

MAXIMUM BODY SIZE AMONG INSULAR KOMODO DRAGON POPULATIONS COVARIES WITH LARGE PREY DENSITY

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Running title: INSULAR SIZE VARIATION IN KOMODO DRAGONS

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ABSTRACT

This study documents variation in maximum body size of Komodo dragons (*Varanus Komodoensis*) among the 4 extant island populations, 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 439%. 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. 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.

KEYWORDS: maximal body size, island populations, prey density, lack of interspecific competition, resource limitations

INTRODUCTION

Across an island archipelago, body size within a single species may span from dwarf to gigantic. A number of mechanisms have been postulated as responsible for this variation in body size among islands, including interspecific competition (Lomolino, 1985; Roth, 1992; McNab, 1994, Petren & Case, 1997), sexual selection (Wikelski & Trillmich, 1997) resource availability, and its interplays (Heaney, 1978; Anderson & Handley 2002; Boback, 2003). 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 & Sarre, 1988; 1990; Petren & Case, 1997; Wikelski & 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 1998; Losos, Warheit & Schoener, 1997). Similar observations of gigantism have been described in Chuckwalla lizards (*Sauromalus*) from two islands. Behavioral comparisons to mainland conspecifics suggests relaxation of predation as the selective force responsible (Petren & Case, 1997). 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 (Boback, 2003; Madsen & Shine, 1992). 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 & 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 & De Boer, 2004). Four of these islands occur within the boundaries of Komodo National Park (KNP). 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 primarily island area, and its interactions with physiogeographic variables (e.g. topographic relief and rainfall; MacArthur & 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 especially adults, 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 predicted that maximal body size would scale positively with the density of ungulate deer and that most-likely 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 manipulate body size, including predation pressure and interspecific competition for food (Dunham et al., 1978; Wikelski, et al., 1997). Fortuitously, 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 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 KNP. Data from each site collected over the 2 consecutive years was pooled. On Nusa Kode, only a small sample size ($N = 9$) was collected after 2 years because of this island's presumably small 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, of 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 difference among samples collected from Nusa Kode between 1998 and samples collected in 2003 and 2004 with respect to mass and snout-vent length (T-test, $t = 0.78$, $P = 0.86$).

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 0.5cm 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 20kg (Jessop, unpublished data). Dragons were permanently marked using passive integrated transponders (Trovan ID100a). Processing time was usually less than 20 minutes 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 & 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 hemiclitoral 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 assessing abundance of Timor deer, were not possible in these study sites due to interchange of habitat types (which comprised the majority of most of the 10 study areas), and other direct methods (e.g., distance sampling) were

inappropriate because deer avoid people and would likely generate severely negatively biased estimates of abundance. We therefore chose to use indirect survey techniques (reviewed in 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 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 meter long transect. Each plot was a circle with a radius of 1 m and an area of 3.14 m². All faecal matter within the plot were recorded. For deer, 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 dung, as additional prey- covariates on influencing body size in Komodo dragons as their distribution is restricted to only 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 and 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 (60-120cm SVL = 57.00%) compared to the Komodo population which contained 26.12 and 45.57% for small and medium sized lizards, respectively. With respect to the largest individual captured in our study, a specimen measuring 154.05

cm SVL (304 cm total body length) and, without obvious distension of the gut due to recent ingestion of prey, weighed 81.5 kg was captured in Loh Liang on Komodo Island.

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 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 largest islands of Komodo, and Rinca were significantly longer and heavier than populations on the smallest islands of Gili Motang and Nusa Kode.

INTER-ISLAND VARIATION IN UNGULATE DENSITY

Density of deer pellet groups varied between islands from 5.86 ± 0.75 groups per transect on Gili Motang to 20.73 ± 1.02 groups per transect on Komodo (Fig. 4). For the islands located within Komodo National Park there was a high correlation between the mean island count of deer pellet groups, an index used to assess deer density, and lizard snout vent length ($R^2 = 0.99$, $F_{1, 3} = 448.64$, $P = 0.002$) and body mass ($R^2 = 0.99$, $F_{1, 3} = 252.82$, $P = 0.004$).

DISCUSSION

Island-dwelling reptiles demonstrate considerable plasticity in body size and may vary over a magnitude in mass among the largest individuals from different populations (Boback 2003; Schwaner & Sarre, 1988; 1990; Petren & Case, 1997; Wikelski & Trillmich, 1997). 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 15% of dragons found on Komodo island compared to the largest 15% of dragons found on Gili Motang, with mass varying by 439%. The two small islands of Gili Motang and Nusa Kode possessed the lowest maximal body sizes within the extant populations persisting within Komodo National Park and in turn Komodo and Rinca, the first 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 KNP also coincided with a 3-4 fold lower density of Timor deer and also lacked the presence of the other two ungulate species. Thus maximal body size in Komodo dragons appear to be strongly associated with the density of large prey in that 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 differences in prey abundance or forage availability and,

equally importantly, the size of prey (Boback, 2003; Case & Schwaner, 1993; Wikelski & 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 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, 1994). Such life-history traits may enable individuals to maintain a viable population in these small island environments.

Do these large differences in body size between small and large islands within KNP represent local genetic adaptation or a phenotypically plastic response by Komodo dragons to the different prey densities available on each island? At this stage this is impossible to resolve without performing 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 (Sears & Angilletta, 2003). However the logistical, bureaucratic and time constraints involved in undertaking such an experiment would be prohibitive for Komodo dragons. Similar constraints have prevented analysis for determining the genotypic or phenotypic basis underpinning large insular difference in body size between marine iguana populations (Wikelski et al., 1997). However, in marine iguanas, Wikelski et al. (1997) suspected that both phenotypic plasticity and genetic factors could drive realised maximal body size obtained due to supplemental feeding.

For the four islands within KNP, previous population genetic studies have indicated variation in gene flow among insular populations (Ciofi et al., 1999). This variation essentially reflects differences in spatial and temporal isolation among the islands. Is it possible that differences in gene flow could underpin the capacity for local adaptation versus phenotypic plasticity to underpin differences in maximal body size among insular Komodo dragon populations? For example, the small island of Nusa Kode is in close proximity (< 800 meters) of the south coast of Rinca, and populations from these localities are genetically very similar. Pair-wise comparisons of three standard genetic distance measures reported non-significant values between sites (Ciofi, 2002). Moreover, 89% of individuals sampled on Nusa Kode had their genotypes assigned to

southern Rinca, indicating high levels of migration between the two islands (Ciofi, 2002). The low deer density on Nusa Kode is therefore likely to be the major factor constraining maximal body size on this small island through phenotypic plasticity. Essentially, if large prey were more abundant, they could be expected to achieve the larger body sizes found on neighbouring Rinca. In contrast, Gili Motang has been isolated from both Rinca and the large island of Flores for approximately 10 000 years, coinciding with the last interglacial period (Chappel & Shackleton, 1986; McCulloch et al., 1999). Extremely low levels of migration between Gili Motang and other islands is thought to be responsible for a high degree of genetic drift leading to the fixation of four of nine microsatellite loci analysed (Ciofi & Bruford, 1999). Thus there is perhaps a greater potential for local adaptation through evolutionary changes to be manifested with respect to a reduction in maximal body size on this island compared to Nusa Kode.

Across the four islands, population body size distributions also exhibited noticeable frequency differences among size classes (Fig. 2). Perhaps of most interest, was 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 cm SVL), ingest deer, albeit less frequently than adults, both directly or indirectly (eg through carrion or scavenging at fresh kills by larger dragons) (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 both intraspecific and broader trophic interactions operating on these tropical island ecosystems.

Conclusions

Among the four extant island populations within Komodo National Park, Komodo dragons exhibit considerable variation in body size. Furthermore, this size variation is strongly associated with the density of Timor deer, the preferred large prey item of this species. At present we are unable to determine the basis, be it genotypic or phenotypic, to these differences in adult maximal body size among island populations. However, scaling of body size to the availability of large prey may result in facultative/obligative survival advantages that could promote fitness of individuals. This far we have addressed the influence of only one covariate (i.e. large prey density) that is strongly associated with maximal body size in insular populations of Komodo dragons. However future research is needed to understand the ultimate mechanisms by which large prey density influences maximal body size. As yet, it remains unknown how important the interaction between large prey availability and the strength of sexual selection is on determining body size and in particular adult male Komodo dragon body size among islands. Interactions between sexual selection and natural selection acting on maximal body size and mediated through food availability have been well documented in other island dwelling reptiles (Madsen & Shine, 1993; Wikelski & Trillmich, 1997). We hope to address similar questions for maximal body size variation among insular population of

Komodo Dragons once the means for genetic based sexing methodologies becomes established within Indonesian research institutions.

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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 \pm 2.4545	23.47 \pm 1.5690	226
Rinca	86.29 \pm 1.9721	20.94 \pm 1.1765	228
Gili Motang	74.76 \pm 2.4686	7.89 \pm 0.8514	39
Nusa Kode	83.14 \pm 3.6973	10.83 \pm 1.4031	20

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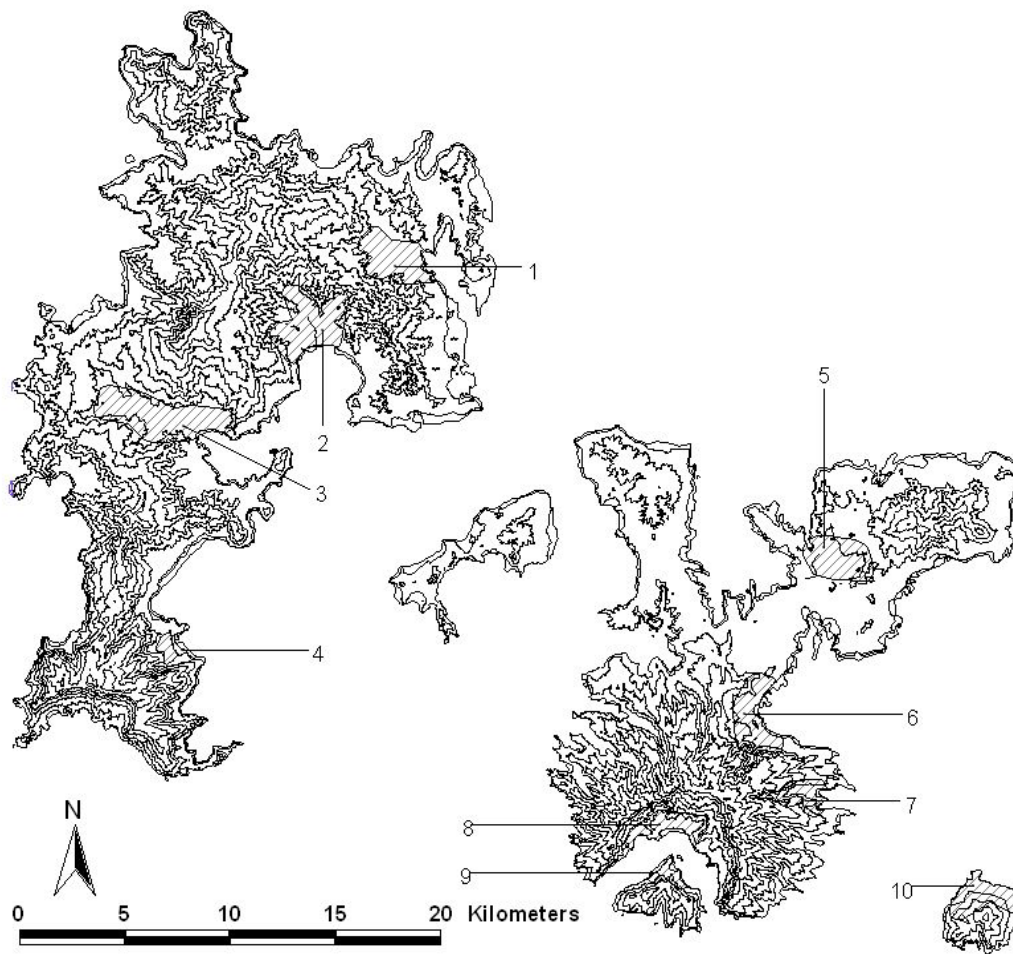


Figure 1. The distribution of Komodo dragon populations across islands in Komodo National Park Indonesia. Sampling sites are marked numerically and were situated across 4 islands and include Komodo Island sites: 1) Loh Sebita 2) Loh Liang, 3) Loh Lawi, 4), Loh Wau,5); Rinca Island sites: Loh Buaya, 6) 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.

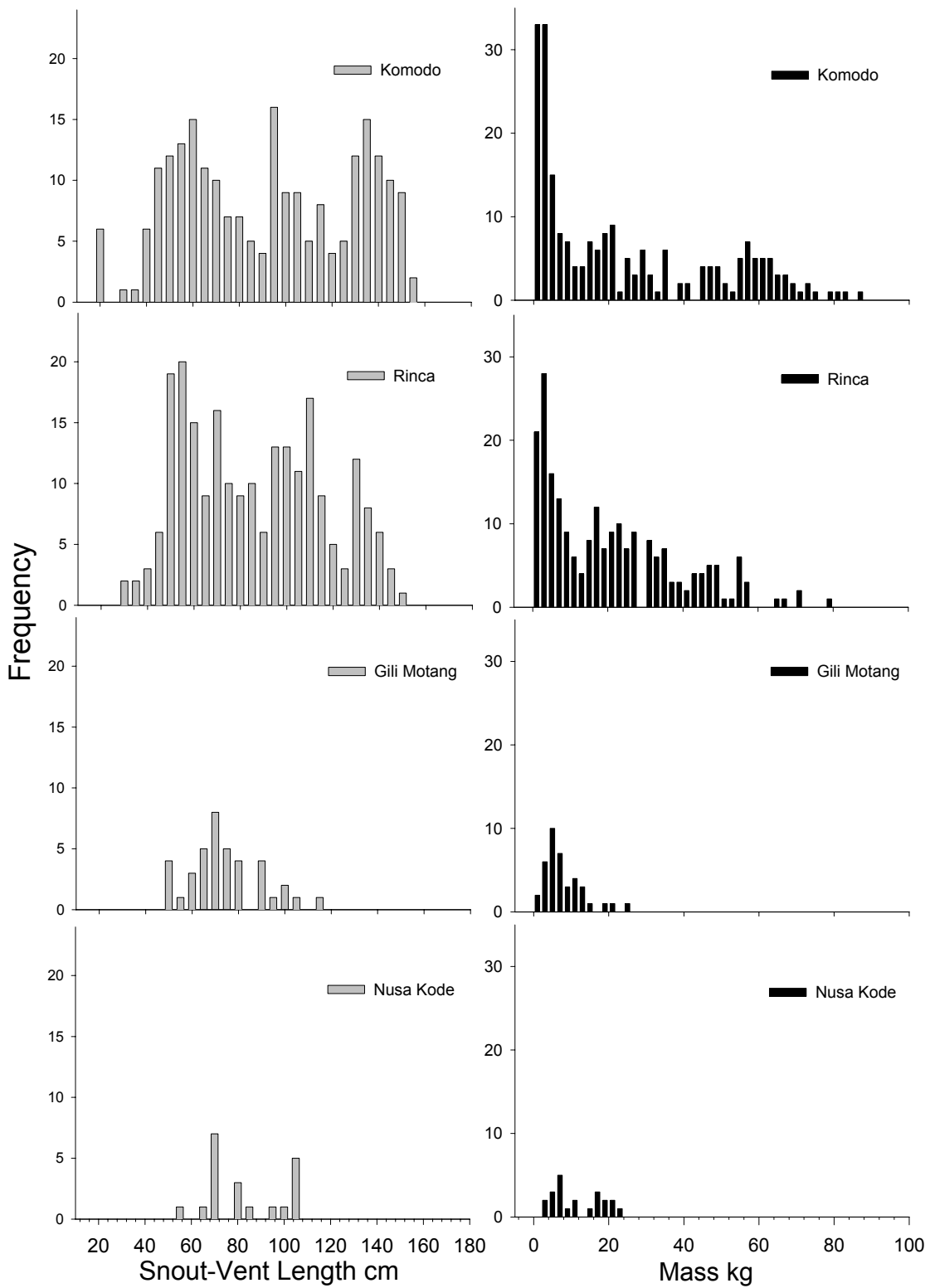


Figure 2. Frequency distribution of snout-vent length (grey bars) and body mass (black bars) of four island populations of Komodo dragons within Komodo National Park.

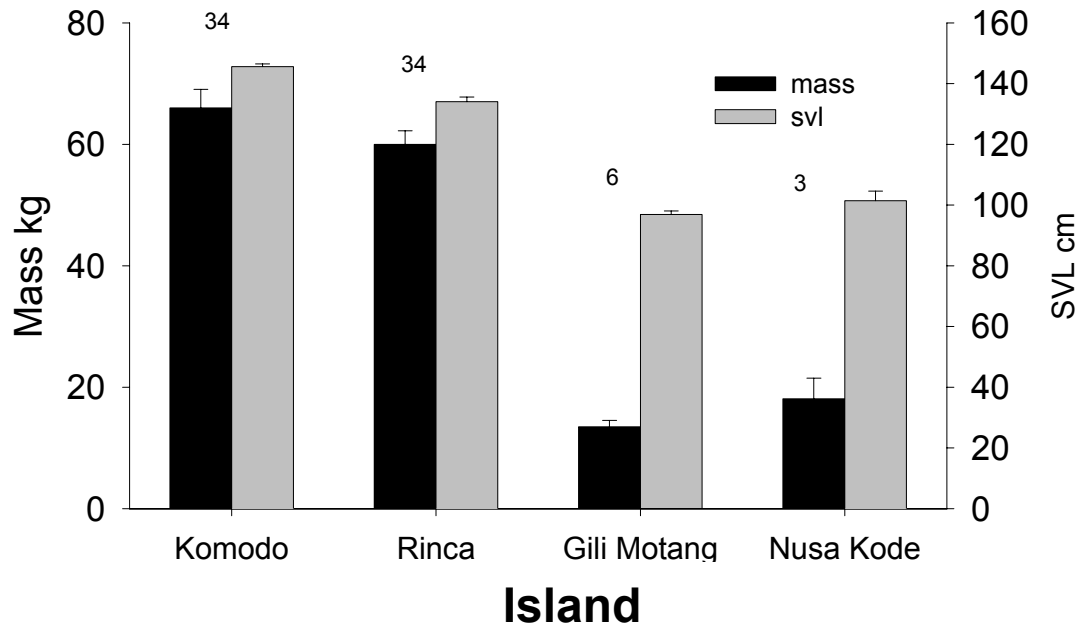


Figure 3. Komodo dragon mass and snout to vent length (SVL) for 4 islands in Komodo National Park, calculated using the largest 15% of individuals in each population.

Sample sizes for each island are presented above the bars. All data was collected in 2003-2004.

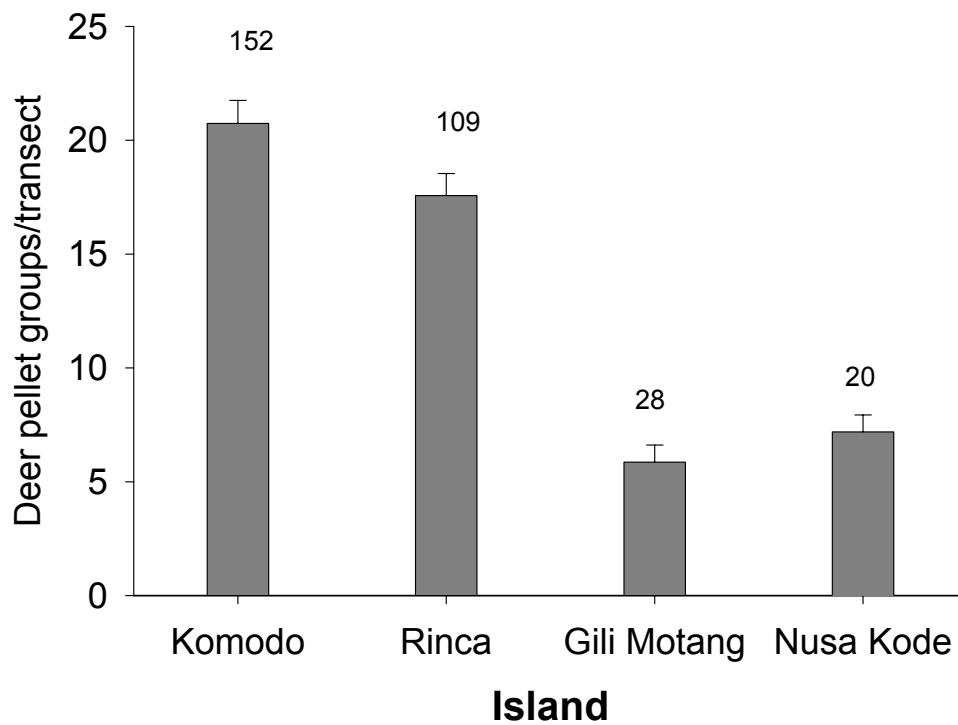


Figure 4. An index of island specific deer density based on the average number of deer fecal pellet groups per transect calculated for each island. Data is presented as the mean and the SEM. The number of transects per island is denoted by the number above the bar.