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TITLE: Behavioral Syndromes in African Bovids: Assay Techniques for Population Planning

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ABSTRACT
To achieve benchmarks of success for captive population planning, managers need reliable measures of animal personalities (i.e. heritable temperament and learned coping styles). Although researchers have identified best practices for measuring behavioral types suitable for specific roles in zoo environments, the approach needs to expand to include measurements of behavior types suitable for specific roles in reintroduction programs designed to meet conservation goals. Selected zoo populations, managed for reintroduction, contain individuals in captive, semi-natural, and free-ranging environments. We focus on the challenge of measuring behavioral syndromes in populations where each individual may be moved multiple times during a lifetime. To address this challenge, we clarify how ethological coding of behaviors from archived video samples can be used to assay behavioral profiles of breeding males and social cohesion of females. We field-tested this behavioral assay system on three species of African bovids (horse antelope) at two sites and report results from case studies of four herds. We discuss the advantages and disadvantages of this case-study approach to measuring behavioral plasticity with applications for optimal management of sustainable herds.

INTRODUCTION

Behavioral monitoring of individual animals in zoo collections provides clear benefits in terms of assessing well-being of animals, husbandry procedures and visitor interest (Watters et al., 2009; Watters and Wielebnowski, 2009). Reporting on a series of workshops about assessing animal personality in zoo settings, Watters and Powell (2012) emphasized the need for assessment tools suitable for related species within broader taxonomic groups, e.g. Felidae. Systematic approaches to objective assessment of behavioral phenotypes, or "personality", exist for a wide variety of taxonomic groups, including invertebrates (Sih and Watters, 2005), fish (Watters et al., 2003), birds (Callicrate et al., 2011), carnivores (Gosling, 1998; Wielebnowski, 1999), primates (Koski, 2011; Margulis et al., 2008), and ungulates(Carlstead et al., 1999; Hausberger et al., 2004; Kileyworthington, 1978). However, no systematic approach exists to assess behavioral profiles of African bovids that are managed for long-term goals such as reintroduction.

The diversity of behavioral profiles within a population, i.e. behavioral syndrome (Sih et al., 2004b), should be considered when managing African bovids for recovery and reintroduction. In general, population planners determine which individuals are most suitable for the roles of "release candidates", "breeders" and non-breeding "social companions". A specific need for bovid behavioral assays emerged from discussions within the network of institutions collaborating in the Sustainable Herds Project of the Conservation Centers for Species Survival (C2S2) (Sawyer, 2011; Sawyer, 2012; Sawyer et al., 2011). Options to diversify the behavioral types available for reintroduction include: (1) environmental enrichment interventions in zoos (Powell and Svoke, 2008; Watters and Meehan, 2007), and (2) semi-natural environments large enough to support animals in diverse social groups typical of free-ranging populations (Sawyer et al., 2011). We focus on the latter.

In this pilot study, we address some of the issues associated with techniques for measuring individual behavioral profiles for the horse antelope (Hippotragini). First, we define the general problem in terms of measuring behavioral syndromes for the purpose of population planning and management. Second, we explain how we use behavioral profiles to monitor results of a specific intervention, "bull switching". Finally, we outline how behavioral assays fit within the benchmarks of success for evaluating (a) diversity of individual behavioral profiles within specific groups and (b) sustainable herd management in general.

Problem Statement: Phenotype Management in Population Planning

The phylogenetic history of African bovids has been shaped by cycles of wet and dry conditions over 3-4 million years (deMenocal, 2004), so ex-situ captive breeding programs would be wise to maintain this behavioral diversity. The diversity of behavioral phenotypes in each free-ranging population is the result of changing risks and resources over evolutionary time (Quinn et al., 2012; Sih et al., 2004a; Sih et al., 2004b). Theoretically, multiple behavioral types were differentially adapted to recurring environmental conditions (e.g. drought and flood), resulting in genetic polymorphism within populations (Dall et al., 2004; Sih and Bell, 2008).

Our challenge is to design and test systems for measuring variation in behavioral traits relevant to maintaining genetic and demographic health of captive populations, in a manner that can contribute to ecological restoration. To assess heritable "behavioral types" in the sense of the terms used by Sih et al. (2004a,b), we would have to be able to show that a behavioral profile is consistent across repeated assessments of the same individual in diverse contexts. Furthermore, heritability of behavioral types would have to be assessed through progeny testing. Collaborating C2S2 institutions maintain the pedigree database and records of individual movements, yet they have been missing accurate and reliable behavioral assays.

Ideally, measurements of behavioral profiles would be integrated into record-keeping systems and population planning, i.e. consistent with recommendations of Association of Zoos and Aquariums (AZA) Taxonomic Advisory Groups and Species Survival Plans. Our goals include moving toward this ideal. Understood by most practitioners as "personality", behavioral phenotypes are a result of the interaction of genetic and environmental diversity (Hausberger et al., 2004). We refer to the genetic component as "temperament" and the learned component as "coping style". Genetic propensities (temperament) can be teased apart by comparing different species in the same environment (Clubb and Mason, 2007). In contrast, environmental influences (learned coping styles) can be detected by comparing the same species in different locations (Gibbons et al., 2009). This implies collection of longitudinal data with repeated assessments as individuals move between groups during their lifetimes (e.g. natal, bachelor/bachelorette, breeding and retirement groups).

Pilot Application to Bull-Switching Intervention

In 2010, the C2S2 initiated the Sustainable Herds Project with the objectives of (a) producing high quality animals for release, (b) maintaining social groups in large areas, and (c) integrating multi-disciplinary expertise and research (Sawyer, 2012; Sawyer et al., 2011). Collectively, the collaborating institutions in the C2S2 consortium maintain at least 64 species of ungulates, including 16 cervids, 4 equids and 44 bovids (A. Eyres, unpublished data). For this initial pilot study, we chose to focus on three species of African bovids that represent diverse risk categories. Sable (*Hippotragus niger*) are "least concern". Addax (*Addax nasomaculatus*) are "critically endangered". Scimitar-horned oryx (*Oryx dammah*) are "extinct in the wild".

Multiple challenges are associated with managing our three target species. Many of these challenges also arise in managing other large hoofstock, which means we can draw from a rich literature addressing options for interventions (Table 1). One of these interventions, "bull-switching", is under investigation at Fossil Rim Wildlife Center (FRWC) to address: (a) optimal outbreeding, (b) management of male-male conflict, (c) socialization of young males, (d) synchronization of births at optimal times, (e) female rejection of inexperienced breeding bulls and (f) male influences on the herd (females with their offspring).

The "bull-switching" intervention consists of rotating two bulls in and out of a herd of breeding females: an intact "breeder" bull and a vasectomized "coach" bull. The "breeder" runs with the herd during the optimal time for conception, usually June and July in the semi-arid wooded grassland where FRWC is located. This schedule results in calving during favorable spring conditions and weaning in the fall after pastures recover from dry summers. Theoretically, one "breeder" should be able to inseminate all females during two months, because females cycle at 21-25 day intervals. During the rest of the year, the "breeder" is replaced with the "coach". The "coach" potentially serves multiple functions in the herd, including (a) detecting non-pregnant females still cycling, (b) "teaching" young males to assess and de-escalate in asymmetric encounters, (c) stimulating puberty in young females, (d) displacing young males that prematurely start to court females, and (e) influencing herd movements.

In addition to assessing the demographic consequences of the "bull switching" intervention, the hoofstock manager at FRWC is assessing the behavioral consequences (A. Eyres, unpublished data). One of the major decisions involves selection of males with appropriate behavioral profiles to serve in the roles of "breeder" and "coach". As recommended by Watters and Powell (2012), our assays include both keeper surveys (Loonam, 2012) and ethological coding techniques. We report here on the quantitative techniques used to code behaviors to document (a) behavioral profiles of bulls and (b) the cohesion of groups, i.e. the social context potentially influencing variation in the individual profiles.

Benchmarks for Success

The "bull-switching" intervention described above is one of several approaches under investigation to meet the benchmarks for success in managing sustainable herds. These six benchmarks include: (1) herd health, (2) genetic diversity, (3) demographic viability, (4) behavioral resilience, (5) ecosystem resilience and (6) economic viability (Sawyer, 2011; Sawyer, 2012; Sawyer et al., 2011). Other research teams within the C2S2 consortium are focusing on ways to assess progress toward their respective benchmarks, e.g. techniques to monitor the genetic diversity of herds without complete knowledge of pedigrees (Armstrong et al., 2011).

Our team focused on valid, effective and efficient systems for measuring behavioral resilience – meaning the ability of individuals to move between physical locations and social groups without management problems. Benchmarks for success of the C2S2 behavioral assay system include: (1) accuracy in measuring actual behavior of multiple species, (2) reliability of measures coded by a team of trained observers, (3) transferability across multiple sites, (4) feasibility within constraints of available staff time and effort, and (5) utility for population planning.

METHODS

As recommended for zoo research that is multi-institutional and multi-disciplinary (Fernandez and Timberlake, 2008), C2S2 has formed strategic partnerships with academic institutions. The capacity for in-house behavioral research is well-developed at certain C2S2 institutions (i.e. San Diego Zoo Global, SDZG; Smithsonian Biodiversity Conservation Institute, SBCI). However, other C2S2 institutions do not have staff dedicated to behavioral research (i.e. White Oak Conservation Center, WOCC). We built on the existing successful internship programs at two institutions (i.e FRWC and the Wilds of Ohio, TW), to develop methods that could be transferred to other C2S2 institutions. These methods include standard approaches to behavioral data collection and analysis (Martin and Bateson, 2011), as described below.

TABLE 1. Challenges and Interventions Associated with Management of Ungulate Herds

Challenge	Options for Intervention	Source
Conflict between breeding males	• Only one breeding male per enclosure (harem group) • Replace rogue bulls that initiate inter-species conflict	(Fureix et al., 2012; Gilbert and Woodfine, 2003; Gordon, 1989; Tilson et al., 1988)
Conflict within bachelor groups	• Increase physical distance from breeding females • Hormonal treatments • Include older dominant "chaperones" • Increase size of enclosure	(Bourjade et al., 2009; Bourjade et al., 2008; Cassinello and Pieters, 2000; Fureix et al., 2012; Gilbert and Woodfine, 2003; Penfold et al., 2002)
Socially maladjusted young males	• Keep pre-reproductive males in their natal group • Socialize young males in a "satellite" role with dominant male • Switch intact and vasectomized males	(Fureix et al., 2012; Gilbert and Woodfine, 2003; Jones et al., 2010)
Inbreeding with daughters	• Replace sire before daughters reach puberty • Disperse daughters at puberty	(Gilbert and Woodfine, 2003; Manski, 1991)
Inbreeding with sisters	• Disperse males at puberty • Disperse females at puberty	(Gilbert and Woodfine, 2003)
Genetic over-representation	• Vasectomize or retire post-breeding males • Suppress ovulation or retire females	(Gilbert and Woodfine, 2003)
Genetic under-representation	• Artificial insemination • Cryopreservation of gametes	(Morrow et al., 2009; Roldan et al., 2006)
Paternity uncertainty	• Estimate relatedness • Whole-herd genetic diversity monitoring	(Heim et al., 2012; Willis, 2001)
Mate choice (female rejection of male)	• Socialize young males in a "satellite" role within a breeding herd • Socialize young males in a group of retired (post-breeding) females	(Quader, 2005)
Aggression to neonates (infanticide by males)	• Provide structure for neonates to hide during post-partum estrus • Avoid replacing male before infants are weaned	(Feh and Munkhtuya, 2008; Manski, 1991; Pluhacek and Bartos, 2005)
Aggression to immigrants	• Female conflict when an immigrant is introduced to a matriarchal group	(Thompson, 1993)
Stable age-structure	• Hormonal suppression of ovulation • Male stimulation of early puberty in females	(Blanvillain et al., 1997; Gilbert and Woodfine, 2003)
Birth synchrony with optimal conditions	• Females in stable matriarchies synchronize estrus • Switch vasectomized and intact males (2-mo breeding window) • Hormonal treatments for estrus synchronization	(Gilbert and Woodfine, 2003; Morrow et al., 2000; Thompson, 1991; Thompson, 1995)

Data Collection: Coordinating Sites, Schedules and Reliability

Techniques for behavioral data collection were developed at FRWC (Jones, 2010; Jones et al., 2010) and adapted for use at TW during May-August 2012. First, staff trained the primary researcher and interns in safety procedures for driving survey routes in the pastures where the target species were located. Second, the primary researcher used a "stepped approach" to train interns and graduate students in data collection.

Observer Training. In Step 1, observers identified focal species and individuals using scan-sampling at a stationary location. In Step 2, observers entered metadata onto data-sheets for each sampling period. In Step 3, observers collected 3-min focal-individual video samples; and in Step 4, they collected group-scan video samples. In Step 5, observers followed a survey route and collected samples (focal and scan) at roving locations each time a group was encountered. Finally, in Step 6, observers learned to archive video samples and metadata in a database (Microsoft Excel Workbook).

Once they had achieved the above criteria, interns were responsible for coordinating with staff to set an observation schedule within the specified time-windows (i.e. within 3 hours of sunrise and sunset). We chose the time-windows based on previous evidence that the target species were most likely to be inactive (or out-of-view) during the middle of the day (J. Packard, unpublished data). Interns scheduled 3 to 5 sampling periods each week, depending on weather conditions and logistical constraints. At FRWC during July, an expanded observation team included students participating in fieldwork associated with a course for graduate credit.

Each sampling period consisted of driving a survey route and stopping at each group to collect data, then continuing to the next group. Observers recorded metadata when they began and finished (e.g. time, weather, number of samples, anecdotes, driver, recorder and videographer). Observers took a scan sample at first encounter of each group visible along the survey route, with a 30-min break before repeating a scan sample of the same group. The videographer started the video scan at the left edge of the group and scanned right, pausing as each new individual came into the viewfinder and ending 10 body lengths after scanning the last individual in the group. By definition, groups were separated by at least 10 body lengths. As many focal-individual video-samples (3-min duration) were collected between scan samples as possible, with at least a 3-min wait between consecutive samples of the same individual (to comply with statistical criteria for quasi-independence). We use the term "quasi-independent" to refer to repeated measures of individuals within observation periods.

We also collected qualitative data in an opportunistic manner. If the focal individual was out-of-view for over 30% of the sample, the focal sample was aborted and the video file was coded as an opportunistic sample. Outside the sampling protocol, rare and salient behaviors were videoed and described in anecdotes. If the focal individual was engaging in social behavior during the wait-period between focal samples, observers turned on the video camera to collect opportunistic records for interpretation of context and analysis of behavior sequences.

Reliability. Observer reliability was tested on a set of video files, selected to represent a variety of observation conditions. As recommended by Watters et al. (2009), an ethogram (Table 2) was compiled from published literature (Estes, 1991; Loeding et al., 2011; Manski, 1991; Penfold et al., 2002; Walther, 1984). Subcategories of behavioral states were defined by lists of action events, as illustrated in Table 3 for social behavior. The subcategories of events allowed us to include actions that were similar across all species in the sub-family as well as actions unique to certain species.

For focal-individual samples, training videos were prepared with freeze-frames at 10- sec intervals. For each freeze-frame, the trainee recorded the activity state of the focal individual, as defined in the ethogram (Table 2). Between freeze frames, the trainee focused on subcategories of social activity (Table 3) and scored each subcategory with a "1" if at least one event from that subcategory was observed (one-zero sampling). We found that one-zero sampling was more reliable than actual counts of behavioral events. The time-span sampling between freeze-frames allowed us to record rare, as well as frequent, events. Using the terms recommended by Martin and Bateson (2011), the recording rules were instantaneous sampling of activity states (freeze frames) and one-zero sampling of rare events (time-span between freeze frames).

Table 2. Ethogram of Activity States: Indicator Behaviors Specific to the Horse Antelope (Hippotraginae).

Activity State	Description of subcategories	Indicator behaviors (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 suggest it is gathering more information about a stimulus that 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 suggest no alarming stimulus has been detected	Scan, chew-pause, ears-forward, ears-flip, turn-head
Feed (FE)		
	High Intensity (ingest): Actor takes food or liquid into the mouth; may chew and swallow.	Graze (grass/forb/hay), browse (leaves/bark), nibble, drink
	Moderate Intensity (handle): Actor manipulates food before ingesting; with head up, grass may be pulled into the mouth with the tongue while chewing	Paw, dig, horn-to-object (e.g. old hay bale)
	Low Intensity (search): Actor looks or moves toward a stimulus or location where food is likely to be	Stare, sniff/look (e.g. food delivery vehicle, trough, area)
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 (lying): 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 (standing): Actor stands on all four feet; not alert; may include maintenance events	Full-body-shake, stretch, defecate, urinate
Social (SO)		
	Conflict: escalate, assess, de-escalate	see Table 3
	Proximity: approach, retain, withdraw	see Table 3
	Sexual: receptive, proceptive, unreceptive	see Table 3

Table 3 Subcategories of Social Activities: Indicator Behaviors Specific to the Horse Antelope

Subcategory	Description of Indicator Behaviors (events)
Conflict	
	Escalate (aggressive): Physical contact forceful enough to injure the opponent if contact is made (lunge, kneel, frontal-horn-jab, horn-tap, frontal-horn-present, sideways-jab); may include physically chasing another individual from the area.
	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).
	De-escalate (submissive/appeasement): Actions that have the consequence of reducing injurious contact or social tension (low-neck-stretch, head shake, bleat); includes movement away from the escalating individual (step-away, walk-away, run-away).
Proximity	
	Approach: Actor decreases distance to recipient; may be in an agonistic, sexual or parental context (sniff, rub-head, lick, nibble, nurse, suckle); may be a response to body odors (ano-genital sniffing, responsive urination) or vocalizations typical of mother/calf join-up (bleat, moo); includes herding (actor positions body in the line of travel, resulting in a change of direction of recipient)
	Retain: Actor directly or indirectly maintains social distance from the recipient, as if there is an "elastic band" between them (follow); although the actual distance may fluctuate around mean, actor maintains acoustic, odor and/or visual contact (bleat, moo, substrate-sniffing, stare); may include drifting with the herd in one direction without direct following (graze-together, parallel-orientation)
	Withdraw: Actor increases social distance from recipient (includes agonistic, sexual or parental contexts); may include actions that reduce acoustic or visual contact (e.g. heading off into the woods away from the group, leaving a calf in a bedding site).
Sexual	
	Receptive (copulation): Actor facilitates copulation (stand, mount, intromission, ejaculation); female is in “standing heat” usually within 24- to 48-h of ovulation (stand-still, spread-rear-legs, tail-moved-to side); in the context of a receptive female, male initiates copulatory sequence (mount, penile-erection, vaginal-intromission, pelvic-thrusting, ejaculatory-jump, dismount); if no receptive female is present, male actions may appear out of sequence (ejaculation may be spontaneous or in response to oral self-stimulation)
	Proceptive (arousal, courtship): Actor interacts with a potential sexual partner without actually copulating; may include alternating approach and withdrawal as if stimulating sexual arousal; indicators of proceptivity in females include approach, follow, rub-body (with face, head or horns), head-flick, responsive-urination, mount, flehmen, sparring, circling; indicators of proceptivity in males include erect-posture, approach, low-neck-stretch, urine-testing, flehmen, fore-leg-lift, chest-bump, partial-mount (no insertion), driving/chasing, sparring, circling, rest-chin-on-rump, sniff- or rub-rump
	Unreceptive (rejection): Actor ignores, avoids or actively discourages proceptive behaviors (stand, move-away, lie-down, brush-off by entering thick bushes or dense herd); females may be in an anestrous or pregnant hormonal state; males may be immature, castrated, exhausted or in a post-ejaculatory quiescent state.

For scan samples of group cohesion, training videos were paused each time a new individual came into view in the video frame. The nearest-neighbor distance between the previous individual and the new individual was estimated to the closest proximity category (defined in terms of animal-body lengths: 1-2, 2-4, 4-6, 6-8, 8-10, over 10). The nearest neighbor of the last individual was scored as "over 10". For each scan sample, all-occurrences of nearest-neighbor distances were tallied for each of the six proximity categories. The sum of these tallies was the group size. Consistent with terms in Martin and Bateson (2011), the observation rule was "focal group" and the recording rule was "all occurrences" (nearest neighbor distance categories).

The data generated by trainees and experienced observers were compared using log-likelihood ratio tests (G-square) and binomial tests (z-score). If the reliability test was significantly different (G-square), the trainees discussed discrepancies, focusing on subcategories that contributed significantly to the difference (based on z-scores for each subcategory). The reliability training procedure was repeated 2-3 times, depending on logistical constraints. Only observers who achieved statistical reliability (G-square test) were involved in subsequent analysis of video samples.

Data Analysis: Behavioral Profiles of Individuals and Social Cohesion of Groups

In this section, we clarify our recommended procedure for analyzing behavior and social context of individual antelope. First, we explain how we calculated behavioral indices (Activity Index, AI; Social Index,SI; Behavior Diversity Index,BDI; Group Proximity Index,GPI; Herd Cohesion Index, HCI). Second, we explain how non-parametric statistics were used to analyze the nominal variables (AI, SI, BDI, GPI). Finally, we explain the use of a parametric statistic to analyze the continuous variable (HCI).

Activity Index (AI). The AI is a measure of the overall activity profile of individuals, given a social context (Figure 1). The broad categories of activity states include: Alert, Feeding, Locomotion, Resting and Social (Table 2). The score in each category (e.g. Alert) was the total frequency of "freeze frames" scored for that category over all the focal samples for a given individual (e.g. the addax breeding bull). To visualize the profile for each individual, we converted the score for each category to a percentage of the total for that individual, resulting in the pie charts in Figure 1. A decision maker can get a quick overview of individual differences from the pie charts. For example, the addax bull clearly rested less and fed more than the sable bull in a social context. The same procedure could be used to calculate behavioral profiles in other contexts, as needed in future studies.

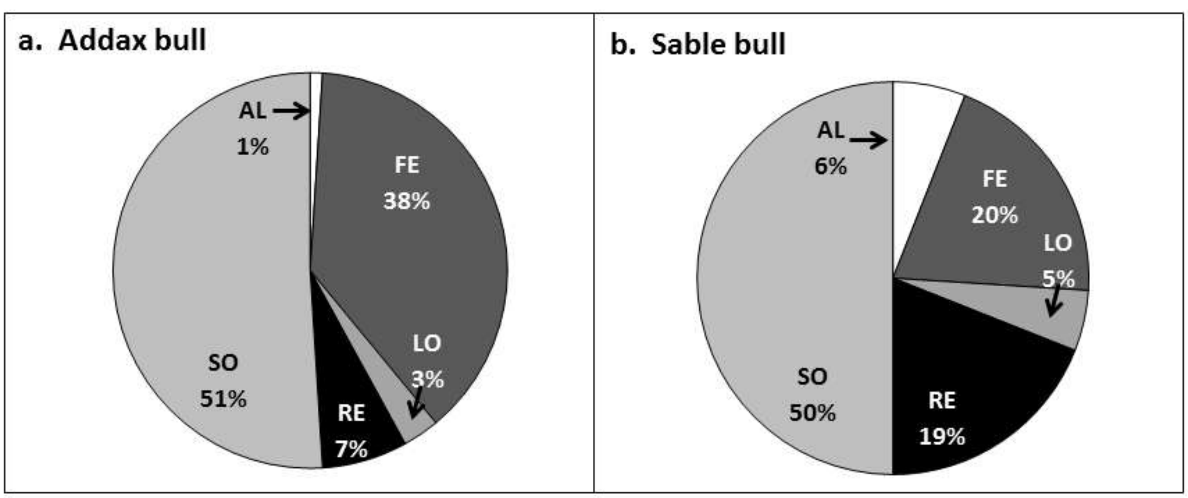

Figure 1. The Activity Index differed significantly between the (a) addax bull and (b) sable bull (G^2=107.74, df=4, p=0.001). Codes indicate behavioral categories defined in Table 2: Alert (AL), Feed (FE), Locomote (LO), Rest (RE), and Social (SO).

Social Index (SI). The SI measures the quality of behavioral interactions within the activity state of "Social" (Table 3). The score in each subcategory (e.g. Conflict) is the total count of intervals (between "freeze frames") where we scored that subcategory as "present". This is not a true frequency of behavioral events. It is a systematic way of sampling events that are short or infrequent, therefore rarely recorded during "freeze frames". The resulting bar chart (Figure 2) provides decision makers with a quick diagnostic about potential problems related to social behavior. For example, in Figure 2, "conflict" and "sexual" behaviors were relatively unlikely compared to "proximity". Such diagnostics are potentially useful for managers who expect a good herd bull to spend time maintaining proximity with the females, but not harassing them.

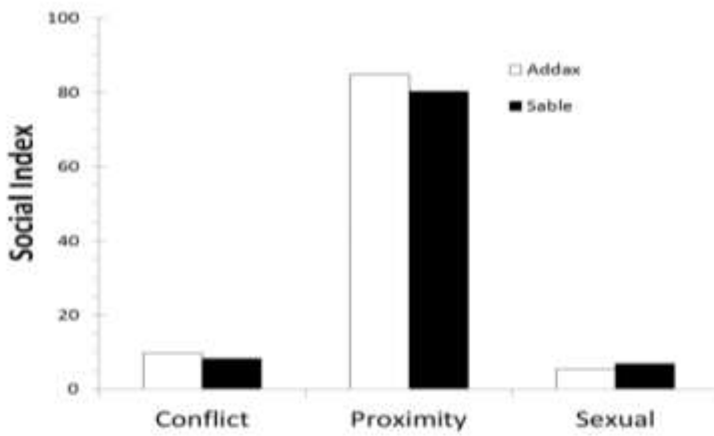

Figure 2. The Social Index did not differ significantly between the addax bull (white bars) and the sable bull (black bars) (G^2=2.82, df=2, p>0.05). The categories for social events (conflict, proximity, sexual) are defined in Table 3.

Behavior Diversity Index (BDI). The BDI is a measure of the variety of behaviors within subcategories. For example, we split the "conflict" subcategory into three descriptors "escalate", "assess" and "de-escalate" (Table 3). Similar to the SI, we counted intervals within which we recorded each of these types of indicator behaviors. For example, Table 4 demonstrates a comparison of the BDI for two bulls. Managers could use this level of detail about social behaviors when they are considering options for behavioral interventions to resolve issues.

Table 4. Behavioral Diversity Indices for Social Subcategories

Social Subcategory	Behavioral Diversity Indices		Statistical test
	Addax bull	Sable bull	
Sexual			G^2=0.01, df=2, p>0.05
Receptive	9	9	
Proceptive	176	183	
Unreceptive	0	0	
Conflict			
Escalate	0	0	not appropriate (too many zeros to calculate expected values)
Assess	48	41	
De-escalate	0	0	
Proximity			G^2=6.57, df=2, p=0.05
Approach	130	99	
Retain	252	145	
Withdraw	38	13	

Group Proximity Index (GPI). The GPI indicates the spatial proximity of individuals within social groups, based on the scan samples (Figure 3). We tallied the distance categories between nearest neighbors and combined the data over all groups. For example, the bar graphs in Figure 3 show the variation within each herd, facilitating the comparison of herds within and between locations. The taller bars on the left of these graphs indicate all the groups were "tight", showing close proximity. Managers would potentially use this information about social context (a) when moving animals between groups, and (b) when interpreting the potential effect of social context on individual behavioral profiles.

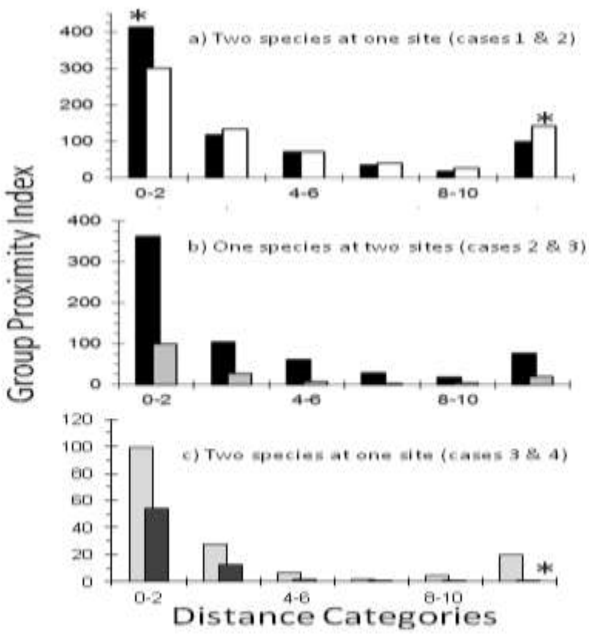

Figure 3. Group Proximity Index comparisons for (a) sable (black bars) and addax at FRWC (G^2= 26.61, df=5, p=0.001), (b) sable at FRWC (black bars) and TW (G^2=9.93, df=5, p>0.05) and (c) sable (light bars) and oryx at TW (G^2=11.44, df=5, p=0.05). Asterisks indicate which categories differed significantly from what would be expected by chance, thereby contributing to the significance. At FRWC (cases 1 & 2), individual sable were more likely to be close to each other (z=3.44) and addax to be distant (z= 3.13). At TW (cases 3 & 4), sable were more likely to be distant (z=2.59) compared to oryx.

Herd Cohesion Index (HCI). The HCI is a measure of how much the whole herd split into groups, in contrast to remaining together as one cohesive social unit. To calculate this index, we divided each group size by the total herd size (similar to a percent of the total). For example, Figure 4 shows the variation around the mean of the HCI for each of four cases. Decision makers could use this type of information when considering options of splitting herds, the effects of each bull on the herd, or the potential risk that one bull will not service all females.

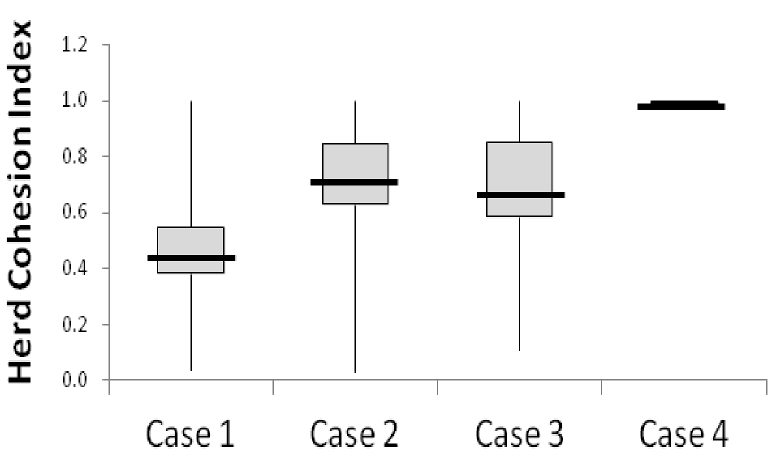

Figure 4. Herd Cohesion varied significantly across cases (ANOVA F-ratio=14.8, df=123, p<0.001). Cases 1 and 4 were significantly different than all other cases (Dunn's Multiple Comparison Test, p<0.05). Cases 2 and 3 did not differ significantly from each other (Dunn's Multiple Comparison Test, p>0.05). Horizontal bars indicate means, boxes indicate 95% confidence intervals and vertical lines indicate high and low values. There was no variation in Case 4, meaning that the whole herd was always seen in close proximity and did not separate into subgroups.

Non-Parametric Statistics (G-square and binomial Z). Four of the five indices defined above (AI, SI, BDI, GPI) are nominal variables. We use the term "nominal" as recommended by Martin and Bateson (2011) to refer to categorical data that can be tallied in matrices. In a statistical sense, these data are "quasi-independent", meaning that we combined data that were not strictly independent. Therefore, we chose the "log-likelihood ratio test" (also referred to as G-square) as the most appropriate measure of association. We phrased our statistical questions in terms such as "given that a behavior was observed in individual X, what is the likelihood that it was also in the category of A or B". The G-square test is based on the distribution of tallies over an entire matrix, comparing observed and expected values (Lehner, 1996). To determine which cells of the matrix contributed to the significance, we calculated the binomial test (z-score; Lehner 1996). These two tests (G^2, z) are easily calculated using an excel workbook that we prepared to analyze matrices ranging from "2 by 2", to "6 by 6" columns and rows (available from the senior author). Simplicity and ease of calculation were important criteria in design of this system for behavioral assays.

Parametric Statistics (ANOVA). One of the indices defined above (HCI) is a continuous variable, meaning that it yields values on a continuous scale of 0 to 1. We chose a One-Way Analysis of Variance (ANOVA) approach for comparing mean values across the four herds in this study (cases 1-4). Our statistical question was framed in terms of "was the variation between cases greater than the variation within each case" (Lehner, 1996). We considered each group to be an independent sample because theoretically individuals could leave or enter any group in the 30-min interval between scan samples. For pairwise comparison of herd means, we used the Dunn Method for Joint Ranking (Lehner 1996:410). We used Microsoft Excel software for calculations, choosing the ANOVA Single Factor option in the Data Analysis toolkit. We chose to use Excel rather than statistical software due to the ease of access for all members of our research team (students, practitioners and scientists).

RESULTS

We field-tested this behavioral assay system, as applied to three species (addax, sable, scimitar-horned oryx) at two locations (FRWC, TW). Below, we briefly describe the results for each of four cases. Cases 1 (addax) and 2 (sable) were breeding herds at FRWC. Cases 3 (sable) and 4 (oryx) were non-breeding female herds at TW (bachelorette herds).

Case 1. Addax Breeding Herd at Fossil Rim Wildlife Center

The breeding herd of addax (4.29) contained 3 immature males as well as the bull and 29 females. It was the least cohesive (Figure 4), with a mean group size of 13 individuals (40-50% of the herd). Within each group, females generally maintained close proximity (Figure 3a) except for a few individuals. When we observed the addax bull in a social context (Figure 1), he was most likely to be socializing (51%) or feeding (38%). His social activity was primarily maintaining proximity with females (Figure 2), as he moved between groups checking for breeding readiness. Conflict and sexual interaction was relatively infrequent. He was more likely to assess than to escalate or de-escalate in the context of conflict (Table 4). Sexual interactions were primarily proceptive courtship. He was receptive when females stood for him to mount and did not reject their courtship (no unreceptive events).

Case 2. Sable Breeding Herd at Fossil Rim Wildlife Center

The breeding herd of sable (4.31), which contained 3 immature males and 31 females, was significantly more cohesive than the addax (Figure 4). Mean group size was 23 individuals (60-80% of the herd). Compared to the addax, sable females were significantly more likely to be in close proximity (Figure 3a). In social contexts (Figure 1), socializing by the sable bull (58%) was similar to the addax bull. However, the sable bull spent significantly more time resting and less time feeding compared to the addax bull. Similar to the addax bull, the social activity of the sable bull consisted primarily of maintaining proximity with females (Figure 2). The sable bull did not differ significantly from the addax bull in receptive, proceptive or unreceptive behaviors (Table 4).

Case 3. Sable Bachelorette Herd at The Wilds

Social cohesion in the bachelorette herd of sable (0.9) did not differ significantly from the larger breeding herd of sable (Figure 4). Mean group size was 6 individuals (60-90% of the herd). Within groups, social distance (proximity) did not differ significantly between the two sable herds (Figure 3b).

Case 4. Oryx Bachelorette Herd at The Wilds

Social cohesion was significantly higher for the female herd of scimitar horned oryx (0.7), compared to the other three herds (Figure 4). The entire herd was always together, with no variation recorded during our observations. Proximity differed significantly from the sable herd in the same pasture (Figure 3c), due to the most distant category (greater than 10 body lengths). One individual sable tended to remain distant from the rest of the herd, a situation not observed in the oryx.

DISCUSSION

The behavioral assay system described above was successful at measuring variation within and across locations. Here we discuss implications for benchmarks of success in achieving our goals relative to (a) behavioral coding approaches, (b) assessment of interventions such as "bull switching" and (c) behavioral syndromes relevant to population management and ecological restoration using herbivores.

Efficacy of Behavioral Coding Approaches

Previously available techniques for assessing temperament in ungulates used (a) questionnaires, (b) scoring criteria and (c) experimental treatments. For example, tests of temperament in cattle have included restraint in a cattle chute (Sebastian et al., 2011), flight speed and social separation (Muller and von Keyserlingk, 2006). In temperament scoring of horses, behavioral observations and heart rate monitoring have been compared to judges' scores during performance testing (von Borstel et al., 2011). These approaches have been highly specific to assessing how individuals behave in human-controlled environments, e.g. the type of work they do for humans (Hausberger et al., 2011).

Our behavioral coding system emerged from the recommendation by Watters and Powell (2012) to apply ethological approaches to assessing personality in zoo animals. We were uncertain how well behavioral coding would work in a variety of field conditions and for diverse species within the horse-antelope tribe. The key to our success was in separating the collection of video samples from the analysis of the video archive. Relatively inexperienced interns at multiple sites successfully collected the data according to protocol. However, more effort by a dedicated few individuals was required to achieve observer reliability in scoring the videos. We realized that "on the spot" observations without the video record were likely to be highly unreliable.

By presenting this behavioral assay system for review by scientists and practitioners, we hope to stimulate productive debate concerning fine-tuning of the system. Ideally, behavioral assays will eventually become as widely accepted as hormonal assays. By working closely with veterinarians and endocrinologists within the C2S2 network we aim to apply appropriate quality control standards to compare data across sites and over the long time-frames necessary for population planning.

Implications for Assessing Bull-Switching Intervention

We are cautious about drawing general conclusions from the four cases in this study. Instead, we choose to emphasize the utility of a systematic approach to documenting cases. For example, the addax bull rested less and fed more than the sable bull in the same FRWC pasture. We are tempted to hypothesize this is a species difference. However, the lifetime experience of the addax bull differed from the sable. The addax was previously in a zoo environment without access to reproductive females. This was his first season in the FRWC pasture. The sable bull was older, vasectomized and periodically had been with the same group of females and their calves for several years.

Currently, working knowledge about the practical utility of "bull-switching" resides in the knowledge base of a few expert practitioners. Sharing that knowledge and subjecting it to the spotlight of scientific review is problematic, due to the infrequent number of cases and the variable conditions associated with each case. However, the systematic recording of behavioral data for each case will contribute to a growing database over decades, suitable for hypothesis testing in the future. In the short-term, practitioners benefited from the anecdotes of unusual behaviors; researchers accumulated more hours of observation than was feasible for staff. For example, the addax bull engaged in sparring with one female. However, his profile indicated this was not a frequent occurrence. Closer examination of the literature confirmed that occasional sparring, circling and chasing are part of the repertoire of natural behaviors in this species.

We recommend expanding the use of this behavioral assay system to document more cases within the C2S2 network, by: (a) adding more cases over time for the same species and institutions, (b) adding in more sites with the same species, and (c) adding more species, e.g. dama gazelles (*Nanger dama*). To accomplish this ambitious goal over the next decade, we propose to build partnerships with internship programs through local colleges near each of the C2S2 institutions, under the umbrella of the San Diego Zoo Global Academy (SDZGA). We used the distance education graduate course offered in collaboration with SDZGA as a mechanism for engaging graduate students, practitioners and scientists in developing, testing and refining the behavioral assay system. We plan to continue the series of webinars associated with the annual graduate course to expand capacity for analyzing behavioral data within and beyond the C2S2 network.

Behavioral Syndromes, Population Management and Ecological Restoration

Within networks of conservation scientists and practitioners, there is a growing awareness that meeting goals for sustainability of zoo populations requires a meta-population perspective extending beyond the short term objective of minimizing genetic decay (Lacy, 2012). Behavior needs to be considered (as well as genetic, physiological and morphological variation) for zoo population management to achieve the ideal of contributing to the ongoing processes of global species conservation (Conde et al., 2011). Maintaining diverse behavioral types within the pool of reintroduction candidates is an important consideration (Watters and Meehan, 2007). For example, "bold" personality types have been associated with more exploration, higher reproductive and lower survival rates; however, implications for captive breeding for reintroduction remain complex (Smith and Blumstein, 2008). Some behavioral types essential for survival under free-ranging conditions, may not be conducive to survival in zoo settings.

Institutions collaborating within the C2S2 consortium recognize that linkages between behavior, nutrition and health have important consequences for maintaining viable populations. Social context can limit not only an individual's access to restricted food resources, but also the expression of genes associated with immune response (Tung et al., 2012). Combined effects (e.g. marginal nutrition and lowered resistance to disease) may negatively impact both reproductive and survival rates. Behavioral implications for health may not seem important during the crisis-motivated phase of assisting small populations recovering from the brink of extinction. However, behavior becomes more important during the secondary recovery phase involving assisted re-colonization into disconnected habitat fragments, as will be needed for ecological restoration initiatives.

In summary, this study addressed "behavioral resiliency" as one of the benchmarks of success for the Sustainable Herds project of the C2S2 consortium. We successfully field-tested a behavioral assay system based on ethological coding of behavioral states and events recorded on video. We met four of our five criteria for success: (1) accuracy in measuring actual behavior of multiple species, (2) reliability of measures coded by a team of trained observers, (3) transferability across multiple sites, and (4) feasibility within constraints of available staff time and effort. The utility of this assay system for population planning was our fifth criteria. Until more cases accumulate for interventions such as the "bull switching" treatment, we remain cautiously optimistic about utility of the behavioral assay system. Whatever the outcome may be, we are confident that the C2S2 initiative has facilitated capacity-building, thereby establishing a strong foundation for future collaboration in addressing these challenging questions about integrating knowledge of behavioral syndromes into population planning.

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