

Varanid combat: perspectives from game theory

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Abstract. Most data on aggressive encounters in varanid lizards are qualitative and often anecdotal. The few quantitative reports have not explicitly tested the predictions generated by game theoretical models of animal combat despite their apparent relevance. The goal of this paper was to investigate whether the patterns evident in varanid contests conform to the predictions of the sequential assessment game with special emphasis on the organization, duration, and outcome of the encounters. Several characteristics of monitor combat are consistent with the sequential assessment game. For instance, contests are organized into distinct phases, displays are repeated within each phase, and asymmetries play a crucial role in determining contest duration and outcome. However, data pertaining to a number of the sequential assessment game's most critical postulations are absent from the current varanid literature (e.g. the consistency of display intensity within each phase). As more quantitative data emerge, the applicability of the sequential assessment game to varanid contests may be better assessed.

Introduction

Combat in varanid lizards has been the subject of a host of anecdotal and descriptive reports dating back at least to the early 1900's (Sterling, 1912; Lederer, 1929; Ali, 1944). Recently, varanid combat rituals have gained more quantitative attention, particularly with respect to the sequences of agonistic behaviour exhibited in the contests and the influence of factors such as body size, social status, and prior residency on fight outcome (Vogel, 1979; Auffenberg, 1981b, 1988, 1994; Daltry, 1991). However, extensive data on aggressive disputes in monitors are still lacking. At least three factors can account for the paucity of data on varanid contest behaviour. First, varanids are generally not observed interacting at high frequencies in nature, making collection of rigorous field data quite arduous. Second, adequate sample sizes needed to conduct powerful statistical inquiries on aggressive interactions in captivity are often difficult, but not impossible, to attain (e.g., Auffenberg, 1981b; Daltry, 1991; foraging behaviour: Kaufman et al., 1994, 1996). Third,

analyses of varanid fighting behaviour have focused primarily on the qualitative aspects of ritual combat rather than on devising experimental tests of the predictions generated by existing behavioural ecological theory on animal conflict (see Carpenter and Ferguson, 1977 for a review).

Game theory — a mathematical tool used to investigate behavioural strategies when one individual's actions depends on those of others in the population — has generated numerous predictions regarding animal combat. Despite the fact that varanid contests conform qualitatively to game theoretical interpretations, reference to such theory in studies on varanid behaviour has only been in passing (Horn, 1985). Our primary objective was to review the literature on varanid combat and to examine whether the existing data on aggressive interactions in monitors are congruent with predictions of game theory. In particular, we focus on a game theoretical model developed by Enquist and Leimar (1983) called the sequential assessment game, which is described in detail below. As most reports on monitor combat are purely descriptive, we do not attempt to formulate any definitive conclusions about the characteristics of aggressive disputes or their outcomes. Rather, we illuminate the potential for testing game theoretical predictions in varanid lizards.

Game theory and animal combat — a primer

Game theory examines how the costs and benefits of individual behaviour influence the emergence and persistence of behavioural strategies and thus, the fitness of individuals adopting those strategies (Dugatkin and Reeve, 1998). Early game theoretical models of animal combat focused on situations in which individuals were virtually identical in all respects (e.g. fighting ability, size) except the strategies that they employed. These were called symmetrical contests. For example, the classic 'hawk-dove' game pitted individuals adopting dangerous fighting tactics (hawk) against those adopting conventional fighting tactics (dove) and revealed that the evolutionarily stable strategy depended both on the value of the resource being contested and the cost of fighting (Maynard Smith and Price, 1973; Maynard Smith, 1982). On the other hand, the 'war of attrition' proposed that contestants may differ only in their willingness to persist in a contest (e.g. time spent displaying) and that the individual that persists longer should emerge as the victor (Bishop and Cannings, 1978). The simplifying assumption of symmetry gave way to analyses of asymmetrical contests (Parker, 1974; Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981; Hammerstein, 1981). Asymmetrical contests describe situations in which the contestants differ in some aspect that may bear on contest outcome such as fighting ability, the value of the contested resource, or ownership. Given that asymmetries are likely to exist between combatants, accurate assessment of such differences should be favored in order to allow weaker individuals to withdraw, injury-free, from interactions they cannot win (e.g. Parker, 1974).

The hawk-dove game, war of attrition models, and their many derivatives established predictions regarding the roles of assessment and asymmetries in resource value, fighting

ability, persistence, or ownership on fight outcome. Though important, these models are of limited value for ascertaining the mechanisms that give rise to display repetition or the escalating sequences of behaviour often performed during aggressive disputes. The sequential assessment game (SAG) was the first model to investigate the temporal organization of contest behaviour (Enquist and Leimar, 1983, 1987; Enquist et al., 1990; Leimar and Enquist, 1984). The SAG envisioned an aggressive contest as a means through which rivals gradually assess relative fighting abilities (i.e. the difference between contestant A and contestant B with respect to physical prowess). The decision to continue to fight or flee is based on each rival's assessment of its opponent's fighting ability relative to its own. An individual will retreat when it assesses its own fighting ability to be considerably lower than its opponent's. More specifically, the SAG predicts that retreats will occur when the costs of continuing outweigh the benefits of obtaining the contested resource (when assessment of relative fighting ability crosses the evolutionarily stable switching line — see figure 2 in Enquist and Leimar, 1983). In the following sections, we outline several key predictions of the SAG as they relate to varanid combat in order to demonstrate the applicability of game theory to this taxon.

Sequential assessment and varanid combat

Contest organization

The SAG assumes that, at the start of an interaction, individuals have relatively little information about one another's fighting ability and that they subsequently gain this information via assessment. Varanids are, for the most part, solitary lizards and often patrol large home ranges (Bennett, 1998; Phillips, 1995; Phillips and Millar, 1998; Pianka, 1968; Tsellarius and Men'shikov, 1994). In addition, the home ranges of many individuals may overlap considerably (Phillips, 1995; Phillips and Millar, 1998; Tsellarius and Men'shikov, 1994; Tsellarius and Tsellarius, 1997a). Hence, though monitors are likely to encounter conspecifics occasionally, interactions are probably few and far between. Intraspecific encounters may also be restricted to certain times of the year as many varanids exhibit strong seasonal activity patterns (Pianka, 1969, 1970; James, 1996). Accordingly, individuals are likely to be unfamiliar with one another's fighting ability and, as a consequence, some form of assessment may be required to settle a dispute.

Another assumption of the SAG is that contests are organized into discrete but increasingly escalated phases, each characterized by novel behavioural elements. Monitor combat rituals conform to a certain sequence and new behaviours, from threat displays and bipedal combat to wrestling matches, emerge as contests progress (Murphy and Mitchell, 1974; Carpenter et al., 1976; Vogel, 1979; Auffenberg, 1988, 1994; Thompson et al., 1992; Horn, 1994; Horn et al., 1994). Horn et al. (1994) identify five distinct phases of varanid combat:

- 1) *display* — both combatants exhibit head-jerks and intense tongue flicking,
- 2) *encompassing* — rivals orient themselves side-by-side often engaging in lateral display and intense head-jerking behaviour,

Table 1. Summary of the phases exhibited in varanid combat, the sex of the participants, the duration of the contest, the contested resource, and the factors involved in determining a winner. The table is arranged alphabetically according to varanid species. Whether the study was done on wild or captive populations is indicated by a 'W' or a 'C' next to the author's name. Male-male combat = 'M'; female-female combat = 'F'; male-female combat = 'F'; intersexual). The phases of combat are abbreviated as follows: D = display, Cl = clinch, Ca = catch, S = subpressive.

Species	Author(s)	D	Cl	Ca	S	Duration (minutes)	Resource	Determination of Victor
<i>V. albigularis</i>	Branch 1991 (C)	M	M ^a	M			Unspecified	Unspecified
<i>V. bengalensis</i>	Ali 1944 (W)		I		I		Unspecified	Unspecified
<i>V. bengalensis</i>	Auffenberg 1981b (C)	M, F, I	M	M	M, F, I	Mean \pm s Ritualized: 3.3 \pm 0.7 Weaponry Use: 1.8 \pm 0.7	Unspecified	Unspecified Size (M)
<i>V. bengalensis</i>	Deriyangala 1958 (W)		M	M			Unspecified	Unspecified
<i>V. caudolineatus</i>	Thompson et al. 1992 (W)			M		5	Unspecified	Disturbed Prior to Victory
<i>V. dumerili</i>	Davis et al. 1986 (C)	M	M		M	> 13	Unspecified	Residency Size (M)
<i>V. exanthematicus</i>	Attum et al. 2000 (C)	M, F		M, F	M, F		Territory (M) Food (M) Basking Site (M, F)	Residency (M, F)
<i>V. exanthematicus</i>	Bayless 1994 (C)	M		M	M		Unspecified	Size
<i>V. gilleani</i>	Carpenter et al. 1976 (C)	M		M	M	> 52	Territory	Residency
<i>V. gilleani</i>	Murphy & Mitchell 1974 (C)	M		M	M	15-30 for symmetrical 6 for resident- intruder fights	Female Territory	Size Residency
<i>V. gouldii</i>	Delean 1981 (C)	F					Unspecified	Unspecified
<i>V. gouldii</i>	Thompson et al. 1992 (W)	M	M	M			Unspecified	Disturbed Prior to Victory

Table 1. (Continued).

Species	Author(s)	D	Cl	Ca	S	Duration (minutes)	Resource	Determination of Victor
<i>V. griseus</i>	Tsellarius & Tsellarius 1997 (W)	M	M			10 – display 14 – fight 2-16	Territory Social Status	Unspecified
<i>V. indicus</i>	McCoid & Hensley 1991 (W)	M		M			Female	Size
<i>V. komodoensis</i>	Auffenberg 1978, 1981a (W)	M			M		Female Food	Size Social Status
<i>V. komodoensis</i>	Horn 1985 (C)	M	M		M	15	Unspecified	Unspecified
<i>V. mertensi</i>	Horn et al. 1994 (W)	M	M		M	1-2	Female	Unspecified
<i>V. niloticus</i>	Clements 1968 (W)		I				Unspecified	Unspecified
<i>V. niloticus</i>	Hagen et al. 1995 (W)			M	M		Female	Size
<i>V. olivaceus</i>	Auffenberg 1988 (C)	M	M		M		Female	Mass, social experience
<i>V. salvator</i>	Daltry 1991 (C)	M, F	F	M, F	M, F		Food (M, F) Social Status	Size (M, F)
<i>V. salvator</i>	Vogel 1979	M	M		M	0.1-2	Social Status Food	Size (relationships unstable)
<i>V. s. cumingi</i>	Horn 1994 (C)	M	M	M	M	3-6	Territory Basking Site	Size
<i>V. semiremex</i>	Horn 1985 (W)	M	M	M	M	15	Unspecified	Unspecified; disturbed prior to victory
<i>V. t. timorensis</i>	Horn 1985 (W)	M					Unspecified	Unspecified
<i>V. t. similis</i>	Horn 1985 (W)	M					Unspecified	Unspecified
<i>V. varius</i>	Horn et al. 1994 (W)	I	I	I		30	Unspecified	Unspecified
<i>V. varius</i>	Twigg 1988 (W)		M	M	M	17-22	Territory	Residency

^a The clinch phase was cited in Horn et al. (1994) as a personal communication from Branch.

- 3) *clinch* — combatants rise up and embrace one another,
- 4) *catch* — contestants twist and tilt around one another in a series of wrestling bouts,
- 5) *subpressive* — a victor is determined and the subordinate male is subsequently mounted by the dominant (pseudocopulation).

The presence or absence of each of these phases in 19 varanid species/subspecies has been noted in table 1. For this table, the display and encompassing phases were combined into 'display' because the two are often not clearly distinguishable in the literature. Though the literature suggests that the ordering of phases described by Horn et al. (1994) is more the rule than the exception in monitor fights, some contests do deviate from this precise sequence (e.g. Auffenberg, 1981b; Thompson et al., 1992; Horn et al., 1994). For instance, members of the *Odatria* clade (e.g. *V. gilleni*, *V. semiremex*, *V. timorensis*) do not exhibit bipedal combat (clinch phase) but instead perform extended wrestling bouts (Murphy and Mitchell, 1974; Carpenter et al., 1976).

Behavioural repetition within phases

Repetition of behavioural displays within each phase of combat is an important aspect of the SAG. By averaging the information content of all display repetitions rather than relying on one possibly erroneous display, contestants are able to gather more precise information about relative fighting ability. This is akin to statistical sampling whereby increasing the sample size reduces random error and gives a more precise estimation of the population mean. Varanids are known to repeat display patterns during aggressive disputes, especially head-jerking and arching-of-the-back which may signal agonistic motivation and size, respectively (Vogel, 1979; Auffenberg, 1981, 1994; Davis et al., 1986; Tselariou and Tselariou, 1997a). In addition, many varanids exhibit repeated bouts of bipedal stance-brachial embrace and wrestling-arching postures which likely act as tests of strength or endurance (Vogel, 1979; Murphy and Mitchell, 1974; Carpenter et al., 1976).

More recently, Bels et al. (1995) analyzed the throat display (i.e. gular expansion), a common threat tactic among monitors, of *V. griseus*. Their functional analysis revealed two characteristics of the throat display — an inhalation phase that they termed the ventilatory bucco-pharyngeal breathing pump display (VBPBD) followed by a long series of bucco-pharyngeal breathing pumps (BPBP), which occur while the body is still inflated. The number of BPPBs within each bout ranged from 3 to 35. The BPBP display is anatomically constrained in the sense that its performance relies on the structure of the varanid hyoid apparatus. As such, the BPBP display may act as an honest signal of size and/or strength, e.g. if stronger individuals are capable of depressing/elevating the hyoid to a greater degree or at a faster rate (see Grafen, 1990; Zahavi and Zahavi, 1997 for a discussion of honest signaling). It is clear that display repetition, whether conspicuous or subtle, is an important component of varanid fighting behaviour.

Contest costs

According to the SAG, escalation occurs only when individuals are not capable of assessing significant differences in fighting ability using non-contact displays. In such cases, the contests may intensify to physical combat involving more costly behavioural elements. Fighting costs may come in two forms: direct costs accrued during physical combat (i.e. injuries or fatigue) or time costs, which involve the loss of feeding/mating opportunity or increased susceptibility to predators as contests progress (especially for small-bodied goannas). The SAG is concerned primarily with direct costs.

Auffenberg (1981b) defined several behaviours falling under the 'weaponry' (biting, tail slapping) and 'combat tactic' (brachial embrace, wrestling) categories. These behavioural elements can be considered the most risky or energetically demanding behaviours of the varanid repertoire and are often those that unambiguously settle escalated contests (e.g. Auffenberg, 1994). Indeed, these acts are often confined to later stages of combat, as predicted by the SAG. For instance, Auffenberg (1981b) revealed that weaponry was never used to initiate aggressive interactions but rather, always followed some other behaviour such as an investigative or dominant act in *V. bengalensis*. Furthermore, the clinch and catch phases normally follow some type of display or investigative behaviour (e.g. gular expansion, head-jerking or tonguing; Murphy and Mitchell, 1974; Carpenter et al., 1976; Vogel, 1979; Auffenberg, 1981b, 1988, 1994; Davis et al., 1986; Branch, 1991; Bayless, 1994; Horn, 1994; Attum et al., 2000). These observations demonstrate that varanids, on the whole, reserve energetically costly or injurious behaviours for situations in which contests cannot be resolved by non-contact display alone.

If aggressive interactions in varanids are in fact costly, how can we measure such costs? To examine visually obvious costs accrued during battle (e.g. lacerations), one could develop a composite injury index and compare the extent of damage suffered in escalated versus non-escalated battles (e.g. Enquist et al., 1990; Neat et al., 1998). Though injuries do occur in varanid duels (Daltry, 1991), they are not commonplace, even after prolonged bouts of apparent biting (e.g. Carpenter et al., 1976; Thompson et al., 1992). Rather, the costs of high-intensity combat in varanids are probably manifest as depletions in energy reserves and/or accumulation of the byproducts of anaerobic metabolism that may impede further activity. As such, a second measure of contest costs could involve the metabolic consequences of battle. In other taxa, measurements of respiration frequencies and lactic acid (or lactate) buildup in the muscle, hemolymph (of invertebrates), or blood often provide good measures of the energetic demands placed upon contestants (e.g. Haller, 1995; Sneddon et al., 1999; Briffa and Elwood, 2001). Bennett's (1982) comprehensive review on reptilian energetics suggested that maximal oxygen consumption places an upper bound on aerobic metabolism and thus, on activity levels. Behaviour that involves sustained, high-intensity activity such as the clinch or catch phases of varanid combat is likely to result in increased anaerobic contributions to metabolism and the production of lactic acid (e.g. Gleeson, 1991). Most studies on varanid metabolism to date have focused

primarily on the energetic demands of locomotory and feeding behaviour (Bennett, 1982; Gleeson, 1991; Christian and Weavers, 1994; Thompson and Withers, 1997; Hicks et al., 2000). Undoubtedly, the methods used in these investigations can be applied to testing predictions generated by the SAG with respect to the accumulation of metabolic cost over the duration of contests.

The SAG predicts not only that overall contest costs increase in later stages of conflict but also that eventual losers accrue costs more rapidly than winners. Though rigorous tests of this prediction are not abundant, empirical evidence in other taxa has revealed that losers score higher on injury indices, have higher respiration rates, and exhibit higher plasma levels of anaerobic metabolites than do winners (e.g. Enquist et al., 1990; Keeley and Grant, 1993; Neat et al., 1998; Schuett and Grober, 2000). For instance, after male copperheads (*Agkistrodon contortrix*) engage in pairwise confrontations, losers exhibit substantially higher levels of plasma lactate than winners (Schuett and Grober, 2000). There are no existing data on discrepancies between the absolute amount of costs or the rate at which winners and losers amass costs in varanid encounters.

Display intensity and phase/contest duration

Three of the most salient predictions of the SAG are: 1) displays within each phase should be performed at constant intensity so as to facilitate accurate assessment (i.e. to promote reduction in the random error associated with each signal), 2) the duration of each phase of combat should be independent of asymmetries in fighting ability between contestants, and 3) contest duration should be longer and more variable when contestants are well-matched.

To our knowledge, empirical support for the first prediction is lacking though there are several studies in other taxa that report decreases in display intensity with time (e.g. Briffa and Elwood, 2000). Davis et al. (1986) reported that *V. dumerili* increase the intensity of head-jerking displays in the initial stages of agonistic interactions. Clearly, this aspect of the SAG is in need of further study across taxa. If varanid contests do not conform to this prediction, then alternative assessment tactics may be explored (see Cumulative Assessment below). The second prediction — that phase duration should not be correlated with asymmetries in fighting ability — has been upheld in numerous studies on fish (Enquist et al., 1990; Koops and Grant, 1993), insects (Hofmann and Schildberger, 2001), and mammals (Jensen and Yngvesson, 1998). However, this issue has not been addressed in enough detail in the monitor combat literature to anticipate its applicability to this taxon.

The third prediction — that contest duration should increase as asymmetries between opponents decrease — has received the most attention in analyses of animal contests. For instance, decreased size asymmetries (e.g. differences in weight, standard length, lateral surface area, head capsule width, etc.) forecast longer contests in invertebrates (Englund and Olsson, 1990; Leimar et al., 1991), fish (Enquist et al., 1990; Koops and Grant, 1993), reptiles (Olsson, 1992; McMann, 1993; Molina-Borja et al., 1998), and mammals (Andersen et al., 2000). Nevertheless, this prediction has not gained ubiquitous support,

suggesting that some animals may use alternative assessment tactics in settling disputes (see Turner and Huntingford, 1986; Marden and Waage, 1990; Marden and Rollins, 1994; Bridge et al., 2000).

Quantitative data regarding this third prediction are unavailable in the varanid literature. However, several descriptive reports suggest that the magnitude of asymmetries between rival monitors may influence contest duration. For instance, fights between *V. salvator* of equivalent social status tend to be significantly more prolonged than fights between a clear dominant and subordinate (Daltry, 1991). Similarly, Murphy and Mitchell (1974) revealed that contests between matched opponents are between two and five times longer than battles involving residency asymmetries (i.e. resident versus intruder; *V. gilleni*). Horn et al. (1994) also claim that fights involving individuals that differ markedly in size are resolved by less expensive means (e.g. body movements, displays) than those between matched contestants.

Oddly, there have been several reports of weaponry tactics (e.g. biting, tail-slapping) being used early on in varanid fights (Vogel, 1979; Auffenberg, 1981b). Auffenberg (1981b) reported that contests in which weaponry was used lasted for significantly shorter periods than those in which tactics such as brachial embrace and catch phase were exhibited (mean \pm standard deviation: 1.8 ± 0.7 versus 3.3 ± 0.7 min, respectively). At first glance, these findings seem to contradict several tenets of the SAG, i.e. weaponry should be reserved for later phases of combat and consequently should be documented only in contests between individuals of similar fighting ability that endure for long periods of time. However, tail-slapping and biting are potentially less costly than the clinch and catch phases of combat. As stated previously, biting rarely causes detectable injuries (but see Auffenberg, 1978 in *V. komodoensis*) and the force of the tail-blow tends to be exaggerated in many reports (Auffenberg, 1978). As such, the tail-blow may act as a low-cost, high-efficiency fighting tactic used by individuals that face intruders or opponents that are obviously inferior (e.g. see example 8 in Tselarius and Tselarius, 1997a). In contrast, the clinch and catch phases of combat may be energetically demanding and thus, reserved for fights between matched combatants. In this sense, the fact that struggles involving the clinch and catch phases endured for longer than those involving weaponry is not entirely unexpected.

The duration of varanid contests ranges from 6 seconds (*V. salvator*) to almost 1 hour (*V. gilleni*; table 1), though there does not appear to be a correlation between the focal species and fight length. Based on the descriptive accounts given in the literature, this variation is most likely to be explained by the degree of asymmetries between contestants (e.g. size, residency, status). Under captive conditions, this prediction of the SAG could be easily tested by establishing several asymmetry regimes (e.g. contestants with slight, intermediate, and pronounced differences in size/status) and assessing fight lengths as a function of these differences. Moya-Laraño and Wise (2000) summarize a statistical technique (survival regression analysis) used to detect the relationship between contest

duration and asymmetry magnitude; this procedure appears to give a better estimate of the relationship than standard correlational analyses.

Asymmetries and contest outcome

In keeping with the predictions of early game-theoretical models, the SAG predicts that contests should be settled on the basis of obvious asymmetries if they are present (e.g. size, resource value, ownership). Two types of outcome-related asymmetries are consistently documented in the varanid literature: size and residency (table 1). Size is clearly an important determinant of contest success in monitors (e.g. snout-vent length, mass; Auffenberg, 1979, 1981b; Vogel, 1979; Bayless, 1994; Bennett, 1998; Attum et al., 2000). For instance, small individuals are considerably more likely to be displaced from feeding or basking sites than are larger individuals (Auffenberg, 1978, 1979). However, there are some instances where smaller individuals do manage to win fights (e.g. Vogel, 1979; Tsellarius and Tsellarius, 1997a). This is consistent with the predictions of the SAG if the probability that the smaller individual wins increases as asymmetries decrease. Under these circumstances, smaller individuals may be expected to win a small proportion of the time due to random errors in the assessment of fighting ability. Indeed, smaller monitors won only under escalated circumstances (e.g. presence of bipedal combat and/or weaponry) which suggests that the contestants may have been well-matched (Vogel, 1979; Tsellarius and Tsellarius, 1997a).

Ownership also influences the outcome of varanid contests, with resident individuals having a higher probability of victory than intruders (Murphy and Mitchell, 1974; Carpenter et al., 1976; Auffenberg, 1978; Twigg, 1988; Attum et al., 2000). In resident-intruder contests, it is often difficult to partition the effects of ownership from the influence of other asymmetric factors (Olsson and Shine, 2000). Empirical studies that separate the effects of residency from those of size and resource value will aid in elucidating the precise contributions of each of these factors to contest resolution in monitor lizards (see Dugatkin and Ohlsen, 1990; Dugatkin and Biederman, 1991 for partitioning asymmetries). Another potential difficulty in analyses of fights with ownership differences is that residency can mediate aggressive contest dynamics through a variety of possible mechanisms. For instance, a resident may have acquired the territory because of its superior fighting ability or ownership status may increase a resident's perceived fighting ability. In addition, resident individuals may be willing to engage in more costly defense tactics than intruders in order to preserve ownership of a valuable resource and thus, should win against an invader. Of course, this proposition assumes that owners are better informed about the resource and thus, can adjust their strategy according to the resource value. On the other hand, intruders are not informed and must choose a strategy based on an average distribution of resource values (Leimar and Enquist, 1984; see Leimar et al., 1991 for additional predictions regarding ownership).

There are a host of other asymmetries that may be considered in analyses of varanid duels including differences in social status, prior dominance or subordination experience, physiological state (e.g. hunger, steroid hormone levels), and intrinsic aggression levels. None of these have been addressed in the varanid literature. Nevertheless, given that these factors are known to influence outcome in a variety of taxa, they may be worthwhile to investigate in varanid encounters (e.g. Stamps and Krishnan, 1994; Knapp and Moore, 1996; Schuett, 1997; Hsu and Wolf, 1999; Earley et al., 2000). Differences in body temperature between contestants may also bear on contest outcome. Maximal oxygen consumption and metabolic efficiency rely, in part, on body temperature and could influence the rate at which energy reserves are depleted (or anaerobic metabolites accumulate) during escalated combat (Bennett, 1982). If there is intraspecific variation in body temperature among active varanids, as has been shown by Tsellarius and Tsellarius (1997b; range: 33-41.5°C), and if body temperature constrains efficient metabolic processes, then it may be important in determining individual persistence times and outcome.

Prior assessment and familiarity

The SAG also makes predictions about contests in which the opponents are familiar with one another or have had the opportunity to assess one another in advance, e.g. through previous agonistic interactions (Enquist et al., 1987; Keeley and Grant, 1993). In particular, contests between acquainted individuals should be shorter than those between strangers because presumably less probing is required to settle the dispute. In addition, the duration of each bout of assessment displays (e.g. arching of the back, gular expansion, head-jerking) should be shorter among familiar individuals. However, if contests between acquainted individuals do escalate to more costly forms of combat (e.g. clinch or catch phase), the duration of these later phases should be independent of familiarity. Several lines of evidence in the varanid literature support the first prediction but the latter two have yet to be addressed in fair detail.

For instance, interactions between acquainted *V. griseus* are far less escalated than those between strangers, indicating that less assessment was needed to settle contests between familiar lizards (Tsellarius, 1994). There is also some evidence that subordinate monitors are capable of recognizing individuals to whom they had previously submitted (Honegger and Heusser, 1969; Auffenberg, 1983). In fact, subordinates appear to adjust their behavioural strategies in order to avoid subsequent costly interactions with dominants, i.e. previous losers often yield immediately (Honegger and Heusser, 1969; Auffenberg, 1983; but see Vogel, 1979; Auffenberg, 1994). Individual recognition in varanids is likely accomplished through olfactory or visual means (e.g. Tsellarius and Men'shikov, 1994). Monitor combat behaviour is consistent with the SAG in that contests between acquainted individuals are shorter and settled by less expensive means than fights between strangers. However, analyses of the dynamics of such interactions remain elusive (e.g. whether the

visual assessment phase itself is shorter in fights between familiar conspecifics or whether the duration of escalated stages is independent of acquaintedness).

Alternative models and summary

Thus far, we have concentrated exclusively on how varanid combat conforms to the assumptions and predictions of the sequential assessment game. From the limited data and available qualitative observations, monitor contests appear to fit nicely within the boundaries of this game theoretical model. However, some of the most crucial aspects of the SAG remain untested. For instance, it is unclear whether displays are exhibited at a constant intensity within each phase and whether the duration of each phase is independent of the relative fighting abilities of the combatants. Since each contestant is essentially calculating an average 'relative fighting ability', displays must also be consistent within each phase to reduce the error associated with signal transmission. In order for the SAG to hold, these predictions need to be supported. Where should we turn if these predictions are not validated? An alternative possibility is that the contestants calculate the sum of all behavioural acts and use this cumulative assessment as a gauge of their own, or their opponent's, fighting ability (Payne and Pagel, 1997; Payne, 1998). In this case, the purpose of repeating a display is to augment, rather than confirm, the information contained in previous displays (see table 1 in Payne and Pagel, 1997).

When an individual's decision to retreat is based on the sum of its own actions, the game is called the 'energetic war of attrition' (e.g. Marden and Waage, 1990). This energetic assessment game is similar to the war of attrition described in the introduction except that the contestants use a currency of energy rather than time in gauging when to give up. As such, the energetic game is one of endurance. This model does not require displays to be performed at constant intensity within each phase, i.e. display vigor may increase, decrease, or remain constant within each phase. In addition, this game predicts that contest duration should be correlated with the absolute fighting ability of the loser since the loser's energy reserves cross the giving-up threshold first; this is in contrast to the 'relative' decision rule used in the SAG. However, it does require that contestants match one another's display, move-for-move, and that the fights rarely, if ever, escalate to dangerous combat (Payne, 1998). Varanid fights do not fulfill the 'matching displays' requirement of the energetic war of attrition. For instance, *V. olivaceus* respond to head-jerking with a variety of tactics including tongue flicking, head jerking, and approaching (Auffenberg, 1988). Moreover, encounters between monitor lizards sometimes escalate to dangerous combat. Though energetic wars of attrition appear to be in conflict with several aspects of varanid combat, some features of this model may be useful in formulating an overall concept of aggressive encounters in these lizards.

A third model — the cumulative assessment game — assumes that an individual's decision to retreat is based on the sum of the costs inflicted by its opponent; when the cumulative costs cross some threshold, an individual should give up (Payne, 1998).

Each contestant assesses only its own cost thus, there is no prerequisite for continuous assessment between opponents. In other words, each individual knows how poorly it is doing and whether the retreating threshold is approaching but does not necessarily know how its opponent is faring (except that the opponent is either still fighting or has fled). As such, the cumulative assessment game may be appropriate in systems where the costs sustained by an opponent are not easily perceived (e.g. depletion of energy reserves and/or buildup of lactic acid in varanid duels) (Payne, 1998). This game is similar to the energetic war of attrition in that each additional display serves to augment previously obtained information, contest duration depends only on the eventual loser's absolute fighting ability, and display intensity can vary within each phase (all of which are contrary to the SAG). However, the cumulative assessment game eliminates the necessity for matching displays and is particularly relevant to interactions that intensify to damaging combat (see Payne, 1998 for an in-depth treatment).

As more quantitative data are collected on varanid fights, we should be able to test the critical predictions of the SAG that are, at present, lacking in the literature. If these aspects of the model are not upheld, then alternative assessment mechanisms, such as those proposed by the energetic war of attrition and cumulative assessment games, should be explored in detail. The vast majority of game theory's predictions remain untested in monitor lizards despite the fact that a wealth of descriptive reports, dating back almost a century, provide the conceptual ammunition to do so. The primary aim of this paper was to provide the impetus for examining varanid fights through the eyes of behavioural ecological theory. In doing so, we will undoubtedly gain a more comprehensive understanding of both the subtleties and overall schema of fighting behaviour in monitor lizards.

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References

- Ali, S. (1944): The 'courtship' of the monitor lizard (*Varanus monitor*). J. Bombay Nat. Hist. Soc. **44**: 479-480.
- Andersen, I.L., Andenaes, H., Boe, K.E., Jensen, P., Bakken, M. (2000): The effects of weight asymmetry and resource distribution on aggression in groups of unacquainted pigs. Appl. Anim. Behav. Sci. **68**: 107-120.
- Attum, O., Earley, R.L., Bayless, M., Eason, P. (2000): The agonistic behaviour of Bosc's monitor (*Varanus exanthematicus* Bosc, 1792) in captivity. Herp. Bull. **73**: 22-26.
- Auffenberg, W. (1978): Social and feeding behaviour in *Varanus komodoensis*. In: Behaviour and Neurology of Lizards: An Interdisciplinary Colloquium, p. 301-331. Greenberg, N., MacLean, P.D., Eds, Rockville, Maryland, National Institute of Mental Health.
- Auffenberg, W. (1979): Intersexual differences in behaviour of captive *Varanus bengalensis* (Reptilia, Lacertilia, Varanidae). J. Herp. **13**: 313-315.
- Auffenberg, W. (1981a): The Behavioural Ecology of the Komodo Monitor. Gainesville, University of Florida Press.

- Auffenberg, W. (1981b): Combat behaviour in *Varanus bengalensis* (Sauria: Varanidae). *J. Bombay Nat. Hist. Soc.* **78**: 54-72.
- Auffenberg, W. (1983): The burrows of *Varanus bengalensis*: characteristics and use. *Rec. Zool. Surv. India* **80**: 375-385.
- Auffenberg, W. (1988): Gray's Monitor Lizard. Gainesville, University of Florida Press.
- Auffenberg, W. (1994): The Bengal Monitor. Gainesville, University of Florida Press.
- Bayless, M. (1994): Zur Fortpflanzungsbiologie des Steppenwarans (*Varanus exanthematicus*). *Salamandra* **30**: 109-118.
- Bels, V.L., Gasc, J.-P., Goosse, V., Renous, S., Vernet, R. (1995): Functional analysis of the throat display in the sand goanna *Varanus griseus* (Reptilia: Squamata: Varanidae). *J. Zool. Lond.* **235**: 95-116.
- Bennett, A.F. (1982): The energetics of reptilian activity. In: *Biology of the Reptilia*. Volume 13 (Physiology), p. 155-199. Gans, C., Pough, F.H., Eds, New York, Academic Press.
- Bennett, D. (1998): *Monitor Lizards: Natural History, Biology and Husbandry*. Edition Chimaira, Frankfurt am Main, Meckenheim, Germany.
- Bishop, A.T., Cannings, C. (1978): A generalized war of attrition. *J. theor. Biol.* **70**: 85-125.
- Branch, W.R. (1991): The Regenia registers of 'Gogga' Brown (1869-1909): "Memoranda on a species of monitor or varan". *Mertensiella* **2**: 57-110.
- Bridge, A.P., Elwood, R.W., Dick, J.T.A. (2000): Imperfect assessment and limited information preclude optimal strategies in male-male fights in the orb-weaving spider *Metellina mengei*. *Proc. R. Soc. Lond. B* **267**: 273-279.
- Briffa, M., Elwood, R.W. (2000): Cumulative or sequential assessment during hermit crab shell fights: effects of oxygen on decision rules. *Proc. R. Soc. Lond. B* **267**: 2445-2452.
- Carpenter, C.C., Ferguson, G.W. (1977): Variation and evolution of stereotyped behaviour in reptiles. In: *Biology of the Reptilia*. Volume 7A (Ecology and Behaviour), p. 138-208. Gans, C., Tinkle, D.W., Eds, New York, Academic Press.
- Carpenter, C.C., Gillingham, J.C., Murphy, J.B., Mitchell, L.A. (1976): A further analysis of the combat ritual of the pygmy mulga monitor, *Varanus gilleni* (Reptilia: Varanidae). *Herpetologica* **32**: 35-40.
- Christian, K., Weavers, B. (1994): Analysis of the activity and energetics of the lizard *Varanus rosenbergi*. *Copeia* **1994**: 289-295.
- Clements, B.N. (1968): Lizard Love. *Lammergeyer* **9**: 53.
- Daltry, J. (1991): The social hierarchy of the water monitor, *Varanus salvator*. *Hamadryad* **16**: 10-20.
- Davis, R., Darling, R., Darlington, A. (1986): Ritualized combat in captive Dumeril's monitors, *Varanus dumerili*. *Herp Rev.* **17**: 85-88.
- Delean, S. (1981): Notes on aggressive behaviour by Gould's goannas (*Varanus gouldii*) in captivity. *Herpetofauna* **12**: 31.
- Deraniyagala, R.Y. (1958): Pseudo-combat of the monitor lizard *Varanus bengalensis* (Daudin). *Spolia Zeylandica* **28**: 11-13.
- Dugatkin, L.A., Biederman, L. (1991): Balancing asymmetries in resource holding power and resource value in the pumpkinseed sunfish. *Anim. Behav.* **42**: 691-692.
- Dugatkin, L.A., Ohlsen, S.R. (1990): Contrasting asymmetries in value expectation and resource holding power: effects on attack behaviour and dominance in the pumpkinseed sunfish, *Lepomis gibbosus*. *Anim. Behav.* **39**: 802-804.
- Dugatkin, L.A., Reeve, H.K. (1998): *Game Theory and Animal Behaviour*. New York, Oxford University Press.
- Earley, R.L., Hsu, Y., Wolf, L.L. (2000): The use of standard aggression testing methods to predict combat behaviour and contest outcome in *Rivulus marmoratus* dyads (Teleostei: Cyprinodontidae). *Ethology* **106**: 743-761.
- Englund, G., Olsson, T.I. (1990): Fighting and assessment in the net-spinning caddis larva *Arctopsyche ladogensis*: a test of the sequential assessment game. *Anim. Behav.* **39**: 55-62.
- Enquist, M., Leimar, O. (1983): Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. theor. Biol.* **102**: 387-410.
- Enquist, M., Leimar, O. (1987): Evolution of fighting behaviour: the effect of variation in resource value. *J. theor. Biol.* **127**: 187-205.

- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y., Segerdahl, N. (1990): A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Anim. Behav.* **40**: 1-14.
- Gleeson, T.T. (1991): Patterns of metabolic recovery from exercise in amphibians and reptiles. *J. Exper. Biol.* **160**: 187-207.
- Grafen, A. (1990): Biological signals as handicaps. *J. theor. Biol.* **144**: 517-546.
- Hagen, H., Horn, H.-G., Hagen, W. (1995): Zu Balz- und Kopulationsverhalten des Nilwarans (*Varanus n. niloticus*) — eine fotografische Dokumentation. *Herpetofauna* **17**: 29-33.
- Haller, J. (1995): Biochemical background for an analysis of cost-benefit interrelations in aggression. *Neurosci. Biobehav. Rev.* **19**: 599-604.
- Hammerstein, P. (1981): The role of asymmetries in animal contests. *Anim. Behav.* **29**: 193-205.
- Hicks, J.W., Wang, T., Bennett, A.F. (2000): Patterns of cardiovascular and ventilatory response to elevated metabolic states in the lizard *Varanus exanthematicus*. *J. Exper. Biol.* **203**: 2437-2445.
- Hofmann, H.A., Schildberger, K. (2001): Assessment of strength and willingness to fight during aggressive encounters in crickets. *Anim. Behav.* **62**: 337-348.
- Honneger, R.E., Heusser, H. (1969): Beiträge zum Verhaltensinventar des Bindenwarans (*Varanus salvator*). *Zool. Garten NF* **36**: 251-260.
- Horn, H.-G. (1985): Beiträge zum Verhalten von Waranen: Die Ritualkämpfe von *Varanus komodoensis* Ouwens, 1912 und *V. semiremex* Peters 1869 sowie die Imponierphasen der Ritualkämpfe von *V. timorensis timorensis* (Gray, 1831) und *V. t. similis* Mertens, 1958 (Sauria: Varanidae). *Salamandra* **21**: 169-179.
- Horn, H.-G. (1994): Der Ritualkampf von *Varanus salvator cumingi*. *Herpetofauna* **16**: 27-30.
- Horn, H.-G., Gaulke, M., Böhme, W. (1994): New data on ritualized combats in monitor lizards (Sauria: Varanidae), with remarks on their function and phylogenetic implications. *Zool. Garten NF* **64**: 265-280.
- Hsu, Y., Wolf, L.L. (1999): The winner and loser effect: integrating multiple experiences. *Anim. Behav.* **57**: 903-910.
- James, C.D. (1996): Ecology of the pygmy goanna (*Varanus brevicauda*) in spinifex grasslands of Central Australia. *Aust. J. Zool.* **44**: 177-192.
- Jensen, P., Yngvesson, J. (1998): Aggression between unacquainted pigs — sequential assessment and effects of familiarity and weight. *Appl. Anim. Behav. Sci.* **58**: 49-61.
- Kaufman, J.D., Burghardt, G.M., Phillips, J.A. (1994): Density-dependent foraging strategy of a large carnivorous lizard, the savanna monitor (*Varanus albigularis*). *J. Comp. Psychol.* **108**: 381-384.
- Kaufman, J.D., Burghardt, G.M., Phillips, J.A. (1996): Sensory cues and foraging decisions in a large carnivorous lizard, *Varanus albigularis*. *Anim. Behav.* **52**: 727-736.
- Keeley, E.R., Grant, J.W.A. (1993): Visual information, resource value, and sequential assessment in convict cichlid (*Cichlasoma nigrofasciatum*) contests. *Behav. Ecol.* **4**: 345-349.
- Knapp, R., Moore, M.C. (1996): Male morphs in tree lizards, *Urosaurus ornatus*, have different delayed hormonal responses to aggressive encounters. *Anim. Behav.* **52**: 1045-1055.
- Koops, M.A., Grant, J.W.A. (1993): Weight asymmetry and sequential assessment in convict cichlid contests. *Can. J. Zool.* **71**: 475-479.
- Lederer, G. (1929): Ein zahmer Bindenwaran. *Waschr. Aquar. Terrar. Kunde* **26**: 19-20.
- Leimar, O., Austad, S., Enquist, M. (1991): A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. *Evolution* **45**: 862-874.
- Leimar, O., Enquist, M. (1984): Effects of asymmetries in owner-intruder interactions. *J. theor. Biol.* **111**: 475-491.
- Marden, J.H., Waage, J.K. (1990): Escalated damselfly territorial contests are energetic wars of attrition. *Anim. Behav.* **39**: 954-959.
- Marden, J.H., Rollins, R.A. (1994): Assessment of energy reserves by damselfies engaged in aerial contests for mating territories. *Anim. Behav.* **48**: 1023-1030.
- Maynard Smith, J. (1982): *Evolution and The Theory of Games*. Cambridge, Cambridge University Press.
- Maynard Smith, J., Parker, G.A. (1976): The logic of asymmetric contests. *Anim. Behav.* **24**: 159-175.
- Maynard Smith, J., Price, G.R. (1973): The logic of animal conflict. *Nature* **246**: 15-18.
- McCoid, M.J., Hensley, R.A. (1991): Mating and combat in *Varanus indicus*. *Herp Rev.* **22**: 16-17.
- McMann, S. (1993): Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. *Anim. Behav.* **46**: 657-668.

- Molina-Borja, M., Padron-Fumero, M., Alfonso-Martin, T. (1998): Morphological and behavioural traits affecting intensity and outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). *Ethology* **104**: 314-322.
- Moya-Laraño, J., Wise, D.H. (2000): Survival regression analysis: a powerful tool for evaluating fighting and assessment. *Anim. Behav.* **60**: 307-313.
- Murphy, J.B., Mitchell, L.A. (1974): Ritualized combat behaviour of the pygmy mulga monitor lizard, *Varanus gilleni* (Sauria: Varanidae). *Herpetologica* **30**: 90-97.
- Neat, F.C., Taylor, A.C., Huntingford, F.A. (1998): Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Anim. Behav.* **55**: 875-882.
- Olsson, M. (1992): Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Anim. Behav.* **44**: 386-388.
- Olsson, M., Shine, R. (2000): Ownership influences the outcome of male-male contests in the scincid lizard, *Niveoscincus microlepidotus*. *Behav. Ecol.* **11**: 587-590.
- Parker, G.A. (1974): Assessment strategy and the evolution of fighting behaviour. *J. theor. Biol.* **47**: 223-243.
- Parker, G.A., Rubenstein, D.I. (1981): Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim. Behav.* **29**: 221-240.
- Payne, R.J.H. (1998): Gradually escalating fights and displays: the cumulative assessment model. *Anim. Behav.* **56**: 651-662.
- Payne, R.J.H., Pagel, M. (1997): Why do animals repeat displays? *Anim. Behav.* **54**: 109-119.
- Phillips, J.A. (1995): Movement patterns and density of *Varanus albigularis*. *J. Herp.* **29**: 407-416.
- Phillips, J.A., Millar, R.P. (1998): Reproductive biology of the white-throated savanna monitor *Varanus albigularis*. *J. Herp.* **32**: 366-377.
- Pianka, E.R. (1968): Notes on the biology of *Varanus eremius*. *W. Aust. Nat.* **11**: 39-44.
- Pianka, E.R. (1969): Notes on the biology of *Varanus caudolineatus* and *Varanus gilleni*. *W. Aust. Nat.* **11**: 76-82.
- Pianka, E.R. (1970): Notes on the biology of *Varanus gouldii flavirufus*. *W. Aust. Nat.* **11**: 141-144.
- Schuett, G.W. (1997): Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim. Behav.* **54**: 213-224.
- Schuett, G.W., Grober, M.S. (2000): Post-fight levels of plasma lactate and corticosterone in male copperheads, *Agkistrodon contortrix* (Serpentes, Viperidae): differences between winners and losers. *Physiol. Behav.* **71**: 335-341.
- Sneddon, L.U., Taylor, A.C., Huntingford, F.A. (1999): Metabolic consequences of agonistic behaviour: crab fights in declining oxygen tensions. *Anim. Behav.* **57**: 353-363.
- Stamps, J.A., Krishnan, V.V. (1994): Territory acquisition in lizards: II. Establishing social and spatial relationships. *Anim. Behav.* **47**: 745-753.
- Sterling, E.C. (1912): Observations on the habits of the large Central Australian monitor (*Varanus giganteus*), with a note on the 'fat bodies' of this species. *Trans. Proc. Soc. (South Australia)* **36**: 26-33.
- Thompson, G.G., Withers, P.C. (1997): Standard and maximal metabolic rates of goannas (Squamata: Varanidae). *Physiol. Zool.* **70**: 307-323.
- Thompson, G.G., Withers, P.C., Thompson, S.A. (1992): The combat ritual of two monitor lizards, *Varanus caudolineatus* and *Varanus gouldii*. *W. Aust. Nat.* **19**: 21-24.
- Tsellarius, A.Y. (1994): Behaviour and mode of life of the monitor in sand desert. *Priroda* **5**: 26-35.
- Tsellarius, A.Y., Men'shikov, Y.G. (1994): Indirect communications and its role in the formation of social structure in *Varanus griseus* (Sauria). *Russian J. Herp.* **1**: 121-132.
- Tsellarius, A.Y., Tsellarius, E.Y. (1997a): Behaviour of *Varanus griseus* during encounters with conspecifics. *Asiatic Herp. Res.* **7**: 108-130.
- Tsellarius, A.Y., Tsellarius, E.Y. (1997b): Thermal conditions of *Varanus griseus* (Reptilia, Sauria) activity. *Zool. Zh.* **76**: 206-211.
- Turner, G.F., Huntingford, F.A. (1986): A problem for game theory analysis: assessment and intention in male mouthbrooder contests. *Anim. Behav.* **34**: 961-970.
- Twigg, L.E. (1988): A note on agonistic behaviour in lace monitors *Varanus varius*. *Herpetofauna* **18**: 23-25.
- Vogel, P. (1979): Innerartliche Auseinandersetzungen bei freilebenden Bindenwaranen (*Varanus salvator*) (Reptilia: Sauria: Varanidae). *Salamandra* **15**: 65-83.

Zahavi, A., Zahavi, A. (1997): *The Handicap Principle: a Missing Piece of Darwin's Puzzle*. New York, Oxford University Press.

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