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Behavioural profiles of African bovids (Hippotraginae)

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Abstract

Behavioural assays for taxon-specific groups aid in assessing individual welfare and in population planning important to ensure sustainability (e.g. choice of enclosures, age/sex structure of groups, candidates for breeding and reintroduction). Personality approaches to measuring individual variation include ethological coding and subjective ratings via keeper questionnaires. We report on an ethological coding technique for measuring behavioural traits under conditions where individuals are in large social groups in semi-natural enclosures with minimal keeper contact. This standardised quantitative approach augments a questionnaire used by decision-makers in choosing appropriate candidates for breeding. This case study was conducted at a conservation breeding centre that is part of a network of institutions managing sustainable herds of ungulates with the long-term goals of recovery, reintroduction and ecological restoration. We developed a behavioural assay system for the subfamily Hippotraginae (African horse antelope) based on ethological coding of video samples. We field-tested this system using focal observations of social behaviour of breeding males in two herds, one each of addax (*Addax nasomaculatus*) and sable (*Hippotragus niger*). We demonstrated how behavioural profiles can be tested for significant differences in the categories of general activity, subcategories within each activity and indicator behaviours within each subcategory. This type of information is needed to develop a long-term database to test the additive effects of multiple variables (age, sex, rearing conditions, group, enclosure, population and species) on variation in individual profiles. We discuss the utility of coding video samples to validate subjective scoring techniques, statistical approaches to assessing variability in individual behaviour profiles, and the value of a hierarchical nested approach to analyse behavioural categories. We recommend applying this evolutionary ecology framework when designing behavioural assay systems, especially for species managed for recovery and reintroduction in sustainable populations.

Introduction

Personality research is at the interface between managing animals for individual well-being in zoo settings and population recovery in native habitats (Powell and Gartner 2010). Watters and Powell (2012) recommended integrating measures of personality into captive population planning processes and databases, which involve multiple institutions in captive breeding programmes. The need to consider variation in individual personality has also been discussed for recovery and reintroduction programmes (Bremner-Harrison et al. 2004; McPhee and Silverman 2004; Watters and Meehan 2007). We address the challenge of developing suitable taxon-specific assays to measure individual variation in behavioural profiles of species managed by conservation breeding centres with the goal of recovery and reintroduction of sustainable populations.

In a review of the debate about whether personality should be measured via "keeper questionnaires" or "ethological coding" in primates, Uher (2008) recommended validating results of questionnaires with ethological observations of actual behaviour. Techniques for comparing results of keeper questionnaires with behavioural observations are available for zoo settings (Baker and Pullen 2013). However, ethological coding may be the preferred option under conditions where (a) keeper experience varies widely, (b) criteria for answering questionnaires requires systematic training, or (c) animals are in large groups and/or enclosures where keeper contact is minimal. Considering that these three conditions are likely to apply to species managed for reintroduction, we focus on an information gap in the use of ethological coding techniques to assay individual profiles, with primary relevance for ungulates.

The need for bovid behavioural assays emerged from discussions within a network of institutions collaborating on sustainable ex-situ management of African antelope (Sawyer et al. 2011), highlighting the value of zoos in contributing to in-situ conservation (Gippoliti 2012). In-situ conservation of desert antelope has been a complex and challenging process that involves holding herds in fenced sanctuaries prior to release (Gordon and Gill 1993; Zafar-ul Islam et al. 2011). Decision-makers raised several challenging questions. Would zoo males show suitable breeding and herd-tending behaviours when placed with large female herds in a fenced sanctuary? Furthermore, what is "normal" for breeding bulls and can individuals raised in a zoo environment transition to species-typical behaviour in a large herd and semi-natural environment? Currently, no systematic approach exists to address these concerns of decision-makers collaborating in this sustainable herds initiative.

In designing suitable techniques for assaying ungulate behavioural profiles for the sustainable herds initiative, we reviewed previously reported techniques for ungulates: ethological coding, observer ratings, and experimental tests. None were directly suitable to the needs of the sustainable herds initiative; however, several suggested useful design elements, such as construct validity (Carter et al. 2013). For example, a study of personality in rutting fallow deer (*Dama dama*) was consistent with theoretical constructs of personality research (Jennings et al. 2013), whereas an earlier study of captive eland (*Taurotragus oryx*) was not (Kiley-Worthington 1978). Although high-construct validity was apparent in questionnaires used to score personality traits for elephants (*Loxodonta africana, Elephas maximus*) (Grand et al. 2012; Lee and Moss 2012; Yasui et al. 2013), these questionnaires were not useful for our purpose because raters needed to be highly familiar with individual animals. Experimental manipulations used to score ungulate temperament have included response to a novel object (Carlstead et al. 1999), chute or capture restraint (Reale *et al.* 2000; Sebastian et al. 2011), aggressive feeding (Gibbons *et al.* 2009), and flight speed and social separation (Muller and von Keyserlingk 2006). However, we needed to focus on social behaviour under conditions that were not manipulated, to meet the needs of the sustainable herds initiative.

The approach that came closest to meeting these needs involved temperament scoring of horses (*Equus caballus*): subjective ratings by judges were compared with behavioural scores from videos taken in the context of working conditions (von Borstel et al. 2011). Collaborators in the sustainable herds initiative have developed a curator questionnaire to assess "bull suitability" (Loonam 2012), analogous to judges' ratings for the horses. In the context of sustainable herds, the "working conditions" refer to the goal of producing resilient individuals for recovery and reintroduction. To compare actual behaviour with the results of the "bull suitability" questionnaire, we needed techniques for ethological scoring of videos taken in the "working conditions" of herds in large enclosures.

We addressed this information gap by designing a behavioural assay system based on ethological coding of videos, which would be suitable for application to the diverse species within one subfamily, Hippotraginae (horse antelope). Because the natural behavioural repertoire of these African bovids is well documented (Walther 1984; Estes 1991), a basis for ethological coding was available. Our objectives were to: (1) develop a system for coding behaviours in a manner that could be applied across species, (2) analyse video samples of unmanipulated, ongoing, social behaviour, and (3) compare behavioural profiles of two breeding males of different species to demonstrate how this technique might be applied in the future to a larger sample size.

Methods

We chose two species of Hippotraginae that differ in habitat and risk category. Sable (*Hippotragus niger*) are "least concern", adapted to forest habitat (IUCN SSC Antelope Specialist Group 2008). Addax (*Addax nasomaculatus*) are "critically endangered", adapted to the Saharan desert (Durant et al. 2014). We used standard ethological approaches to data collection and analysis (Martin and Bateson 2011) as described below.

Study site

Data were collected at Fossil Rim Wildlife Center, a conservation breeding centre accredited by the Association of Zoos and Aquaria (Spevak et al. 1993). Located in the savannah ecoregion of Texas (32.180556°N, 97.796389°W), the vegetation includes grassy meadows and wooded patches, similar in structure to in-situ antelope habitat in Africa. Sable (n = 35) and addax (n = 33) were observed in a fenced area of 182 ha, which also included five other ungulate species. Only one breeding male was in each herd due to the need to document paternity in the controlled breeding programme. Both males had been scored as "suitable" using the subjective scoring procedure (Loonam 2012).

Data collection

Observations occurred within three hours of sunrise and sunset, totaling 36 observation periods during May through July 2012 (averaging 12 samples per period). Observers drove a survey route and stopped at each group encountered. If the breeding male was in the group, observers collected focal-individual video samples (three minutes duration); otherwise, they continued along the survey route to the next group. To comply with statistical criteria for quasi-independence, consecutive samples of the same individual were separated by at least three minutes. We experimented with focal videos and "rest" periods of different durations; however, the "three minute" rule was optimal based on duration of activity bouts, consistency of data collection by a team of observers, and transferability of the technique to other institutions.

Data analysis

An ethogram (Table 1) was compiled from published literature (Walther 1984; Estes 1991; Manski 1991; Thompson 1993; 1995; Penfold et al. 2002; Loeding et al. 2011). Subcategories of activity states were defined to match ethological concepts of the hierarchical control of motivational systems (Packard et al. 1990). The list of indicator behaviours (action events) within each subcategory allowed us to include actions that were similar across all species of Hippotraginae as well as actions unique to certain species.

We used instantaneous sampling of activity states (freeze frames) at 10-second intervals and "one-zero" time-span sampling of indicator behaviours (action events) during the intervening 10 seconds (Martin and Bateson 2011). We found that one-zero sampling (1 = present, 0 = absent) was more reliable than counts of indicator behaviours (events) during time-spans (see techniques for observer reliability assessment below). The time-span sampling between freeze-frames allowed us to record both rare and frequent events. Activity profiles were tallied from point samples. Subcategories within the category of social activity were tallied from time-spans.

Observer reliability was assessed using a test set of six video files selected to represent a variety of observation conditions ranging

Table 1. Hippotraginae behavioural repertoire defining broad activity states (alert, feed, locomote, rest, social), subcategories within each activity state, and indicator behaviours (events) within each subcategory. Events marked with an "a" superscript were only observed in addax.

Activity state (CODE)	Activity state subcategories	Indicator behaviours (events)
Alert (AL)	*High intensity (alarm):* Actor switches from assessment to attack (fight) or flight away from the stimulus (not a conspecific)	Horn swipe (anti-predator context), startled turn away, fast walk, trot, gallop, run
	Moderate intensity (assess): Actor stands in a high posture with head up; movements of ears, eyes, nose and feet indicate stimulus has been detected	Alert posture, freeze, style-trotting, stamp (one foot on ground); object-manipulate, mob, bleat
	Low intensity (vigilant): Actor briefly raises and drops head; briefly stops ruminating; slight movements of eyes and ears indicate no alarming stimulus detected	Scan, chew-pause, ears forward, ears flip, turn head
Feed (FD)	*High intensity (ingest):* Actor takes food or fluid into the mouth; chews, swallows.	Graze (grass/forb/hay), browse (leaves/bark), nibble, drink
	Moderate intensity (handle): Actor manipulates food before ingesting; grass may be pulled into the mouth; no swallowing	Paw, dig, horn to object (e.g. old hay bale), chewing
	Low intensity (search): Actor looks or moves toward a stimulus or location where food is likely to be	Stare, sniff/look (e.g. vegetation on ground, food delivery vehicle, trough)
Locomote (LO)	*High intensity (run):* Spontaneous rapid directional movement; no stimulus indicative of AL, FE, SO	Run
	Moderate intensity (other gait): Spontaneous directional movement that is not running or walking; no stimulus indicative of AL, FE, SO	Trot, gallop, self-play (jump in place, gambol around enclosure, frolic, leap over objects)
	Low intensity (walk): Spontaneous slow directional movement; no stimulus indicative of AL, FE, SO	Walk
Rest (RE)	*High Intensity (sleep):* Actor closes eyes while lying on chest, not ruminating	Prone (head on substrate), head tucked against side
	Moderate intensity (lie): Actor is lying on chest with eyes partially closed; may ruminate or graze; may include maintenance events (scratch, lick, rub)	Yawn, snort, sneeze, stretch neck, chew cud, scratch
	Low intensity (stand): Actor stands on all four feet; not alert; may include maintenance events	Full body shake, stretch, defaecate, urinate
Social-conflict (SO-c)	*Conflict-escalate (aggressive):* Agonistic movement forceful enough to injure the opponent if contact is made; may include physically chasing another individual from the area.	Lunge, kneel, frontal horn jab, horn tap, frontal horn present, sideways jab, rush, charge, pursuit march, foreleg strike, fight (clash, push, thrust, lever, circle, air-cushion, parallel)
	Conflict-assess (threat display): Any agonistic social interaction that is not an escalation or de-escalation, also includes actions that are not directed towards specific individuals but serve to communicate conflict readiness – advertising and dominance displays.	Stand high, circle, displace, scent-mark[a], horn-object, high step, nodding, horn sweep, chin level, chin up, head turned away, face opponent, stiff-legged approach, horn present (low, medial, high, angle), stare, roar
	Conflict-de-escalate (submissive/ appeasement): Actions that have the consequence of reducing injurious contact or social tension; includes movement away from the escalating individual.	Low neck stretch, head-shake, bleat, step away, walk away, run away, humped back, chin in, lying out, pass behind, look away, gape
Social-proximity (SO-p)	*Proximity-approach:* Actor decreases distance to recipient; may be in an agonistic, sexual or parental context; may be a response to vocalisations (or body odour) typical of mother/calf join-up.	Approach conspecific, herd females, sniff, rub head, lick, nibble, nurse, suckle, ano-genital sniff, responsive urination, bleat, moo
	Proximity-retain: Actor directly or indirectly maintains social distance from the recipient, as if there is an "elastic band" between them; although the actual distance may fluctuate around a mean, actor maintains acoustic, odour and/or visual contact; may include drifting with the herd in one direction without direct following.	Follow conspecific, bleat, moo[a], substrate sniff, stare, graze together, parallel orientation
	Proximity-withdraw: Actor increases social distance from recipient; may include actions that reduce acoustic/visual contact.	Leave group (includes leaving another individual), leave calf (e.g. as in a lying out site)
Social-sexual (SO-s)	*Sexual-receptive (copulation):* Actor facilitates copulation; female is in "standing heat" usually within 24 to 48 h of ovulation; in the context of a receptive female, male initiates copulatory sequence; if no receptive female is present, male actions may appear out of sequence.	Stand, mount, intromission, ejaculatory hop, stand still, spread rear legs, tail moved to side
	Sexual-proceptive (arousal, courtship): Actor interacts with a potential sexual partner without actually copulating; may include alternating approach and withdrawal as if stimulating sexual arousal.	Approach, follow, rub body, head-flick, responsive urinate, mount, flehmen, sparring[a], circling, low-neck stretch, urine-testing, foreleg lift, chest bump, partial mount (no insertion), driving/chasing, rest chin on rump, sniff, rub rump.
	Sexual-unreceptive (rejection): Actor ignores, avoids or actively discourages proceptive behaviours; females may be in an anestrous or pregnant hormonal state; males may be immature, castrated, exhausted or in a post-ejaculatory quiescent state.	Stand, move away, lie down, brush-off[a] (e.g. entering thick bushes or dense herd)

from good to poor. Trainees and an experienced observer used the same technique to score each video (point-sample and span-sample). Summed scores tallied for each behaviour category were compared between each trainee and the experienced observer using log-likelihood ratio tests (G^2). For trainees who did not achieve statistical reliability (G^2; $p < 0.05$), we used the binomial z-score to examine which categories were coded unreliably. The coding criteria were discussed and the trainee was allowed to retest one time. Only trainees who achieved statistical reliability were chosen to code data entered into the data set for analysis.

We used a hierarchical approach to data analysis of video samples (addax, n = 41; sable n = 37); thus, we analysed activities associated with social behaviour, subcategories within social behaviour and the indicator behaviours within each social subcategory. We had previously estimated that social interaction comprised less than five percent of the daily activity budget (Packard, unpub. data). To achieve sufficient resolution to examine such relatively infrequent behaviour, we only analysed video samples containing social activity. By selecting video samples that included social activity, we controlled for variation in motivational state (e.g. excluding long bouts of feeding or resting behaviour); this provided a consistent criteria for comparison of individual profiles.

All of our analyses are reported as "in the context of social behaviour": during each 3-min video sample, the focal animal potentially switched among the activity states, one of which was social (Table 1). If research questions focused on a different motivational state (e.g. feeding), the same procedure could be followed with a different criteria for selecting videos from the larger archived data base shared among cooperating institutions.

To be consistent with emerging models for comparing individual variation across populations and species (Dingemanse et al. 2010), we applied an "information theoretic" approach. We used the G^2 statistic to test for individual differences in behavioural categories, and the binomial z-score to determine which cells of each matrix contributed to the significance of the G^2 statistic. Our statistical hypotheses were: (1) "given that individual X was observed, what was the likelihood that activity A was also observed", (2) "given that activity A was observed in individual X, what was the likelihood that subcategory A1 was also observed". Our intent was to document how this technique for analysing individual behavioural profiles could be applied across closely related species, not to generalise from our limited sample to species comparisons.

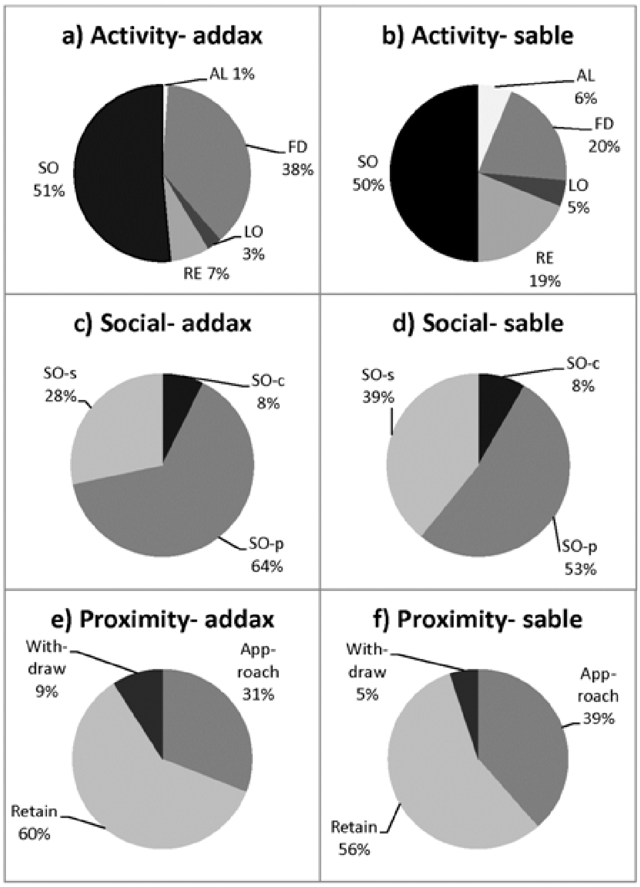

Figure 1. Nested comparison of behavioural profiles for two breeding males (addax, sable): general activity categories (a, b), subcategories within social activity (c, d), and indicator behaviours within the social-proximity subcategory (e, f). Behaviour codes are defined in Table 1. Codes for activity states are Alert (AL), Feed (FD), Locomote (LO), Rest (RE) and Social (SO). Social activity subcategories are Conflict (SO-c), Proximity (SO-p), Sexual (SO-s).

Results

For this case study, we compared the behavioural profiles of two sexually mature males consisting of one sable and one addax, which subjectively had been scored by facility managers as "suitable" for breeding purposes (Figure 1). Activity profiles (Figure 1a, 1b) differed significantly between the breeding males ($G^2 = 107.74$, df = 4, $p < 0.001$). In the social context in which these samples were collected, the addax male rested less (7%; z = -6.15) than the sable male (19%) and fed more (38%; z = 6.01). Both rarely showed alert ($\leq$ 6%) or locomotion activity ($\leq$ 5%) in the social context of these samples. Social activity was similar in both males (addax, 51%; sable 50%).

The type of social behaviour (Figure 1c, 1d) differed significantly between individuals ($G^2 = 16.99$, df = 2, $p < 0.001$). Compared to the sable (39%), the addax was less likely to show sexual behaviour (28%; z = -2.53) and more likely to show proximity behaviour (64%; z = 2.65). Conflict was relatively infrequent in both individuals (8%). All conflict actions for both males were in the category "assess" (addax, n = 48 sable, n = 41), which some authors interpret as threat display (with no physical contact). Neither male escalated (aggressive) nor de-escalated (submissive/appeasement). Sexual actions were primarily proceptive (e.g. courtship; addax, n = 176; sable, n = 183) with relatively infrequent receptive actions (e.g. copulation: addax, n = 9; sable, n = 9) and no rejection of female courtship.

Both males actively tended females. In the subcategory of proximity behaviour (Figure 1e, 1f), males differed significantly ($G^2 = 6.57$, df = 2, $p < 0.05$). The sable was slightly more likely to approach females (39%; z = 1.59) than the addax (31%). Both males actively retained proximity to females (addax 60%; sable 56%). Withdrawal was relatively unlikely for both males ($\leq$ 9%).

Discussion

Our pilot study provides a valuable standardised protocol for systematically quantifying individual profiles of African antelope. Based on an "ethological coding" approach (Uher 2008), this protocol augments the questionnaire used by decision-makers to select bulls suitable for breeding purposes. The hierarchical nested approach to analysing the data is innovative, allowing comparisons at multiple scales (eg. activity state categories, subcategories, indicator events within subcategories). Although we demonstrated this assay system using samples from only two individuals, we suggest the technique has broader applicability to answer questions raised by managers of sustainable herds, not only for Hippotraginae, but also for other taxonomic groups.

We recommend measures based on ethological coding under conditions where animals have minimal contact with keepers (and hence personality questionnaires are not valid), such as populations managed for recovery and reintroduction. In a review of comparative personality research, Uher (2008) recommended statistical approaches that examine sources of variation in trait dimensions at several levels of the biological hierarchy: species, populations, contexts, individuals. Causal factors can be conceptualised as intrinsic (e.g. species, sex, age, reproductive state) or extrinsic (e.g. rearing, social group, enclosure type). The behavioural assay system we report here could be applied to females as well as males of diverse ages.

Uher (2008) emphasised the value of using ethological coding rather than personality questionnaires when the research is based on an evolutionary ecology framework in contrast to a conceptual model of animal welfare. From an evolutionary ecology framework (Carter et al. 2013), the goal is to understand how individual genetic variation is expressed in the context of social groups, nested within populations, rather than examining how well human personality dimensions are reflected in other species (i.e. dominance, neuroticism, agreeableness, curiosity, impulsiveness). We could not envision how human personality dimensions such as "neuroticism" or "agreeableness" would be measured in ungulates. However, with a larger behavioural data set in the future, appropriate dimensions for ungulates will emerge through the use of statistical analyses such as a generalised linear models approach (Guisan et al. 2002) or analysis of covariance (Dingemanse et al. 2010).

Currently, managers of sustainable herds make several types of decisions that would be better informed by systematic records of individual behavioural profiles. Our results suggest that decision makers scored breeding bulls as "suitable" based on several behavioural traits: (a) engaging in minimal conflict behaviour, (b) more likely to assess than fight or flee, and (c) actively tending females by retaining proximity and assessing their readiness for copulation. Alternatively, questions might be raised by some of the statistical differences we documented. For example, given equal genetic value, will a potential breeding male from a zoo enclosure (eg. our addax bull) forage as efficiently as a male from a pasture enclosure (eg. our sable bull), thereby maintaining body condition needed for breeding? At what age is a male sufficiently confident to transfer into an established herd of females without being rejected by females or unduly harassing them? The addax bull in this study was younger than the sable bull, and more likely to retain proximity to females than to show sexual behaviours. However, we can not make such generalisations about the effects of rearing conditions, age or species differences without a larger sample size.

Ideally, decision-makers would choose to keep diverse individuals in the population, with a range of scores related to subcategories of alarm activity (otherwise referred to as bold/shy in the personality literature). In one case, a released male addax unsuccessfully attempted to defend a calf from predators (Gordon and Gill 1993). Anecdotes like this raise questions about whether selection for anti-predator behaviour has been relaxed in captivity. Alternatively, issues arise in managing aggression within bachelor groups of antelope (Penfold et al. 2002). Typically, each bull is moved from the natal group to a bachelor group prior to maturity to reduce inbreeding. Perhaps, individuals that scored relatively high on "assess" would be more likely to be resilient when introduced to a new group, compared to those that scored high on either "escalate" or "de-escalate", thereby likely to escalate to injurious fights. With a larger sample size of behavioural profiles we would be able to ask whether the variation in anti-predator behaviour is correlated with variation in social conflict. However, a systematic technique for behavioural assays is needed.

In summary, we addressed the information needs of decision-makers managing sustainable herds of African bovids, by developing an ethological coding technique to measure variation in individual behavioural profiles. We demonstrated how the technique could be applied by comparing behavioural assays of two breeding bulls. We recommend future expansion of the sample size to look at the additive effects of potential predictive variables (e.g. species, population, group, age, sex). The technique is theoretically grounded in an evolutionary ecology framework and practical (in terms of validating an existing subjective rating technique for choosing breeding candidates). We designed this nested hierarchical approach for comparing individual behavioural profiles in Hippotraginae, keeping in mind the potential utility for other taxonomic groups managed by networks of conservation breeding centres.

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