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ENCOUNTER RATES, AGONISTIC INTERACTIONS, AND SOCIAL HIERARCHY AMONG GARBAGE-FEEDING WATER MONITOR LIZARDS (*VARANUS SALVATOR BIVITTATUS*) ON TINJIL ISLAND, INDONESIA

LINDA T. UYEDA[1,4], ENTANG ISKANDAR[2], RANDALL C. KYES[3], AND AARON J. WIRSING[1]

[1]*School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA*
[2]*Primate Research Center, Bogor Agricultural University, Bogor, West Java, Indonesia*
[3]*Departments of Psychology & Global Health, Center for Global Field Study, and Washington National Primate Research Center, University of Washington, Seattle, Washington, USA*
[4]*Corresponding author, e-mail: ltuyeda@gmail.com*

Abstract.—**Predictable anthropogenic resource subsidies have the potential to influence the behavior of wildlife populations. Concentrated, human-provided food resources in particular have been associated with increases in encounter rates, agonistic interactions, and the development of dominance hierarchies. While the effects of food subsidies on wildlife have been well researched, few studies have focused on reptile populations. Through behavioral observations of garbage-feeding, free-living Water Monitor Lizards (*Varanus salvator bivittatus*) on Tinjil Island, Indonesia, we documented a higher incidence of intraspecific encounters in a garbage-feeding area as compared to areas where animals foraged naturally. The number of agonistic interactions observed was also higher in the presence of food compared with interactions observed in the absence of food. Moreover, our data suggest the presence of a primarily size-based dominance hierarchy among *V. salvator* frequenting the area of human-provided resources. Although agonistic interactions were frequent among garbage-feeding individuals on Tinjil Island, our observations indicate that in this population of *V. salvator*, intense fighting is not essential for hierarchy maintenance.**

Key words.—anthropogenic food subsidies; behavioral ecology; dominance hierarchy; Java; sociometric matrix; Varanidae

INTRODUCTION

Anthropogenic resource subsidies have the potential to influence ecosystems by affecting wildlife behavior and abundance (Newsome et al. 2014). Human-provided food subsidies have been recognized as a primary concern (Oro et al. 2013), with documented effects ranging from increased abundance (Coyotes, *Canis latrans*, Fedriani et al. 2001; Common Ravens, *Corvus corax*, Boarman et al. 2006) altered space use (Spotted Hyenas, *Crocuta crocuta*, Kolowski and Holekamp 2007), increased interactions (Banded Mongoose, *Mungos mungo*, Gilchrist and Otali 2002) and increased incidence of aggression within wildlife populations (e.g. Herring Gulls, *Larus argentatus*, Pons 1992; Barbary Macaques, *Macaca sylvanus*, Alami et al. 2012). When food subsidies are concentrated, competition for feeding opportunities may even lead to the establishment of social hierarchies among conspecifics that would otherwise forage alone (e.g., Chuckwallas, *Sauromalus obsesus*, Berry 1974; wild lizard populations, Stamps 1977). Concentrated food subsidies that bring humans and wildlife into close contact, as in the case of refuse, may also increase the potential for conflict, especially when larger species that easily habituate to human presence are involved (e.g., Coyotes, Timm et al. 2004; Polar Bears, *Ursus maritimus*, Stirling and Parkinson 2006; Lemelin 2008; American Black Bears, *Ursus americanus*, Spencer et al. 2007). Previous research on the effects of garbage-feeding and other forms of anthropogenic resource subsidies has focused primarily on mammals and birds. Thus, there is a need for studies examining the implications of these subsidies for herpetofaunal populations. Here, we explored the impacts of garbage feeding on the behavior of the Water Monitor Lizard (*Varanus salvator bivittatus*).

Varanus salvator (Fig. 1) is a large (ca. 2 m total length) predator and scavenger. This species habituates well to areas of human disturbance and has been documented feeding on human garbage (Traeholt 1994; Uyeda 2009). *Varanus salvator* is not considered territorial, and free-living *V. salvator* do not generally interact with each other at high frequencies (Traeholt 1997; Gaulke et al. 1999; Gaulke and Horn 2004). However, in captive varanid populations, high population densities and concentrated resources may facilitate the formation of social hierarchies (*V. salvator*, Daltry 1991; *Varanus varius*, Hoser 1994, 1998). Such dominance structures have also been noted in free-living varanid populations under similar conditions. For example, Cota (2011) noted a hierarchy among a high-density wild population of *V. salvator macromaculatus*

FIGURE 1. The Water Monitor Lizard (*Varanus salvator bivittatus*) on Tinjil Island, off the south coast of Java in Banten, Indonesia. (Photographed by Linda Uyeda).

at the Dusit Zoo (Thailand), while Auffenberg (1981) documented a hierarchical system among free-ranging *Varanus komodoensis*, noting that the most commonly observed agonistic interactions occurred around carrion. Gaulke (pers. comm.; 1989) also observed a hierarchy among wild, carrion-feeding *V. salvator marmoratus* (now *V. palawanensis*). Such varanid dominance hierarchies are largely based on size, with larger individuals dominating over smaller ones (Auffenberg 1981; Daltry 1991; Hoser 1994, 1998; Cota 2011).

Previous literature on agonistic behavior and social hierarchy in *V. salvator* has focused on either captive populations or free-living populations foraging primarily on naturally available resources. In contrast, our research was designed to investigate behavior in a population of garbage-feeding free-living *V. salvator*. Research was conducted on Tinjil Island, Indonesia, a largely undisturbed habitat with a small area of localized human activity. On Tinjil Island, we were able to observe the behavior of free-living individuals with consistent access to both anthropogenic resource subsidies and natural resources. We conducted behavioral sampling of *V. salvator* in garbage-feeding and non-garbage-feeding areas of Tinjil Island to compare encounter rates between areas with and without this resource, and to compare the ratio of agonistic interactions associated with food to agonistic interactions in the absence of food in both areas. We also created a sociometric matrix to assess the presence of a dominance hierarchy, and related hierarchy data to morphometric measurements.

We predicted that, compared to the area where garbage feeding did not occur, we would observe: (1) an increased encounter rate in the garbage-feeding area; (2) an increased agonistic interaction rate in the garbage-feeding area; and (3) a greater percentage of the agonistic interactions involving individuals engaged in foraging as compared to interactions occurring in the absence of food. In assessing the presence of a dominance hierarchy, we predicted that individuals engaging in regular agonistic interactions associated with garbage-feeding would have established a dominance hierarchy, and that any dominance hierarchy established among *V. salvator* would be largely based on size. Our aim was to increase understanding of *V. salvator* behavior in an area of concentrated anthropogenic resources while facilitating the prevention and mitigation of human-lizard conflict.

MATERIALS AND METHODS

Study site.—We studied lizards on Tinjil Island, Indonesia, located at 6°56'97'S, 105°48'70'E, approximately 16 km off the south coast of Banten, Java, Indonesia. Tinjil Island is ca. 600 ha (6 km long and 1 km wide), with an average elevation of ca. 20 m. Tinjil Island has been managed by the Primate Research Center of Bogor Agricultural University (IPB) as a

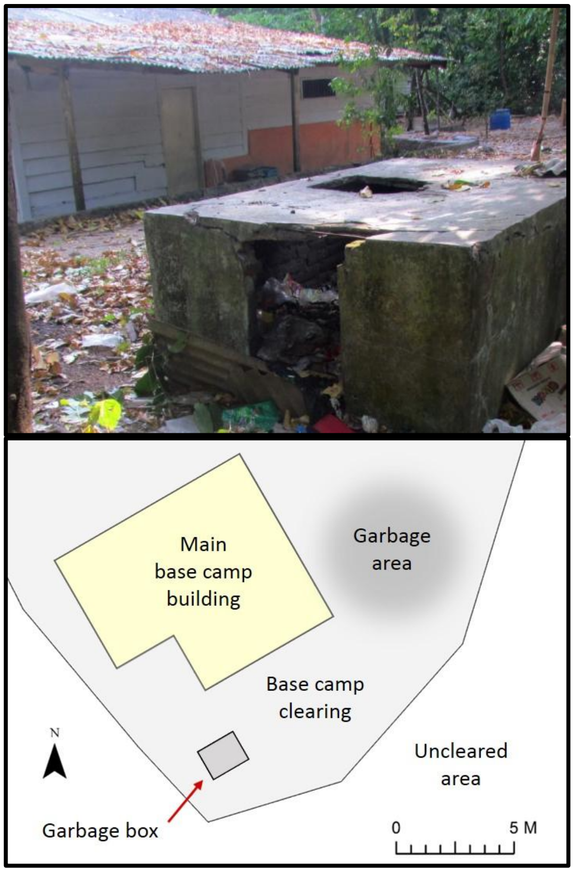

FIGURE 2. Top: overview of the main base camp building and garbage-feeding area frequented by Water Monitor Lizards (*Varanus salvator bivittatus*) on Tinjil Island, Indonesia. Bottom: the garbage box outside of the main base camp building. The photographer of this photo (Linda Uyeda) was oriented in the position indicated by the red arrow labeling the garbage box in the top overview.

Natural Habitat Breeding Facility for Long-tailed Macaques (*Macaca fascicularis*) since 1987 (Kyes et al. 1997). As such, the island has limited accessibility to humans and all visitors to the island must obtain permission to conduct activity there. Although there are officially no permanent residents on Tinjil Island, staff members provide a year-round human presence (5–8 people at any given time). *Varanus salvator* are found throughout Tinjil Island, and individuals are frequently seen around a small base camp area where most human activity on Tinjil Island is concentrated. Leftover food scraps and food waste are routinely discarded either 1–5 m away from a main base camp building in a cleared area, or in a large, ca. 1.5 × 2 × 1 m cement garbage box, located approximately 3 m south of the building (Fig 2). *Varanus salvator* are not fed directly by humans in the base camp area but commonly gain access to forage in the garbage box via openings in the side and top and are regularly observed foraging in human-discarded food and garbage (Uyeda 2009; Uyeda et al. 2013). *Varanus salvator* and the Reticulated Python (*Malayopython reticulatus*) are the largest predators found on Tinjil Island. Long-tailed Macaques are the largest species of non-human mammal on the island, and generally avoid contact with *V. salvator*. The Saltwater Crocodile, *Crocodylus porosus*, the Small Asian Mongoose, *Herpestes javanicus*, and the Common Palm Civet, *Paradoxurus hermaphroditus*, species found on the mainland of Java, are not present on Tinjil Island. Unauthorized removal of flora and fauna from Tinjil Island is prohibited per official policy of IPB, and *V. salvator* on the island remain unharvested (see Uyeda et al. 2014).

Tinjil Island experiences two distinct seasons, a dry season and a wet season, with each season characterized by markedly different conditions. In the dry season there are no natural fresh-water sources on the island other than an occasional ephemeral puddle. In the wet season, frequent rains provide an abundance of water throughout the island; water pools in tree hollows, a swampy area develops in the center of the island, and puddles are omnipresent. Natural food resources (e.g., land crabs) are also more plentiful in the wet season. The peak of dry season is generally from June to August, while January to March represents the middle of the wet season. Tinjil Island consists of lowland secondary Tropical Rainforest and coastal beach vegetation, with comparable flora and fauna throughout. Representative vegetation types include *Ficus* spp., *Gnetum gnemon* (Melinjo), and *Dracaena elliptica* (Hernowo et al., unpubl. report; McNulty et al. 2008).

Data collection.—Following anecdotal observations of agonistic behavior of the base camp population of *V. salvator* on the island in 2008 and 2011 (Linda Uyeda, pers. obs.), we undertook systematic documentation of *V. salvator* behavior from 5 July 2012 to 11 August 2012 (dry season) and 13 January 2013 to 27 March 2013 (wet season) to better understand the social behavior of this species in an area where garbage-feeding frequently occurred. During these periods, we collected behavioral data in conjunction with a larger study involving the use of radio-telemetric harnesses to determine activity and resource use of *V. salvator* in food-subsidized areas.

We captured *V. salvator* in the Tinjil Island base camp area primarily using baited wooden box traps, but we also captured lizards by hand. Following capture, we assigned an identifying number to each lizard and we applied a superficial mark with a non-toxic crayon that rubbed away in time or was shed off with the skin. We measured and weighed each individual, and we outfitted each with a backpack-style radio-telemetric harness. The harnesses used in this study were modified versions of a custom-designed LPR-3800 unit (Wildlife Materials, Murphysboro, Illinois, USA) used in a July

2011 pilot study (Uyeda et al. 2012). We removed all harnesses following completion of our research.

Throughout both study periods, a single observer used *ad libitum* sampling (ALS) and focal animal sampling (FAS) techniques (Altmann 1974) to collect behavioral data and to complete a sociometric matrix. Prior to each behavioral follow, the observer located focal animals by tracking lizards on foot using a TRX-48S receiver and 3-element yagi directional antenna (Wildlife Materials, Murphysboro, Illinois, USA). *Varanus salvator* are generally diurnal and we did not observe study animals to be active at night (with the exception of one individual whose nocturnal activities were not included in this report; see Uyeda et al. 2013). Thus, FAS was generally conducted between 0600 and 1800. The majority of the sampling periods were 2-h time blocks, although we conducted two 12-h focal animal observations and one 6-h observation in the 2013 season. We sampled focal animals across each of the six 2-h time blocks in an effort to observe a representative sample of activity throughout the day. Although we made attempts at FAS with all instrumented individuals, several animals had clearly altered behavior in the presence of an observer, regardless of the distance of the observer. Thus, we conducted FAS on only a subset of the instrumented animals, individuals that appeared undisturbed by the presence of the observer, as evidenced by the willingness of individuals to continue engaging in daily behaviors such as sleeping, foraging, and drinking while being observed.

Encounter rates and agonistic interactions.—To compare the incidence of encounters in the area where garbage-feeding occurred (in the base camp) to encounter rates in areas where such food resources were not available (outside of the base camp), we documented all observed encounters between pairs of individuals, with interactions characterized as In Camp, or Out of Camp. We defined In Camp as the cleared base camp area plus a 3 m perimeter of brush surrounding the camp clearing, while Out of Camp included any location beyond this perimeter. The observer documented all encounters, defined as instances in which two *V. salvator* were within 3 m of one another, including all observed agonistic interactions as well as instances in which no interaction was observed (noted as No Response). We calculated encounter rates for each area as the total number of encounters / total FAS time. In addition, the observer noted whether or not each encounter involved food or foraging by one or both of the individuals. Because we could not accurately quantify agonistic interactions observed through ALS by time, we did not include those observations in calculations of interaction rate. However, we included additional interactions observed through ALS in the base camp area in comparing the number of agonistic interactions associated with food to the number of agonistic interactions that occurred in the absence of food. We used chi-square to compare observed encounter rates and agonistic interaction rates in each area (In Camp and Out of Camp). The expected frequencies were based on the assumption that the proportion of observed encounters and agonistic interactions in each area were equal. We also used this test to compare the number of agonistic interactions associated with food to the number of agonistic interactions which occurred in the absence of food. Significance for all tests was set at $P \leq 0.05$.

Dominance hierarchy.—We assessed the existence of a hierarchy among lizards competing for concentrated food resources in the Tinjil Island base camp area by entering agonistic interactions observed between dyadic pairs of known individuals into a sociometric matrix. Data were entered into the matrix based on interaction outcomes (i.e., dominant and submissive) as a means to determine the direction and degree of one-sidedness of each relationship. The observer noted agonistic interactions, which were grouped into four categories based on type: (1) avoid; (2) displace; (3) short pursuit; and (4) stand ground/concede. The avoid category referred to a clear avoidance behavior (i.e., running away, veering off course to create a wide berth around a stationary dominant individual) demonstrated by the submissive individual, and did not involve any noticeable aggressive behavior from the dominant individual. Displace behaviors were defined as instances in which the dominant individual approached the submissive individual directly until the submissive individual gave way (typically running 1–2 m away), allowing the dominant individual to take over its previously occupied space (Fig. 3). Although individuals engaging in displace behaviors generally did not appear to be aggressive (i.e., did not engage in a Threat Walk posture), we considered interactions displace regardless of whether the approaching individual appeared to be in a relaxed or threatening posture. Short pursuit involved a dominant individual actively chasing a submissive individual a short distance (< 7 m). We observed three scenarios associated with the short pursuit: (1) the two individuals would encounter one another, at which point the individuals would approach closely and stand snout to snout, licking the snout of each other for several seconds before one of the two initiated a short pursuit; (2) the dominant individual initiated the pursuit, beginning chase as it approached a submissive individual (e.g., while the submissive individual was foraging in a desirable location), after which the dominant individual would return to take over activity (i.e., foraging) in the desirable location; or (3) a submissive individual slowly approached a dominant individual (e.g., while the

FIGURE 3. Displace behavior between two *Varanus salvator bivittatus* on Tinjil Island, Indonesia. Top: lizard 44 approached lizard 23 as it was consuming some human food leftovers outside the main base camp building. Bottom: lizard 23 ran away while lizard 44 took over foraging in the desired location. (Photographed by Linda Uyeda).

dominant individual was foraging in a desirable location), at which point the dominant individual would chase the submissive one away a short distance before returning to resume its activity. We also occasionally observed tail slaps in conjunction with this third scenario; the dominant individual would continue foraging while tail slapping the approaching individual. Following 1–3 tail slaps, the approaching individual would either change direction and retreat (noted as stand ground/concede), or the dominant individual would then initiate a short pursuit before resuming its foraging activity (noted as short pursuit). Stand ground/concede also included situations in which two individuals met snout to snout (usually at a foraging location), with one holding its ground and the other turning away after a few seconds.

We used data from the completed sociometric matrix to calculate Kendall's coefficient of linearity, *K* (Appleby 1983), an index used to describe the strength of a hierarchy among a group of individuals (Langbein and Puppe 2004). Specifically, *K* is a measure of the degree of linearity of a dominance hierarchy calculated

Table 1. Encounter rates observed through focal animal sampling (FAS) of *Varanus salvator bivittatus* on Tinjil Island, Indonesia. All encounters (agonistic interactions and those that produced no response) versus hours of focal animal sampling (FAS), and encounter rate per hour. IC = in camp; OC = out of camp.

Year	Total encounters/hrs FAS-IC	Total encounters/hrs FAS-OC	Encounter/hr of FAS-IC	Encounter/hr of FAS-OC
2012	32/15.6	2/20.5	2.05	0.10
2013	0/3.00	4/59.3	0	0.07
Total	32/18.6	6/79.8	1.72	0.07

by considering the actual number of circular triads (*d*) relative to the total number of possible triads. *K* is represented as a number between zero and one, with one corresponding to a completely linear hierarchy.

For even values of N,

$$K = 1\text{-}\frac{24d}{N^3\text{-}N}$$

for a group size of N, where *d* is the number of circular triads. Linearity of the hierarchy can be tested statistically by comparing the observed number of circular triads with the probability that such linearity would be observed by chance (Appleby 1983).

We calculated a dominance index (DI) for each individual based on the ratio of the number of individuals dominated by the individual relative to all individuals with which it interacted. DI is represented as a percentage of individuals dominated (Lamprecht 1986; Langbein and Puppe 2004):

$$DI_{dom} = \frac{\text{submissive individuals}}{\text{submissive individuals + dominant individuals}} \times 100$$

We then compared the size of the individuals involved in the linear hierarchy and dominance indices to measurements of weight and total length to qualitatively assess the role of size in the establishment of the hierarchy.

Results

We captured 10 *V. salvator* in the base camp area of Tinjil Island. Of these, we fitted eight with radio-telemetric harnesses. Two individuals were smaller sub-adults and were thus marked with crayon for identification, but we did not fit them with harnesses. Individual weights ranged from 4.5–21.5 kg. We measured seven of the 10 lizards in both the 2012 and 2013 seasons, and individual averaged total lengths (including three individuals with missing tail tips) ranged from 138.0–222.2 cm. We also recorded tail base circumference, maximum girth, snout-vent length, and thorax-abdomen length (Appendices I and II). We observed two individuals (53 and 23) with everted hemipenes and we thus considered them to be males. We did not determine the sex of the other individuals.

We conducted 98.4 h of focal animal sampling (FAS) across the 2012 and 2013 field seasons, including 18.6 observation hours in the garbage-feeding/base camp area and 79.8 observation hours conducted outside of the base camp. We observed five individuals for 36.1 h in the 2012 (dry) season, and three individuals for 62.3 h in the 2013 (wet) season. Individuals 04 and 44 were observed in both the 2012 and 2013 season. In 2012 these two individuals spent equal amounts of time in camp and out of camp (12.8 h in each area), but in 2013 the same individuals spent 22.5 of a total 25.5 observed hours outside of camp.

Encounter rates and agonistic interactions.—Encounter rates were significantly higher in the garbage-feeding area (In Camp) than in the area outside of camp ($X^2 = 4.869$, df = 1, $P = 0.027$). Of 38 total encounters documented through FAS, we observed 32 encounters in the base camp area, while we observed only six outside of the base camp area, despite 79.8 of the 98.4 FAS hours having been conducted outside of base camp (Table 1). We observed 26 agonistic interactions through FAS in the garbage-feeding area compared to one interaction observed outside of the camp area. Overall interaction rates were low in both areas, with an average of 1.4 interactions per hour in camp and 0.01 interactions per hour outside of camp. There was not a significant difference in agonistic interaction rates between the two areas ($X^2 = 1.52$, df = 1, $P > 0.100$).

We included an additional 31 interactions observed through *ad libitum* sampling (ALS) in comparing the number of agonistic interactions associated with food to the number of agonistic interactions that occurred in the absence of food. The number of agonistic interactions that occurred in the presence of food was significantly higher than the number occurring in the absence of food ($X^2 = 36.48$, df = 1, $P < 0.001$). Only one encounter in the presence of food resulted in no response, while 52 encounters in the presence of food resulted in an agonistic interaction (Table 2). In the absence of food, 10 encounters resulted in no response while six encounters resulted in an agonistic interaction. All but

TABLE 2. Agonistic interactions and encounters resulting in no response among *Varanus salvator bivittatus* on Tinjil Island, Indonesia. Observed encounters were grouped according to whether they involved food and foraging, or were in the absence of food. Numbers in parentheses represent values inside/outside the base camp area.

Year	Total interactions	Interaction, food	Interaction, no food	Percentage of interactions involving food	no response, food	no response, no food
2012	55 (55/0)	49 (49/0)	6 (6/0)	89.0%	1 (1/0)	7 (5/2)
2013	3 (2/1)	3 (2/1)	0 (0/0)	100%	0 (0/0)	3 (0/3)
Total	58 (57/1)	52 (51/1)	6 (6/0)	89.6%	1 (1/0)	10 (5/5)

one of the 58 total agonistic interactions we observed through FAS and ALS across the 2012 and 2013 seasons occurred in the base camp area. Of the 57 total *V. salvator* interactions we observed in the base camp, 55 occurred in the dry season as compared to two agonistic interactions observed in the wet season.

Dominance hierarchy.—Of the 58 observed agonistic interactions, short pursuit was the most commonly observed interaction (36.2%), followed closely by displace (29.3%), and avoid (22.4%). We only observed stand ground/concede on seven occasions (12.1%). Among known individuals, there did not appear to be a predictable pattern of similar interaction types among the categories recorded. For example, individual 04 was dominant over individual 44 fourteen times, consisting of four avoid, five displace, four short pursuit, and one stand ground/concede. We did not observe long pursuits, where an individual chased another for an extended (≥ 7 m) distance, biting, ritual/bipedal combat, or wrestling during the course of the study.

Forty-two of the observed interactions occurred between dyads of known individuals (Fig. 4). Individual 07, the largest individual by weight and total length, was consistently dominant over all other individuals. Due to the high number of unknown dyads between known individuals (i.e., dyads for which we did not observe an agonistic interactions, even though it was possible for members to have done so), we assessed the linearity of the relationships between only four of the study individuals, 07, 04, 44, and 23. There were no circular dyads among these individuals. Thus, simple calculations yielded a Kendall's coefficient of linearity K of 1 (complete linearity). However, with small sample sizes such as this one (n = 4), the probability that such linearity would be observed by chance is 0.375. Therefore, this result cannot be considered statistically significant (Appleby 1983).

Similarly, calculations regarding Dominance Index (DI) and individual rank among these four individuals were straightforward. High ranks corresponded to larger overall size as indicated by weight and total length of the two top ranked individuals, 07 (DI = 100) and 04 (DI = 66.6), although 23 (DI = 0) ranked fourth to a slightly smaller but similarly sized 44 (DI = 33.3). Based on our observations, individuals 04 and 44 appeared to be residents of the base camp area, while 07 and 23 were less commonly seen in the base camp area.

DISCUSSION

Varanid lizards commonly engage in agonistic behavior at feeding places such as carcasses (Auffenberg 1981; Horn et al. 1994). When feeding behaviors occur at a concentrated, human-subsidized resource, regular agonistic interactions may also occur in areas of human activity. We documented increased encounter rates in such an area of anthropogenic resources at the base camp of Tinjil Island, Indonesia. On Tinjil Island, agonistic interactions among *V. salvator* were associated with the presence of food, and agonistic interactions among garbage-feeding *V. salvator* appear to have given rise to a dominance hierarchy largely based on size.

Encounter rates and agonistic interactions.— Our data showed an increased encounter rate in the garbage-feeding area as well as a significantly higher proportion of agonistic interactions involving food as compared to those occurring in the absence of food. However, we did not document a significant increase in agonistic interaction rates at the garbage-feeding site despite a difference in observed agonistic interaction rates between the two areas (1.4 vs. 0.01 per hour). Agonistic behavior among *V. salvator* in proximity to food sources (e.g. carcasses) has been well documented (*V. s. salvator*, Vogel 1979 *in* Horn et al. 1994; *V. s. marmoratus*, Maren Gaulke, pers. comm.; Gaulke 1989), so increased agonistic interaction rates in the Tinjil Island garbage-feeding area would also be expected. Restricting the analysis to interactions observed through FAS for this comparison may have resulted in insufficient data, with a larger sample size potentially producing a significant result. There is also a possibility that the presence of an observer may have led to a reduction of encounters between focal animals and those individuals who were less tolerant of human interaction. Although the presence of the observer was consistent in both study areas, a repellent effect could have been more

Dominant (columns) / **Submissive** (rows)

	07	93	15	63	04	53	23	44	02	01
07										
93	1									
15	1				1					
63										
04	7									
53	1				1					
23	1				5			2		
44	3		2		14					
02										
01							1	2		

FIGURE 4. Results of a sociometric matrix based on observations of agonistic interactions between known dyads of *Varanus salvator* on Tinjil Island, Indonesia. Matrix values represent the number of agonistic interactions recorded between pairs of individuals in each direction (e.g. individual 07 was observed to be dominant over individual 04 seven times, while individual 04 was not observed to be dominant over individual 07). Individuals are listed along the axes by weight from heaviest (07) to lightest (01).

pronounced in the areas outside of camp, as most individuals in the base camp appeared habituated to humans (Uyeda 2009). Due to these considerations, the potential for increased agonistic interaction among garbage-feeding *V. salvator* requires further attention.

Our data also suggest that there may be a seasonal shift in behavior on Tinjil Island. Namely, we observed 55 *V. salvator* interactions in the garbage-feeding area in the dry season whereas only two agonistic interactions in the same area in the wet season. Such differences may be explained by increased availability of natural food resources in the wet season, which could have alleviated a dependence on human food resources. Seasonal changes in behavior related to food availability have been noted by Traeholt (1997), who documented larger wet season home ranges in *V. salvator* as compared to those in dry season, when the lizards fed on seasonally available concentrated food leftovers from tourists on Tulai Island in Malaysia. Similarly, despite human subsidized food resources being available year-round on Tinjil Island, individuals 04 and 44 appeared to spend more time outside of the garbage-feeding area in the wet season as opposed to the dry season. It is likely that water availability also affects the behavior of *V. salvator* on Tinjil Island across seasons, as this species prefers habitats in close proximity to fresh-water sources (Auffenberg 1981; Bennett 1995; Gaulke and Horn 2004). Anthropogenic activities in the base camp area provide a consistent source of fresh water, an additional concentrated resource that may be particularly important for *V. salvator* in the dry season. Despite the difference in number of interactions observed between seasons, we conducted far fewer hours of FAS in the base camp area in the wet season and we observed only two individuals in both wet and dry seasons. Thus, meaningful statistical comparisons of seasonal encounter rates and agonistic encounter rates in the base camp area were not possible. We recommend that future research efforts on Tinjil Island include comparisons of agonistic behavior across seasons to further assess temporal differences.

***Dominance hierarchy*.—**Agonistic interactions observed between *V. salvator* on Tinjil Island demonstrated a consistent directionality that strongly suggests the existence of a dominance hierarchy among garbage-feeding individuals. Despite numerous unknown dyadic relationships within our data, we documented a linear hierarchy based on size. The few differences we observed in expected outcomes based on size may also be explained by additional factors. For example, resident individuals have been known to dominate over transient individuals in varanid populations (Auffenberg 1981; Earley et al. 2002). Such a trend may explain the higher ranking of the resident lizard 44 of the base camp as compared to the slightly larger, but likely transient individual 23.

Throughout the course of our study, we did not observe bipedal combat, biting, and wrestling. The lack of extended or escalated interactions between individuals in our study is consistent with the predictions of game theory in which familiar individuals refrain from engaging in risky or energetically costly physical contact if a dominance relationship has already been established (Earley et al. 2002). While the necessity for prolonged, high energy expenditure contests may have been diminished by familiarity among individuals, interactions between known individuals continued to occur regularly in the Tinjil Island garbage-feeding area. For example, we observed 04 and 44, two individuals commonly seen around the base camp area, engaging in short pursuit four times throughout the study period, despite 04 dominating over 44 in 100% of their 14 observed interactions. Such non-contact interactions would be less energetically costly while still serving to resolve contests and maintain dominance relationships.

Our observations challenge the results of Heller et al. (1999), who observed agonistic behavior among *V. salvator* but did not see evidence of a social hierarchy, concluding that social structure establishment in this species may be "considered as an artefact developed after long periods of forced close contact between the same individuals". The interactions we observed among *V. salvator* on Tinjil Island were not forced, with regular contact between the same individuals coming about through competition for concentrated, human-provided food resources. Whereas our study was based on the natural behaviors of a free-living wild population of *V. salvator*, Heller et al. (1999) observed captivity stress among wild-caught *V. salvator* placed in enclosures for 3-day periods. It is likely that differences in methodology between the two studies resulted in differing conclusions.

Female *V. salvator* have been documented engaging in combat (Daltry 1991) and have also been known to be victorious over males (Horn et al. 1994). However, as we did not document the sex of every individual in our study, the role of gender in the establishment of the Tinjil Island base camp hierarchy could not be determined. Overall condition (Horn et al. 1994), individual differences in aggressiveness (Daltry 1991), and aggression related to mating behavior (Cota 2011) are also considerations that were not directly addressed by our research.

Future directions.—On Tinjil Island, the establishment of size-based dominance hierarchies in garbage-feeding areas could result in increased presence of larger individuals in the base camp area. Although large individuals engaging in intraspecific aggressive behavior in areas of human activity may raise concerns about the potential for human-lizard conflict, the types of agonistic interactions observed among *V. salvator* frequenting the Tinjil Island base camp were of short duration and low intensity. Further, *V. salvator* on Tinjil Island were generally passive towards humans when encountered in the base camp area when food was not involved (Linda Uyeda pers. obs.). However, we not only observed bolder individuals approaching humans in the possession of food (e.g., fresh fish), but occasionally caught them attempting to enter the base camp kitchen, even when it was occupied by people. As most agonistic interactions between *V. salvator* on Tinjil Island occurred in the garbage-feeding area and in the immediate presence of food, efforts to mitigate human-lizard conflict should focus primarily on decreasing garbage-feeding in areas of human activity. Human food leftovers should be discarded far from the main areas of human activity, particularly during periods in which natural food resources for *V. salvator* are limited (i.e., the dry season). If unavoidably located in areas of human activity, human refuse receptacles should be lizard-proofed whenever possible to discourage garbage-feeding behavior in these areas.

Our research indicates that *V. salvator* on Tinjil Island are not deterred from garbage feeding in close proximity to human activity and in addition may favor human-provided food in the dry season when natural prey is less abundant. In addition to comparisons of agonistic behavior across seasons, future directions should include evaluating the temporal ecological effects of garbage feeding on natural prey populations. Uyeda (2009) reported that *V. salvator* on Tinjil Island were more abundant in the base camp area than in areas of the island with less human activity. Although *V. salvator* populations artificially increased by anthropogenic subsidy could deplete prey populations, frequent garbage feeding could alternately decrease the use of natural food sources. Alterations to the composition of prey populations could result in trophic cascades, as has been noted in systems involving terrestrial mammalian predators (Newsome et al. 2014). Further research is crucial to better understanding the effects of anthropogenic resource subsidies on the behavior of large, predatory herpetofauna and the influence of behavioral changes on both ecosystems and human-wildlife relationships.

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LINDA T. UYEDA received her Ph.D. in Wildlife Science at the University of Washington (Seattle, USA), and is a member of the IUCN Monitor Lizard Specialist Group. She is interested in the study of both wildlife behavior and human dimensions as an interdisciplinary basis for informing conservation. Her dissertation focuses on the behavioral ecology of the water monitor lizard (*Varanus salvator*) in Banten, Indonesia and the attitudes and perspectives of the local people who coexist with this species. She received an M.A. in International Studies (2010), an M.Sc. in Biology for Teachers (2008), and a B.A. in Zoology (1995) from the University of Washington. (Photographed by Linda Uyeda).

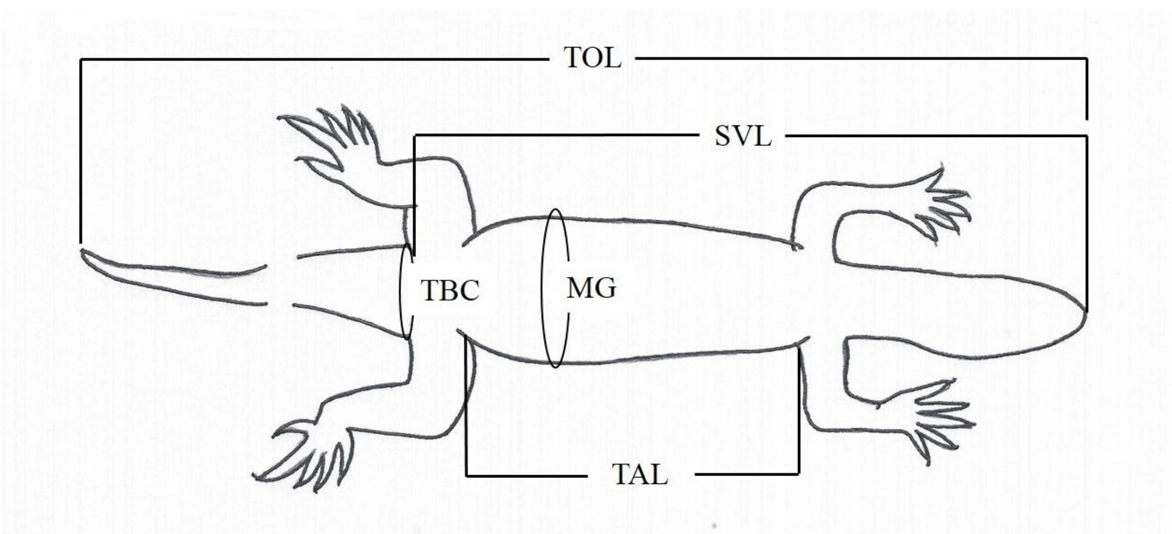
ENTANG ISKANDAR is the head of conservation programs at the Primate Research Center of Bogor Agricultural University, Indonesia. His research interests focus on the areas of ecology and behavior with a specialty in non-human primates. He also conducts studies on the human-primate interface. He received his B.A. in Forestry from Bogor Agricultural University (1992), a M.Sc. (1998) and Ph.D. (2007) in Primatology from Bogor Agricultural University. (Photographed by Noorkhairiah Salleh).

RANDALL C. KYES (second from the right) is a Research Professor in the Depts. of Psychology and Global Health, Director of the Center for Global Field Study (http://depts.washington.edu/cgfs/), and Core Scientist in the Washington National Primate Research Center at the University of Washington (Seattle, USA). His work has a strong international focus with collaborative research, training, and educational outreach programs in a number of countries. His research focuses on field-based studies of nonhuman primates and other wildlife in the areas of Conservation Biology and Global Health, at the human-environment interface. Prof. Kyes received a B.A. in Psychology from the University of Maine-Orono (1981), an M.A. in Animal Behavior from Bucknell University (1985), a Ph.D. in Biopsychology from the University of Georgia (1989), and completed a Postdoctoral Fellowship in Medical Primatology from Wake Forest University School of Medicine (1992). (Photographed by Pensri Kyes).

AARON J. WIRSING is an Associate Professor of Wildlife Science in the School of Environmental and Forest Sciences at the University of Washington (Seattle, USA). His research program addresses the ecology and conservation of large carnivores, and focuses especially on how predators shape their environments through interactions with their prey. Dr. Wirsing received an A.B. in Biology from Bowdoin College (1996), a M.Sc. in Wildlife Resources from the University of Idaho (2001), and a Ph.D. in Biology from Simon Fraser University (2005). (Photographed by Ramona C. Hickey).

APPENDIX I. Morphometric measurements of *Varanus salvator bivittatus* on Tinjil Island, Indonesia. Weights were measured to the nearest 0.5 kg, lengths measured to the nearest 0.5 cm. All individuals except 93, 02, and 01 were measured in both the 2012 and 2013 season. Table values represent the mean and range (in parentheses) for each measurement. An asterisk (*) indicates that the individual had a missing tail tip. In each of the three cases it appeared very little of the tail had been lost. TOL = total length; SVL = snout-vent length; MG = maximum girth; TBC = tail base circumference; and TAL = thorax-abdomen length.

Individual	Weight	TOL	TBC	MG	SVL	TAL
07	21.5 (21.0–22.0)	222.2* (221.5–223.0)	34.5 (34.0–35.0)	66.5 (66.0–67.0)	95.5 (94.0–97.0)	40.5 (38.0–43.0)
93	20.5	211.5	33.5	65.0	92.0	43.0
15	18.5 (18.0–19.0)	213.0 (208.0–218.0)	32.0 (31.5–32)	60.0 (57.0–62.5)	92.0 (208.0–218.0)	41.75 (36.0–47.5)
63	17.5 (17.0–18.0)	206.5 (206.0–207.0)	31.0 (30.5–31.5)	61.7 (60.0–63.5)	93.2 (92.5–94.0)	43.7 (42.0–45.5)
04	17.7 (17.5–18.0)	215.0* (213.0–217.0)	31.7 (31.5–32.0)	62.0 (61.0–63.0)	94.5 (92.0–97.0)	44.5 (43.0–46.0)
53	16.7 (16.0–17.5)	215.7 (214.5–217.0)	29.0 (29.0–29.0)	62.7 (59.5–66.0)	96.2 (96.0–96.5)	44.0 (44.0–44.0)
23	16.2 (16.0–16.5)	214.5 (213.5–215.5)	31.0 (31.0–31.0)	61.5 (59.5–63.5)	93.5 (90.5–96.5)	40.0 (37.0–43.5)
44	15.0 (13.0–17.0)	208.2 (206.5–210.0)	28.7 (28.0–29.5)	59.5 (55.5–63.5)	96.2 (94.5–98.0)	43.5 (43.0–44.0)
02	7.0	159.0*	21.5	42.0	64.0	32.0
01	4.5	138.0	20.5	35.0	56.0	28.5



APPENDIX II. Key to morphometric measurements recorded of *Varanus salvator bivittatus* on Tinjil Island, Indonesia. Measurements were total length (TOL), snout-vent length (SVL), maximum girth (MG), tail base circumference (TBC), and thorax-abdomen length (TAL).