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Effects of human activities on Komodo dragons in Komodo National Park

Ardiantiono[1,5] · Tim S. Jessop[2] · Deni Purwandana[1] · Claudio Ciofi[3] · M. Jeri Imansyah[1] · Maria Rosdalima Panggur[4] · Achmad Ariefiandy[1]

Abstract

Understanding how threatened wildlife can coexist with humans over the long term is a central issue in conservation and wildlife management. Komodo National Park in Eastern Indonesia, harbors the largest extant populations of the endemic Komodo dragon (*Varanus komodoensis*). Consistent with global trends, this species is expected to be increasingly exposed to human activities and in particular growing ecotourism activities. Here we comprehensively evaluated how human activities affected individual and population level attributes of Komodo dragons. We compared Komodo dragons phenotypic (behaviour, body size, and body condition) and demographic (age structure, sex ratio, survival, and density) responses to variation in human activities across national park. Komodo dragons were found to exhibit pronounced responses to high human activity level relative to sites with low and negligible human activities. Komodo dragons exposed to ecotourism exhibited significantly less wariness, larger body mass, better body condition, and higher survival. These results are entirely consistent with ecotourism activities that provided Komodo dragons with long-term and substantial nutritional subsidies as a consequence of feeding and human food refuse. However, we also noted the potential negative consequences of altered behaviour and adult-biased populations in ecotourism areas which may influence demographic processes through intraspecific competition or predation. To address this issue, we recommend that three management strategies to be implemented in future include: (1) removal of human-mediated nutritional subsidies, (2) alternative ecotourism, and (3) spatial regulation of ecotourism. Furthermore, we advocate the development of approaches to achieve a socio–ecological sustainability that benefits both people and wildlife conservation.

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✉ Ardiantiono
   ardiantiono.tjokro@gmail.com

Extended author information available on the last page of the article

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Introduction

Humans have caused broad scale changes in the ecological and evolutionary dynamics of natural systems (Vitousek et al. 1997). Key human mediated processes that affect biodiversity and ecosystems include exploitation, degradation, and loss of natural resource via habitat modification, encroachment, and illegal harvesting (Vitousek et al. 1997; Butchart et al. 2010). Ecotourism is a relatively recent human activity that has experienced substantial growth in the past few decades and now raises concern for its complex effects on wildlife and habitats (Krüger 2005; Buckley 2011).

It is currently estimated that terrestrial protected areas receive eight billion tourists visits per year (Balmford et al. 2015). Tourism is a major human activity in protected areas and includes multiple types of tourism (e.g., often classified into two branches mass tourism and alternative tourism) (Beaver 2005). In this study we focus on ecotourism, as one sector of alternative tourism, which is increasingly recognized for its capacity to provide both benefits and costs to biodiversity (i.e., wildlife and habitats). Ecotourism is defined as the human visitation of relatively undisturbed natural areas and is undertaken for the specific purpose of enjoyment of natural (e.g., scenery, animals and plants) or cultural values (Rai 2012). Positive effects of ecotourism include increased political and financial support and may promote research and conservation efforts with local stakeholders and tourist operators (Buckley et al. 2012; Higginbottom 2004). Ecotourism can provide increased protection to wildlife and their habitat through increased supervision in protected areas (Macdonald et al. 2017). Additionally, this activity can promote public knowledge and enhance positive attitudes toward wildlife and habitats (Curtin and Kragh 2014). Furthermore, ecotourism can also provide alternative socio-economic opportunities and improve the livelihoods for local communities around protected areas and this may even help abate impacts within protected areas (Goodwin 2002; Higginbottom 2004).

However, ecotourism may also have important consequences for wild animals and associated habitats. As such there is an increasing interest to understand how ecotourism activities influence animal behaviour, health, breeding success, and survival (Schoenecker and Krausman 2002; Ellenberg et al. 2006; Amo et al. 2006). Although ecotourism effects on animals are often predicted to be commensurate with the volume of human visitation and associated infrastructure development (Krüger 2005), the effects nevertheless can be highly variable and contextual with both positive and negative effects being reported. For example, some animals exposed to ecotourism activities increased their antipredator behaviour including vigilance and flight responses (Papouchis et al. 2001; Dyck and Baydack 2004). These behaviours are potentially costly as they reduce the animals' time, energy, and opportunities to engage in other fitness-enhancing activities (Ellenberg et al. 2006). Alternatively, animals may also adapt to tourists by muting their reactions and become habituated (Herrero et al. 2005; Rodriguez-Prieto et al. 2009).

Additionally, supplementary feeding or food provision to wild animals is a common ecotourism-related activity. This practice is used to aggregate animals to specific locations and improve tourist's ability to encounter wild animals (Orams 2002; Massé et al. 2014). For large predators that are often cryptic, supplemental feeding may increase tourist-wildlife interactions (Brunnschweiler and Baensch 2011) but eventually lead to a range of complex behavioural and physiological consequences for wild animals (Orams 2002; Jessop et al. 2012; Smith and Iverson 2016).

Ultimately, ecotourism mediated effects on animal's phenotype can lead to changes in fitness (e.g., survival, reproduction) and in turn influence population dynamics (Buckley

et al. 2016). Physiological responses to human disturbance such as increased heart rate, stress hormone levels, and energy expenditure can have population level consequences such as reduced breeding success and survival (Dyck and Baydack 2004; Ellenberg et al. 2006). Conversely, ecotourism related food subsidies consumed by animals can influence demographic parameters such as improved fecundity, survival, and population growth (Orams 2002; Jessop et al. 2012). Thus, in order to understand the effect of human activities on wild animals and evaluate potential conservation management implications it is necessary to investigate anthropogenic consequences on both individuals and populations.

The world heritage listed Komodo National Park is a major protected area in Eastern Indonesia and comprises both marine and terrestrial island habitats. A key reason for the establishment of this protected area was to conserve the endemic Komodo dragon (Iriyono et al. 2012). Komodo dragons are large (up to 87 kg; 3 m), long-lived (up to 60 years) predatory lizards (Auffenberg 1981; Jessop et al. 2006; Laver et al. 2012). These lizards have a highly restricted distribution range and extant populations persist on five islands, four of which are in Komodo National Park (Ciofi and de Boer 2004). These dragons are flagship species and represent the main tourist attraction in Komodo National Park (Walpole 2001).

Whilst recent studies have reported how environmental or ecological processes influenced phenotypic and population characteristics of Komodo dragons, there remains limited understanding of how human activities affect dragon ecology across Komodo National Park (Purwandana et al. 2014, 2015). A previous study reported how tourist related supplementary feeding conducted during 1980s–1990s led to six fold density increases of Komodo dragons at feeding sites compared to adjacent areas (Walpole 2001). However, a limitation of this study was that it not determined if density related feeding effects arose because food attracted individuals, or supplemental nutrition improved reproduction or survival which then resulted in increased density. Nevertheless, this study suggested that ecotourism activities could alter the ecology of Komodo dragons, a point that deserves more detailed investigation given that human activities, given that up to 107,000 tourists per year currently visit Komodo National Park (Balai Taman Nasional Komodo 2017).

This study aimed at understanding to what extent different levels of human activities affected Komodo dragons by documenting changes in behaviour (initial reaction to human encounters and approach distance), morphology (body size and condition) and demography (population age structure, sex ratio, survival, and density). In particular, we investigated how Komodo dragon phenotypic and demographic responses were influenced by three levels of human activities that were categorized into (1) high activities from ecotourism, (2) low but routine activities from Komodo National Park rangers, and (3) negligible human activities. In Komodo National Park, because of management related zonation practice, differences in these human activities are largely spatially regulated and thus provide an excellent opportunity to understand how scales of human interactions influence Komodo dragon ecology (Ramono et al. 2000; Iriyono et al. 2012).

Materials and methods

Study area

We studied the effects of human activities on Komodo dragons across Komodo (393.4 km^2) and Rinca (278.0 km^2) Islands, the two largest islands in Komodo National Park (8°35′22″S, 119°36′52″E; Fig. 1). These islands have a tropical monsoonal climate,
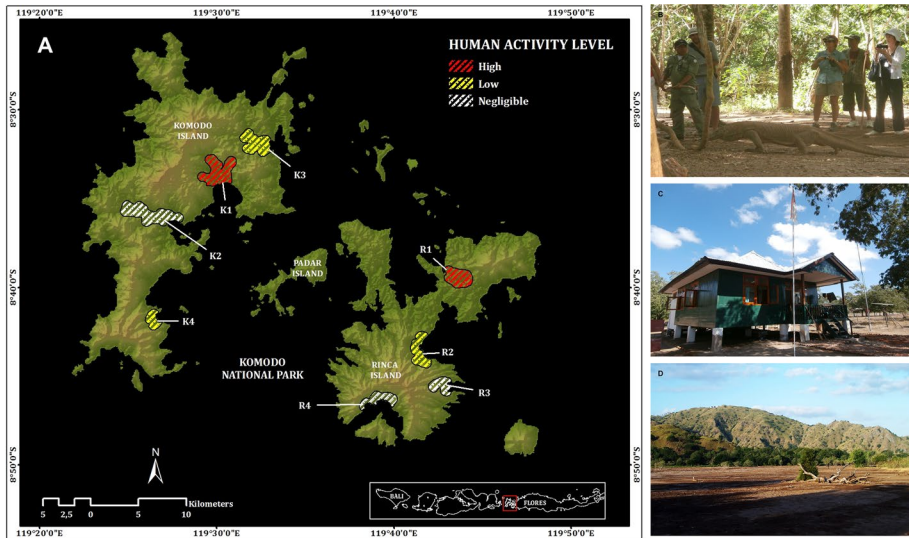
Fig. 1 Locations (**a**) of the eight study sites in Komodo National Park used to assess different levels of human activities on phenotypic and demographic attributes of Komodo dragons. Study sites and their corresponding human activity level are represented by (K1) Loh Liang, (K2) Loh Lawi, (K3) Loh Sebita, (K4) Loh Wau on Komodo Island; whilst (R1) Loh Buaya, (R2) Loh Baru, (R3) Loh Tongker, (R4) Loh Dasami were located on Rinca Island. Inset depicts location of Komodo National Park within Indonesia. Examples of different human activities considered in this study included **b** tourist visitation in high human activity areas (K1, R1), **c** ranger posts in low human activity areas (K3, K4, R2) and **d** areas where Komodo dragons were exposed to negligible human activity (K2, R3, R4)

with most annual rainfall (mean ~ 850 mm) occurring between December and February (Monk et al. 2013). We selected eight sites across these two islands to conduct our study. Four sites were located on Komodo Island: (1) Loh Liang (K1; 5.6 km^2), (2) Loh Lawi (K2; 9.2 km^2), (3) Loh Sebita (K3; 3.8 km^2) and (4) Loh Wau (K4; 1.6 km^2). Another four sites were located on Rinca Island: (5) Loh Buaya (R1; 4.5 km^2), (6) Loh Baru (R2; 3.4 km^2), (7) Loh Tongker (R3; 3.1 km^2) and (8) Loh Dasami (R4; 2.3 km^2). These eight sites were divided into three categories based on their human activity levels:

1. High human activity areas: Sites K1 and R1 (Fig. 1) harbor the highest level of human activities (~ 500/people/day/site) as a consequence of been designated areas for tourist visitation (mean 30,757 with range of 11,587–63,801 visitors per year between 2002 and 2013) and a permanent presence of Komodo National Park staff (~ 10–15/people/day/site). These sites have permanent buildings (~ 600 m^2 floor area) that provide accommodation, offices and cafeterias for Komodo National Park staff or tourists. Habitat adjacent to these buildings (~ 1 ha) were converted from adjacent wooded vegetation types to lawn.

   Additional human activities at these sites included supplementary feeding from goat meat to attract Komodo dragons for visitor watching, or from food refuse produced by the permanent presence of Komodo National Park staff and cafeterias. Adjacent natural habitats in these sites were regularly exposed to human visitation through multiple daily guided walks for tourists and regular ranger patrols (i.e., used to monitor wildlife and

illegal activities). These activities were largely concentrated along a specific network of walking trails.

(2) Low human activity areas: Sites K3, K4 and R2 (Fig. 1) harbored a low level of human activities (~ 3 people/day/site). Each site has one small building (~ 144 m^2) permanently occupied by 2–3 rangers. Here limited supplementary feeding was present due to ranger food refuse. Routine ranger patrols were conducted every other day and infrequent guided tourist visitation occurred.

(3) Negligible human activity areas: Sites K2, R3 and R4 (Fig. 1) comprised park core areas that are exposed to negligible human activities as they lack permanent buildings, absence of tourist visitation, and infrequent human presence.

Field protocols

Evaluation of Komodo dragon behaviour responses to human activities

Assessment of Komodo dragons' behavioural responses occurred at all eight sites during August–September in 2013 coinciding with annual monitoring activities. This activity followed after we finished our capture-mark-recapture based population monitoring activities (described below). The delay in behavioural assessment reflected that, unlike demographic parameters which required multiple years of monitoring to allow for robust demographic estimates in long-lived species, this data could be collected rapidly. However, because of logistical reasons, we could only allow for a single annual behavioural estimate that would be best indicated by data collected following completion of the population monitoring activities.

We collected behavioural data for 2–3 days at each study site between 0700 and 1600 h coinciding with the peak daily activity period of Komodo dragons (Auffenberg 1981). Observations were made during routine walks along trails (~ 20 km/day). Behaviour of each individual of Komodo dragon encountered was measured once only. To recognise, and prevent repeated observations, of individuals, we relied on the presence of unique paint codes (applied to lizards during complimentary mark recapture study) or other physical attributes including an individual's body size, presence of scars and the extent of partial tail loss. Additionally, we discounted subsequent observations that were within 30 min or less than 200 m from the previously recorded encounter. We recorded two behaviours of Komodo dragon to human encounters:

1. *Approach distance*—this behaviour represented the proximity that an observer could approach a Komodo dragon before the lizard turned their head and looked at the observer. To standardize the scoring of approach distance, observers (AR/AA) approached Komodo dragons in a straight line and at a constant speed (3 km/h). The approach distance was measured using a 30 m long tape measure to estimate the straight line distance between the observers and the Komodo dragon's position at which the behavioural response was initiated.

2. *Initial reaction type*—this behaviour was defined as the immediate reaction of the Komodo dragon to the approaching observer and scored as either no response (the

animal continued its normal activity) or avoidance (the lizard moved away from the observer).

Evaluation of Komodo dragon morphological and demographic responses to human activities

Trapping protocols During the dry season (March–November) from 2002 to 2012, annual capture-mark-recapture of Komodo dragons occurred at each of the eight study sites (Fig. 1). We used aluminum cage traps (300 cm long × 50 cm high × 50 cm wide) baited with goat meat to capture Komodo dragons. Nine to 32 trapping locations (mean = 22 ± site, N = 175) were established at the eight study sites. Trapping locations were located predominantly in deciduous monsoon forest landscape that is considered as high quality habitat for the dragons (Purwandana et al. 2014). Trapping at each site took between eight and 14 days to complete. Within sites, trapping were set for three consecutive days, with each trap checked twice daily between 0800–1100 and 1400–1700 h.

After capture, dragons were restrained with rope and their mouths taped closed, and several morphological measurements recoded as described below. Each dragon was permanently identified using a passive integrated transponder (Trovan ID100a, Microchips Australia Pty Ltd., Australia) inserted in the upper right hind leg. All dragons were released at their point of capture.

Body size and condition

We used two morphological measures to infer Komodo dragon phenotypic responses to different human activity levels. As a measure of Komodo dragon body size we recorded each individual's body mass (in kilograms) using a digital scale at the time of capture. We also recorded the Komodo dragon total body length (TBL) that was measured from the tip of the snout to the end of tail for each individual. As an index of body condition, a measure often used to describe the energetic, and hence health status of animals, we used the residuals from the regression equation of natural log transformed mass plotted against total body length (TBL, natural log transformed) (Schulte-Hostedde et al. 2005). This commonly used index infers that individuals with negative residuals for body condition have a lower than average body mass for their body length compared to individuals with positive residuals who have a higher than average body mass for their body length. This body mass index has been widely used in reptiles to infer physical change in body mass that reflect underlying changes to tissue (e.g., muscle and adipose), organ and skeletal mass that would arise from broad scale changes to the energetic (i.e., health) status of individuals (Schulte-Hostedde et al. 2005; Jessop et al. 2007). Log transformation was used to ensure there is no non-linear allometry in the relationship between body mass and total body length that could confound the use of this index (Jessop et al. 2007). Similarly the use of log transformed derived residuals provides a body condition index that is not correlated with an individual's body mass or body length (Schulte-Hostedde et al. 2005; Jessop et al. 2007).

Sex determination for sex ratio estimation

Sex was determined using molecular methods for a subset of 383 individual Komodo dragons (138, 58 and 187 individuals in high, low and negligible human affected

habitats, respectively). Genomic DNA was extracted from blood in lysis buffer using a DNeasy Blood and Tissue Kit (Qiagen), following the manufacturer's protocol. To determine potential sex ratio differences between treatments, dragon blood samples were genetically sexed using PCR primers that amplified sex specific alleles (Halverson and Spelman 2002). Amplifications were performed in a 20 μL total volume, containing 2 μL of DNA (diluted 1:10 in TE buffer), 10 μL Gotaq (Promega), 0.5 μL of each primer (10 μM) and 7 μL of H_2O. PCR amplifications were performed on a Corbett Palm-Cycler using a touchdown thermal cycle program with the following parameters: initial denaturation at 94 °C for 5 min, followed by two cycles of 94 °C for 30 s, an annealing step at 65 °C for 30 s and 72 °C for 90 s; 2 cycles each with annealing temperatures of 60 °C, 55 °C and 50 °C; 30 cycles with an annealing temperature of 48 °C; then a final extension step of 10 min at 72 °C. Amplifications were checked on a 1.2% agarose gel and amplification patterns were compared to those of a male and female whose sex had been verified anatomically.

Population survival

All survival analyses were conducted on capture-mark-recapture data using the Cormack–Jolly–Seber (CJS) model in program MARK (White and Burnham 1999). These analyses estimate apparent survival rather than true survival because mortality and emigration cannot be distinguished within the CJS model (Schaub et al. 2004). Apparent survival is an underestimate of true survival, but because emigration occurs rarely in our study system the difference is likely to be small.

Analyses were performed on a single combined dataset in which each site was coded based on its level of human activities (i.e., negligible, low, and high). To estimate survival, we developed a set of candidate models for analysis, evaluated goodness-of-fit, and estimated an overdispersion parameter ($\hat{c}$) for the data set. We used an information theoretic approach to select the most parsimonious model, based on the AICc model selection criterion (lower AICc values represented better fitting models). Models were then ranked using the quasi-likelihood AIC_c value (QAICc) to account for any overdispersion and their respective model weights (*w*) estimated to evaluate their strength of model support. We used estimated survival parameters from the top ranked model when there was clear support for a single model (i.e., model weight ≥ 0.9), otherwise we used a model-averaging approach that incorporated model selection uncertainty for all models with substantial model support (ΔAIC < 2 from top ranked model).

A candidate set of 16 models was assessed to evaluate group-specific survival estimates in Komodo dragons. These models considered variation in parameter combinations influencing Φ (apparent survival) and p (recapture probability). To model group variation in survival, we also considered null and fully time- and group-dependent models to enable assessment of models fitted with group specifications. Here, the survival and capture probability parameters were fitted with combinations of time (t), group (g, i.e., human activities levels) or constant terms.

Population density estimation Population density estimates were derived using the POPAN formulation of the Jolly–Seber (JS) method (Arnason and Schwarz 1995; Schwarz and Arnason 1996). The following parameters could be estimated from POPAN JS models: Φ, p, PENT (probability of entry into the population at each occasion), and N (size of superpopulation, i.e., the total number of individuals present within the population during the

entire study period). This JS model is assumed to be 'open', and allows additions (births and immigration) and losses (deaths and emigration) between successive sampling occasions (Schwarz and Arnason 1996).

A set of 32 Jolly–Seber models were tested on the data set where survival (Φ) and recapture (p) parameters were estimated by considering all combinations of time constant (.) or variable (*t*) time, and group (i.e., human activities levels) effects (models). The PENT parameter was modelled as time variable or group by time combination. The N parameter was modelled as function of group (i.e., N_g). POPAN produces two different estimates of population abundance: the super population estimate (N) and the derived annual abundance parameter ($N_{g,t}$) for each human activity level (g) at each annual sampling period (t). In this study we refer to the latter as we only wanted to estimate total abundances each human activity area. We assessed goodness-of-fit of the global model and estimated overdispersion using the median $\hat{c}$ implemented in program MARK. Komodo dragon population abundances were then estimated for each human activities level using only the 2011/2012 (i.e., final sampling period) derived estimate of annual population abundance (plus SEM; upper and lower 95% CI). To obtain population density estimates we divided annual abundance estimates for each site by its area.

The key assumptions of the CJS models are: (1) equal capture probabilities for individuals within a population; (2) capture occasions are non-lethal and instantaneous events; and (3) emigration is permanent (Williams et al. 2002). These assumptions are not likely to be violated for the following reasons. Komodo dragons exhibit year-round activities and hence are not overly sensitive to seasonal thermal variation; nor do they exhibit undue site-specific behavioural variation in trapping responses that could influence capture probabilities, which is necessary for robust estimates of lizard survival (Purwandana et al. 2014). Komodo dragon capture events are of short duration (< 3 h), and no mortality was recorded from our trapping or capture activities. Finally, incidents of Komodo dragons moving between sites (i.e., emigration) were rare during our study (Imansyah et al. 2008).

Statistical analyses

The study's statistical analyses comprised the use of six generalized linear mixed effect models (GLMM) that tested for the fixed effects of human activity level on each of the six uncorrelated dependent variables (i.e., reaction type, approach distance, body mass, body condition, sex ratio and density). As these dependent variables comprised data drawn from both Gaussian and non-Gaussian distributions, each model was fitted with its appropriate distribution and canonical link. For normally distributed data (i.e., approach distance and population density data), models were fitted with a Guassian distribution and identity link. For models that tested the effects of human activity levels on Komodo dragon reaction type and sex ratio data (i.e., categorical data), these were fitted with a binomial distribution and logit link. The model evaluating the effect of human activity levels on Komodo dragon age category data (i.e., ordinal type categorical data) was specified with a multinomial distribution and identity link. To each of these six models we included the random effect of site to account for data being collected from different localities. A second random effect comprising Komodo dragon identity (i.e., PIT tag number) was added to the two models that tested for the effect of human activity on body mass and body condition data, respectively. This additional random effect was necessary to account for multiple data measurements

obtained from the same individual being present within each of these data variables. All models were run using SPSS v.23 (IBM Corp, Amronk, USA).

Results

Behavioural responses of Komodo dragons

We recorded 54 behavioural responses of Komodo dragons across study sites: (1) high human activity area ($N=29$ responses); (2) low human activity area ($N=11$); and (3) negligible human activity area ($N=14$). We found that different levels of human activities were associated with significant differences in the initial reaction type of Komodo dragons (GLMM, $F_{2,51}=3.92$, $P = 0.026$; Fig. 2a). Komodo dragons in the high human activity
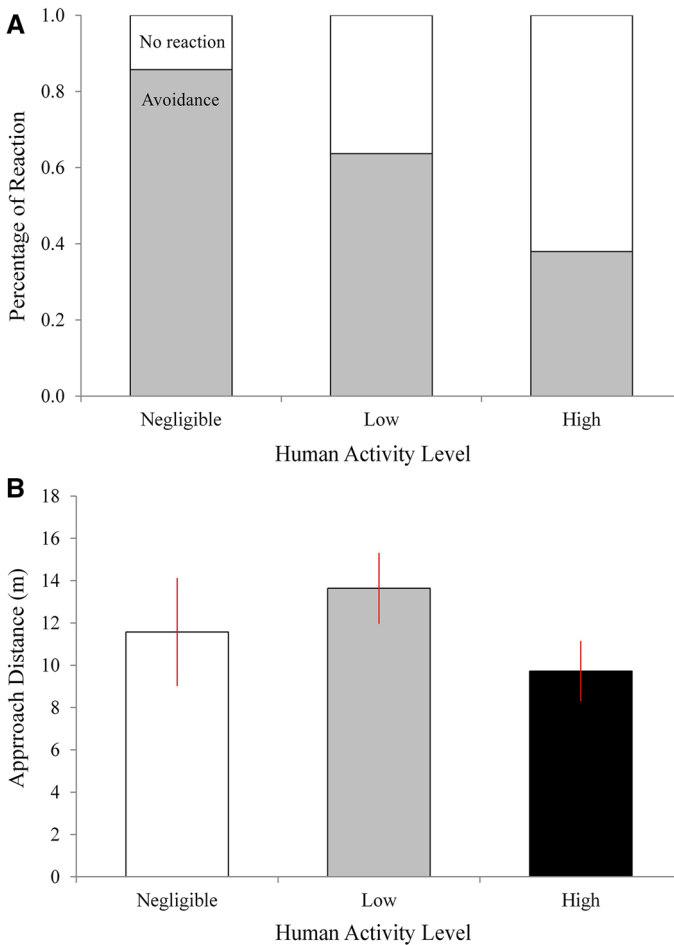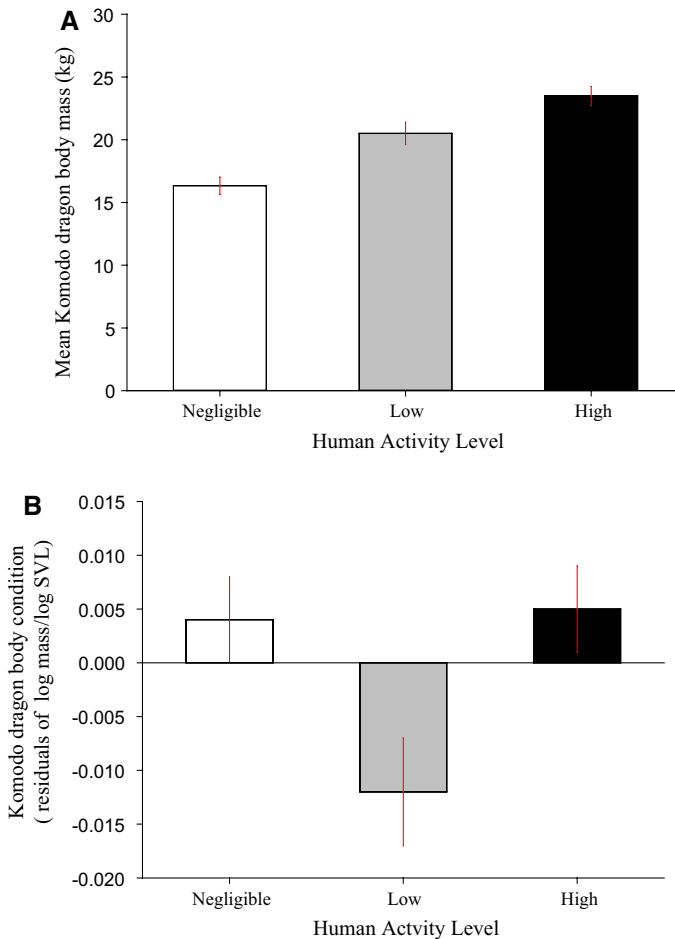

Fig. 2 The effects of three different levels of human activities on Komodo dragon behavioural responses including the **a** initial reaction type and **b** mean approach distance (± SEM)

areas had a significantly higher proportion of no reaction whilst in negligible human activity areas they tended to run or walk away (avoidance) when encountered. However, Komodo dragons approach distance did not differ among sites with different human activity levels (GLMM, $F_{2,51} = 0.86$, $P = 0.44$; Fig. 2b).

Morphological Responses of Komodo dragons

There was a highly significant effect of human activities on the body mass of Komodo dragons among sites (GLMM, $F_{2,1871} = 21.36$, $P < 0.001$). Body mass in high and low human activity areas were found to be significantly heavier than those from negligible human activity areas (Post-hoc tests, $P < 0.05$; Fig. 3a). There was no significant difference in lizard body mass between high and low human activity areas (Post-hoc tests; $P = 0.165$).
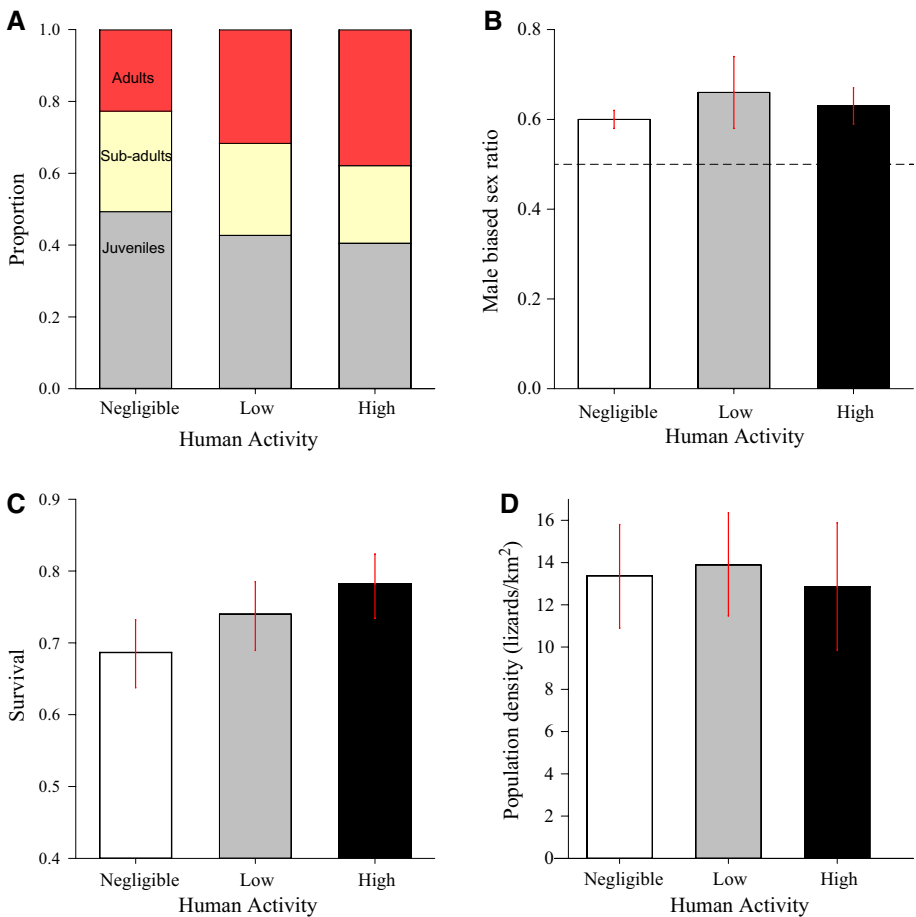

Fig. 3 The effects of three different levels of human activities on phenotypic attributes of Komodo dragons. Phenotypic attributes measured comprised **a** body mass and **b** body condition (residuals of log mass/log total body length ± SEM)

The body condition (residuals of body mass/TBL) of captured Komodo dragons significantly varied among the three human activity areas (GLMM$_{2,1871}$, F = 3.94, P = 0.020; Fig. 3b). Body condition of Komodo dragons in low human activity areas was significantly decreased ($P < 0.05$) compared to individuals in either high or negligible human activity areas.

Demographic responses of Komodo dragons

Age class proportion

Komodo dragon age class composition was significantly influenced by human activities (GLMM$_{2,1871}$, F = 9.28, $P < 0.001$; Fig. 4a). As human activity levels increased, the relative

Fig. 4 The effects of three different levels of human activities on demographic attributes of Komodo dragons. Demographic attributes measured comprised **a** age structure, **b** sex ratio ($\pm$95% SEM), **c** survival ($\pm$95% CI), and **d** population densities ($\pm$95% CI)

proportion of adult dragons and juveniles within populations increased and decreased, respectively.

Sex ratio

There was no evidence that Komodo dragon sex ratio was influenced by human activities (GLMM$_{2,380}$, F = 0.28, P = 0.76; Fig. 4b). The sex ratio of Komodo dragon populations comprised 0.60 ± 0.02, 0.66 ± 0.08, and $0.63 \pm 0.04\%$ of males for low, neglible and high human activity habitats, respectively.

Survival estimates

From 2003 to 2012, we encountered 825 individual lizards during 1856 capture events. The top model [Φ (g) p (t)] received high model support (ω = 0.92) and indicated that survival of Komodo dragons was strongly influenced by human activities (Table 1). Here, apparent survival (Φ) was highest for Komodo dragons occupying high human activity areas, followed by low and negligible human activity areas, respectively (Fig. 4c).

Table 1 Cormack–Jolly–Seber analysis on capture-mark-recapture data used to estimate survival for Komodo dragons populations across sites with three human activities levels in Komodo National Park between 2003 and 2012 (n = 825)

Model	QAICc	Δ QAICc	ωi	ML	K	QDeviance
Φ(g) p(t)	2246.48	0.00	0.92	1.00	9.00	2228.37
Φ(.) p(t)	2251.69	5.22	0.07	0.07	7.00	2237.62
Φ(g*t) p(t)	2256.36	9.88	0.01	0.01	23.00	2209.67
Φ(t) p(t)	2257.61	11.13	0.00	0.00	11.00	2235.44
Φ(g) p(g*t)	2258.77	12.29	0.00	0.00	21.00	2216.19
Φ(.) p(g*t)	2260.50	14.02	0.00	0.00	19.00	2222.02
Φ(g) p(.)	2262.67	16.19	0.00	0.00	4.00	2254.64
Φ(g) p(g)	2264.79	18.31	0.00	0.00	6.00	2252.74
Φ(t) p(g*t)	2266.38	19.90	0.00	0.00	23.00	2219.69
Φ(.) p(g)	2267.32	20.85	0.00	0.00	4.00	2259.30
Φ(.) p(.)	2268.09	21.62	0.00	0.00	2.00	2264.09
Φ(g*t) p(g*t)	2270.16	23.68	0.00	0.00	33.00	2202.75
Φ(g*t) p(.)	2270.83	24.35	0.00	0.00	19.00	2232.35
Φ(t) p(g)	2271.17	24.70	0.00	0.00	9.00	2253.06
Φ(t) p(.)	2271.97	25.49	0.00	0.00	7.00	2257.90
Φ(g*t) p(g)	2273.08	26.60	0.00	0.00	21.00	2230.51

Shown are models are ranked by Quasi Akaike Information Criterion (QAIC$_c$) corrected for small sample size (QAICc) and overdispersion. Delta Quasi Akaike's information criteria (ΔQAICc) indicating parameter fit differences among models, the QAICc weight (ω_i), model likelihood (ML), the number of parameters (K) and the deviance for each model. Parameter terms are specified as follows: Φ survival, p probability of capture, t time, (.) time invariant, g human activities levels

Table 2 POPAN Jolly–Seber analysis on capture-mark-recapture data used to estimate derived population abundances for Komodo dragons populations across sites with three human activities levels in Komodo National Park between 2003 and 2011/2012 ($n = 825$)

Model	QAICc	Δ QAICc	ωi	ML	K	QDeviance
Φ(g) p(.) pent(t) N(.)	2379.13	0.00	0.39	1.00	11	2356.9636
Φ(g) p(.) pent(t) N(g)	2379.78	0.66	0.28	0.72	13	2353.5569
Φ(.) p(.) pent(t) N(.)	2382.15	3.02	0.09	0.22	9	2364.0381
Φ(g) p(g) pent(t) N(g)	2382.44	3.31	0.07	0.19	15	2352.1434
Φ(g) p(g) pent(t) N(.)	2382.68	3.55	0.07	0.17	13	2356.4499
Φ(.) p(g) pent(t) N(.)	2384.08	4.95	0.03	0.08	11	2361.9175
Φ(.) p(g) pent(t) N(g)	2384.72	5.59	0.02	0.06	13	2358.491
Φ(.) p(.) pent(t) N(g)	2384.94	5.82	0.02	0.05	11	2362.7805
Φ(t) p(.) pent(t) N(.)	2386.14	7.01	0.01	0.03	14	2357.8763
Φ(g*t) p(.) pent(t) N(.)	2388.00	8.87	0.00	0.01	26	2335.1211
Φ(t) p(g) pent(t) N(.)	2388.21	9.09	0.00	0.01	16	2355.8746
Φ(t) p(g) pent(t) N(g)	2388.83	9.71	0.00	0.01	18	2352.407
Φ(t) p(.) pent(t) N(g)	2388.95	9.82	0.00	0.01	16	2356.6076
Φ(g*t) p(.) pent(t) N(g)	2389.23	10.11	0.00	0.01	28	2332.2171
Φ(g*t) p(g) pent(t) N(.)	2389.78	10.65	0.00	0.00	27	2334.8346
Φ(g*t) p(g) pent(t) N(g)	2390.01	10.88	0.00	0.00	29	2330.918
Φ(t) p(g*t) pent(t) N(.)	2393.95	14.82	0.00	0.00	33	2326.5389
Φ(.) p(.) pent(t) N(g)	2475.37	96.25	0.00	0.00	10	2455.2381

Shown are models ranked by Quasi Akaike Information Criterion corrected for small sample size (QAICc) and overdispersion. Delta Quasi Akaike's information criteria (ΔQAICc) indicating parameter fit differences among models, the QAICc weight (ω_i), model likelihood (ML), the number of parameters (K) and the deviance for each model. Parameter terms are specified as follows: *Φ* survival, *p* probability of capture, *pent* probability of entry, *N* superpopulation abundance, *t* time, (.) time invariant, *g* human activities levels

Population density

The top ranked POPAN model [Φ (g) p (.) pent (t) N (.)] indicated that the abundance parameter (N) was best formulated as a constant parameter (Table 2). Mean annual Komodo dragon population densities did not differ substantially in response to different human activity levels (GLMM$_{2,53}$, F = 0.14, P = 0.87; Fig. 4d).

Discussion

The degree to which threatened wildlife can coexist with humans over the long term is of central importance in conservation science and policy (Carter et al. 2012). Komodo National Park, a world heritage site, remains the largest protected areas for Komodo dragons. As a general result, given their continued presence, Komodo dragons appear to persist with the current levels of human activities occurring within Komodo National Park. This stands in contrast to incidences of local extirpations and range contractions observed in other Komodo dragon populations exposed to pervasive human activities (e.g., habitat modification) elsewhere across their range (Ariefiandy et al. 2015). Nevertheless, exposure

to existing human activities and in particular ecotourism can affect the ecology, through diverse effects on the phenotype and demography, of Komodo dragons.

Effects on phenotypic attributes of Komodo dragons

Komodo dragons from high human activity areas exhibited pronounced differences in behaviour and morphology compared to individuals inhabiting areas characterized by low or negligible human presence. In high human activity areas, Komodo dragons showed habituation to humans with reduced negative reactions (avoidance) recorded. Such responses may arise in animals when their encounters with humans are perceived as neutral and present little risk (Knight and Cole 1991; Rodriguez-Prieto et al. 2009). Habituation by Komodo dragons would reduce the costs associated with increased anti-predator behaviours (Romero and Wikelski 2002). However, habituation of Komodo dragons to humans may have two undesirable consequences. These include increased livestock predation around villages and more importantly an increase in non-lethal attacks by Komodo dragons on humans within ecotourism areas (Ardiantiono, unpublished data).

Physical changes including increased body size and condition were observed in individuals resident in high human activity areas compared to dragons inhabiting other types of human activity areas. These responses are consistent with Komodo dragons receiving supplementary feeding resulting from ecotourism activities and food refuses from ranger posts. Such phenotypic changes are based on mean site level measures taken from individuals captured across several square kilometers of habitat, suggesting that even highly localized food subsidies can have broad scale effects on Komodo dragons. These phenotypic effects are entirely consistent with those first reported by Walpole (2001) and now indicate that food subsidies have had long-term effects on Komodo dragons. Interestingly, in low human activity areas (e.g., sites with ranger stations), whilst the body mass of Komodo dragons was heavier than that of individual's resident in negligible human activity areas, we recorded a decrease in body condition. Given the substantially lower levels of food subsidies provided in such areas due to the absence of supplementary feeding (i.e., used in ecotourism areas), it is possible that larger Komodo dragons are nonetheless attracted to ranger stations because of olfactory food related cues that do not provide similar energetic subsidies and possibly act as deterrents to natural foraging behaviour which may explain their reduced body condition at these areas.

Effects on demographic attributes of Komodo dragons

Human activities were also associated with demographic consequences for Komodo dragons. We found evidence that Komodo dragons' resident to high human activity areas exhibited an adult biased age structure, had higher survival, but importantly their sex ratio and population densities were not significantly different from those estimated at other sites. These results again suggested that food subsidies provide additional nutrition with significant effects on population size structure and survival rates (Oro et al. 2004; Dempster et al. 2011; Jessop et al. 2012).

Komodo dragons in high human activity areas were disproportionally biased towards heavier adult lizards, but this was not further exaceberated by any sex ratio skew towards large male individuals as observed in other monitor lizard populations exposed to supplemental feeding (Jessop et al. 2012). Hence phenotypic effects may arise not only from

direct food subsidies, but also because these areas attracts larger individuals, who can monopolise food by aggressively displacing smaller dragons. Adult individuals, provisioned with nutritional benefits, would also account for the higher survival observed in high human activity (Laver et al. 2012). It is also conceivable that because large individuals compete for food subsidies, that may lead to local selection for high fitness individuals. This, in turn, would contribute to greater survival and differences in population dynamics compared to natural populations (Oro et al. 2004). Similar results could arise if high human activity areas had relatively large densities of prey, however no evidence for an increase in ungulate prey density was ever recorded across the studied areas (Purwandana et al. 2015; Ariefiandy et al. 2016).

An adult biased population structure may present some negative consequences for local Komodo dragon populations. For example, Komodo dragon population densities were not significantly different among the different human activity areas. This may indicate that adult biased populations could displace or predate smaller individuals (Auffenberg, 1981) to reduce overall densities. If present, both types intraspecific interactions would potentially limit recruitment beyond the apparent survival benefits from supplemental feeding and thus in part constrain local population growth and limit population densities (Kvarnemo and Ahnesjo 1996; Buckley et al. 2016). In this sense, high human activity areas may act as a weak ecological traps, with low-quality habitats preferred over adjacent higher quality habitats with higher carrying capacity and potential for increased fitness (Gilroy and Sutherland 2007). An ecological trap is a habitat that is attractive to animals, yet functions demographically as a population sink or at least constrains population growth (Fletcher et al. 2012). Ecological traps can arise when there is a decoupling between the habitat preference of individuals and the fitness consequences of their habitat choice (Battin 2004). Thus, to some extent, high human activity areas may function as ecological traps by providing cues to adult Komodo dragons that potentially influence the potential for younger individuals to normally demographically function (i.e., via recruitment and survival) and contribute to broader population processes.

Implications for Komodo dragon management

Our study indicated that in sites considered to have high level of human activities, which cater for ecotourism, had some important effects on Komodo dragon ecology. These effects arise not only from tourist visitation, but also from food subsidies (e.g., supplementary feeding and food refuse) provided within Komodo dragon habitats.

Properly managed ecotourism can generate long-term conservation benefits for Komodo dragons. At present, ecotourism has provided additional economic resources for KNP management and employment opportunities (e.g., as tourist guides, hospitality/transport services and souvenir sellers) for local communities (Walpole and Goodwin 2000; Goodwin 2002). The increasing popularity of Komodo dragons and KNP (especially after its establishment as one of the New Seven Wonders of The Natural World in 2011) has also greatly increased public and government support for this threatened species (Erb 2015; Hakim 2017). In addition, education presented by tourist guides may contribute to helping tourists increase positive attitudes toward Komodo dragons, as predators are often perceived as scary and dangerous animals which can hinder conservation efforts (Macdonald et al. 2017).

Nevertheless, expansion of ecotourism activities must be carefully considered to limit negative impacts on animal populations as well as human-Komodo dragon conflicts. In order to reduce long-term effects of human presence on Komodo dragon populations, we recommend three management strategies to be considered by Komodo National Park authority.

First, supplementary food resources made available to Komodo dragons for either enhancing visitor experience or as a refuse from ranger stations should be regulated. Ideally, additional food resources should be eliminated entirely and waste disposal improved through, for instance, recycling and transport of waste out of Komodo National park boundaries. Such practices are likely to lead to a decrease in anthropogenic induced phenotypic and demographic effects observed in Komodo dragons.

Second, Komodo National Park managers should consider alternative ecotourism activities to reduce human influence on Komodo dragons and their habitats. This may include devising additional walking trails to show visitors a wider variety of Komodo and Rinca Island terrestrial habitats as well as specific tours targeting flagship species other than Komodo dragons, such as yellow-crested cockatoos (*Cacatua sulphurea*). Improved facilities and interpretation and welcome centers for visitors along with diversified nature and wildlife tourist attractions would reduce detrimental effects of direct interactions between humans and Komodo dragons.

Third, the rapid, foreseeable growth in ecotourism will probably intensify its direct impact on Komodo National Park. Currently, almost all existing tourism facilities and infrastructure (e.g., airports, resorts, hotels, restaurants) are located out of Komodo National Park, on the neighboring island of Flores. However, if future resorts were to be built inside the park, then careful evaluation should be made on how planned infrastructure are likely to impact Komodo National Park's environmental assets. Visits to the park should remain regulated through use of specific and spatially limited sites where tourists can observe Komodo dragons. Additionally, we advocate a regional management approach where future ecotourism and infrastructure are developed in areas adjacent to other reserves that would limit ongoing tourism impacts on Komodo National Park.

Conclusions

This study emphasizes the importance of assessing the effects of ecotourism on wildlife in Indonesia. A key strength of this study was that it considered human effects at large spatial and population-level scales, attributes needed to best inform management for the potential of broad scale effects on wildlife. Currently, the Indonesian government aims at attracting 21.5 million tourist visitations (20 million local and 1.5 million international visitors) to protected areas during the 2015–2019 period (Kehutanan 2015). This would likely increase the impact of tourism on wildlife. It is therefore timely that stakeholder meetings are undertaken to develop approaches that evaluate how to integrate political, economic, and ecological objectives to ensure that Indonesia's astonishing biodiversity is valued and protected through social–ecological sustainability that benefits both people and wildlife conservation (Walsh and Mena 2016).

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Affiliations

Ardiantiono[1,5] · Tim S. Jessop[2] · Deni Purwandana[1] · Claudio Ciofi[3] ·
M. Jeri Imansyah[1] · Maria Rosdalima Panggur[4] · Achmad Ariefiandy[1]

[1]   Komodo Survival Program, Denpasar, Bali 80223, Indonesia

[2]   School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Geelong, VIC 3220, Australia

[3]   Department of Biology, University of Florence, Sesto Fiorentino 50019, Italy

[4]   Komodo National Park, Labuan Bajo, Flores 86554, Indonesia

[5]   Wildlife Conservation Society-Indonesia Program, Bogor 16151, Indonesia