaney 1978). Both Gili Motang and Nusa Kode are extremely small ($<11 \text{ km}^2$) relative to Komodo and Rinca ($>230 \text{ km}^2$), and their deer density is low; suggesting that availability of preferred large prey has limited the upper body size in this species. Further, given the small land mass of these two islands, stochastic influences would be predicted to have greater impacts on these dragon populations than those living on larger islands. Reduced maximal body size in the two island populations may, however, be a local evolutionary strategy for dealing with a small island environment. A reduced body size for dragons could maximize fitness via several mechanisms: a reduction in body size could enable dragons to access a broader range of prey and thus retain the capacity to switch between smaller and more varied prey species, rather than relying on a single species of larger prey. In addition, because absolute energetic requirements scale with body size (Schmidt-Nielsen 1984), a reduction in maximal body size on small islands would result in a decreased requirement for prey, making smaller sized dragons more efficient with respect to absolute energetic requirement relative to island populations with a larger body size. Concurrently, life-history traits tend to scale with body size, so that smaller-sized dragons may exhibit a reduced age to maturity and perhaps reduced interbreeding intervals for females (Calder 1984). Such life-history traits may enable individuals to maintain a viable population in these small island environments.

At present we can not conclude if these large differences in body size between small and large islands within Komodo National Park represent local genetic adaptation or a phenotypically plastic response by Komodo dragons to the different prey densities available on each island. To distinguish between genetic and/or phenotypic differences in Komodo dragon body size would require use of a common garden experiment, in which hatchlings from the four islands are raised under identical conditions to observe whether inherited differences are reflected in different growth patterns (Niewiarowski and Roosenburg 1993, Tracy 1999, Sears and Angilletta 2003). However the logistical, bureaucratic and time constraints involved in undertaking such an

experiment would be prohibitive for Komodo dragons. For the four islands within Komodo National Park, previous population genetic studies have indicated variation in gene flow among insular populations (Ciofi et al. 1999, Ciofi and Bruford 1999, Ciofi 2002). This variation essentially reflects differences in spatial and temporal isolation among the islands. These differences in gene flow could also underpin the capacity for local adaptation versus phenotypic plasticity to explain differences in maximal body size among insular Komodo dragon populations. Island populations that receive little gene flow, such as the relatively isolated Gili Motang (Ciofi 2002) might be predicted to exhibit a greater potential for local evolutionary responses, rather than phenotypic processes, to influence body size. In contrast the island of Nusa Kode, which also possesses a dwarf population, is in close proximity ($<800 \text{ m}$) to Rinca and these two populations exhibit high levels of migration (Ciofi 2002). Thus the homogenising effects of high gene flow (Slatkin 1973) could be expected to prevent adaptive differentiation in body size on Nusa Kode. Thus phenotypic constraints on growth due to a low density of prey on this small island could explain the observed differences in body size between these two neighbouring islands.

Across the four islands, population body size distributions also exhibited noticeable frequency differences among size classes (Fig. 2). Perhaps of most interest was the fact that on Komodo Island there was a greater proportion of large individuals compared to Rinca, where similar maximal body sizes are attained. These population differences in size structure could presumably influence community structure, population dynamics and even intraspecific interactions. For example, smaller dragon size classes ($>50 \text{ cm SVL}$) also ingest deer, both directly or indirectly (e.g. through carrion or scavenging at fresh kills by larger dragons), albeit less frequently than adults (Auffenberg 1981). Thus the effects of having a higher frequency of large adults in the population might lead to differences in the survival and energy intake of smaller size classes. Further research is needed to assess how both the frequency (with density incorporated) of large adult dragons could presumably underpin intraspecific and broader trophic interactions operating in this tropical island ecosystem.

Acknowledgements – Special thanks to Deni Purwandana and Jeri Imansyah and to the many Komodo National Park rangers and technical staff who assisted in the field work. Mats Olsson made helpful comments on the manuscript, as did David Forsyth with respect to deer census methods. This research was conducted as a collaborative program with staff from Komodo National Park. Approval for research was conducted under a MOU between the Zool. Soc. of San Diego, The Nature Conservancy (Indonesia program) and the Indonesian Dept of Forest Protection and Nature Conservation (PHKA). Financial support for research was provided by a Millennium post-doctoral fellowship from the Zool. Soc. of San Diego (to TSJ), and grants from the Amerman Family Fund, the Offield Family Fund, and an IMLS grant # IC-10161-01. Further

support (to CC) came from Columbus Zoo, Denver Zool. Foundation, Miami Metro Zoo and Woodland Park Zoological Society.

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Subject Editor: Tim Benton