

Individually Consistent Behavioural Patterns in Wild, Breeding Male Grey Seals (*Halichoerus grypus*)

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Abstract

Recent research demonstrates remarkable consistency in interindividual differences in behaviour patterns across time or across situations indicating that within populations, individuals have different behavioural types or personalities. Examples of behavioural consistency have been shown in taxa ranging from molluscs to mammals. However, there remain few such studies of wild populations and none of pinnipeds. This study presents preliminary evidence of behavioural types in wild male grey seals (*Halichoerus grypus*). Activity budget analyses revealed highly repeatable individual patterns of alertness across successive breeding seasons unrelated to local environmental context. While field studies of behavioural types can be challenging, it is essential to develop techniques for identifying behavioural types in natural populations in order to begin to understand the ecological and evolutionary relevance of animal personalities.

Key Words: behavioural type, behavioural plasticity, personality, fitness, pinniped

Introduction

Traditionally, individual variation within populations is often considered as deviation from an adaptive optimum (Dall et al., 2004; Bell, 2007a); however, growing research is demonstrating remarkable consistency in interindividual behavioural differences across a wide range of taxa (Bell, 2009). Much of this research has focused on the existence of behavioural syndromes and evidence of personality in nonhuman species. A *behavioural syndrome* is defined as individual behavioural differences that are consistent over time and/or across contexts (i.e., functional behavioural categories such as feeding, mating, or parenting) or situations (e.g., spatially and/or temporally varying environmental conditions) within contexts (Sih et al., 2004a, 2004b; Dingemanse & Réale, 2005; Bell, 2007a, 2007b; Réale et al., 2007; Sih & Bell, 2008). Typically, behavioural syndrome studies test

for rank order correlations in individual behaviour across two or more behavioural axes (Sih & Bell, 2008). The behavioural assays used vary across studies but are generally designed to represent behavioural axes such as shyness-boldness (based on reactions to risky but not novel situations), exploration-avoidance (based on responses to novel situations), activity (in non-novel or risky scenarios), aggressiveness towards conspecifics, and sociality (Réale et al., 2007). Within such syndromes, individuals express a behavioural type (or personality), which “refers to the particular configuration of behaviours that an individual expresses” (Bell, 2007b, p. 755). For example, an individual with an aggressive behavioural type in a mating context also tends to be more aggressive than conspecifics in foraging contexts. Other studies use measures of repeatability of a single behaviour over time to infer behavioural types, such as measures of handling response in bighorn ewes (*Ovis canadensis*) (Réale et al., 2000), and aggressive and mating behaviours in bluefin killifish (*Lucania goodie*) (McGhee & Travis, 2010). In such studies, distinct time points are assumed to represent different situations or, at the very least, different age points (Bell, 2009).

The key element of all studies of personality in nonhuman species is the relative consistency of individual behaviour through time and/or across contexts (Martin & Réale, 2008; Sih & Bell, 2008; Bell, 2009). Evidence of such consistency in individual behaviour has now been identified in a remarkable range of taxa, from molluscs to mammals (Réale et al., 2007; Smith & Blumstein, 2008; Bell, 2009). The existence of such consistent individual expression of behaviour poses challenging questions to behavioural and evolutionary ecologists, particularly in terms of how such consistent individual differences in behaviour can be maintained in the face of selection and whether personalities result from mechanistic constraints or reflect individually differing adaptive solutions to complex physical and social environments (Dall et al., 2004; Sih et al., 2004a, 2004b; Dingemanse & Réale, 2005; Bell, 2007a, 2007b; Réale et al., 2007). Various adaptive solutions

have been postulated and supported by theoretical models and empirical studies (Bell, 2009), including frequency or state dependent mechanisms (Dall et al., 2004) and life history strategies (Stamps et al., 2007; Wolf et al., 2007).

In resolving the debates about the evolutionary and ecological causes and consequences of individual consistency in behaviour, it is essential that we understand more about the prevalence of behavioural types in natural populations and ultimately the consequences for individual fitness (Réale & Festa-Bianchet, 2003; Sih et al., 2004a; Dingemanse & Réale, 2005; Bell, 2007a, 2007b; Réale et al., 2007; Martin & Réale, 2008; Sih & Bell, 2008; Smith & Blumstein, 2008). Most studies of behavioural types are laboratory based or animals are extracted from the wild to controlled test arenas where standardised tests of personality can be performed. There remain very few studies that have examined consistent interindividual differences in wild populations, and there are no such studies of pinnipeds. Demonstrating behavioural types in field situations, where there is limited scope for controlled and repeated exposure of known individuals to standardised stimuli, is a significant challenge. This challenge is exacerbated when attempting to repeatedly test individuals over multiple behavioural axes. However, repeated tests of individuals based on a single behaviour are more tractable, especially where individuals are site-faithful and therefore able to be relocated over time points. Grey seals (*Halichoerus grypus*) present such an opportunity as both males and females show high levels of interannual site fidelity (Pomeroy et al., 1994; Twiss et al., 1994). This preliminary study adopts a purely observational approach to present evidence of high levels of interannual consistency in interindividual behavioural differences indicative of individual behavioural types in wild, breeding male grey seals.

Grey seals are polygynous, colonial breeders, gathering annually, typically at remote island sites. Males compete to maintain positions among female aggregations and mate when females enter oestrus towards the end of lactation (Twiss et al., 2006). Male mating success provides a good proxy for reproductive success (Twiss et al., 2006). The length of an individual male's stay on the breeding colony is the primary determinant of his mating success (Twiss, 1991). Most male behaviours exhibited on the breeding colony are related to maximising individual mating success. For example, time spent engaged in sexual activity (approaches to females and attempted copulations) correlates with mating success (Twiss, 1991); increased time resting reduces mass loss rates potentially extending stay (Anderson & Fedak, 1985); and aggressive behaviour is required to maintain positions on the colony (Anderson & Fedak, 1985;

Twiss, 1991; Twiss et al., 1998). Time spent alert, however, although a substantial portion of activity budgets (mean = $12 \pm 1\%$; Twiss, 1991), is less obviously linked to success. Note that the classification of *alert* used here includes all instances when a male had his head raised and was looking around but at a nonspecific target (i.e., excluding looking directly at conspecifics in the context of aggressive or sexual interactions). The amount of time that individual males spend alert may depend on local environment (e.g., density of potential mates or competing males), but equally it could be hypothesised that alertness indicates *nervousness*, akin to the *shy-bold* personality axis (Réale et al., 2007). Therefore, this study re-examines existing detailed time-activity budgets of individually identified male grey seals over two consecutive breeding seasons (1988 and 1989) at the North Rona colony ($59^{\circ} 06' N$, $05^{\circ} 50' W$), Scotland, for evidence of individual consistency in time spent alert.

Materials and Methods

Behavioural Observations

Observations were made from a hide (observation blind) overlooking the North Rona study site throughout daylight hours (0700 to 1800 h BST) and spanning the entire breeding season (22 September 1988 to 16 November 1988 and 22 September 1989 to 23 November 1989) (Twiss, 1991; Twiss et al., 2006). All behavioural observations were made by the first author (SDT). All males present on the study site for a discrete period of greater than 1 h were identified by pelage and scarring patterns or brands (Twiss et al., 1994). Individual time-activity budgets were derived from instantaneous scan sampling of each male's behaviour at 5-min intervals during observation hours using the following broad behavioural categories: resting, alert, locomotion, sexual behaviour, aggressive behaviour, and out of sight (definitions for these categories are presented in Twiss, 1991; Twiss et al., 1998).

All occurrences of inter-male fights and chases and all attempted and successful copulations were also recorded (Altmann, 1974), including date and time of occurrence, participant identities, initiator, interaction duration, and outcome (Twiss, 1991). These behaviours are sufficiently rare and attention grabbing to enable all occurrences during observation periods to be recorded (Altmann, 1974). These data permitted computation of daily rates of male-male aggression and sexual behaviour for each male. Individual male mating success was defined as the number of successful copulations with females not observed copulating previously with either the same or other males (Twiss et al., 2006). Male dominance rank was

calculated from the outcomes of observed intermale aggressive encounters as described in Twiss et al. (1998). Dates and times of arrival and departure of males to and from the study area were also noted. Locations of males at the study site were recorded daily, allowing calculation of potential male home range area (Twiss et al., 1994).

Although detailed activity budgets for males were only available from 1988 and 1989, long-term brand sighting effort on North Rona from 1980 to 2008 provided records of the number of years that each male was present on the colony and the span of years from the first to last time each male was sighted, thus providing two indices of reproductive longevity.

Measuring Male Size, Mass, Mass Loss, and Age

Since male grey seals fast during the breeding season, mass loss incurred by a male is a useful indicator of energy expenditure. The subsample of males in the present study were weighed and measured (linear nose-to-tail length) at least twice during each season to provide estimates of mass on date of arrival at the colony, rate of mass loss, and overall body size (Twiss, 1991). First captures in each season were timed to be close to each individual's arrival at the colony (between 30 September and 18 October), and subsequent captures were spread through the breeding season (from 21 October to 6 November). The number of days between the first and last mass collection for individual males ranged from 10 to 33 d (Twiss, 1991). These males also had a single lower incisor tooth removed under local anaesthesia to permit estimation of age per male (Twiss, 1991). All animal handling was conducted under the UK Home Office Licence.

As this study examines repeatability of behaviour over two consecutive breeding seasons, only males that were present in both seasons could be used in this analysis. Males present on the colony adopt a spectrum of behavioural strategies from subordinate mobile (transients) to dominant resident (tenured) males, with the former spending relatively more time alert than the latter (Twiss, 1991). Moreover, males that are present across successive seasons tend to be tenured males (Twiss et al., 1994, 1998). The goal of this study was to compare like with like, therefore only males adopting the same dominant, resident, and tenured strategy were included in this study. This provided a sample of eight males that were present in both 1988 and 1989 as tenured, resident males (maintaining positions among the females for approximately half of the breeding season or longer).

Statistical Approach

To test for interannual consistency in time spent alert, the intraclass correlation (ICC) was

employed as a measure of repeatability (Lessells & Boag, 1987; Bell et al., 2009). Correlations (Spearman's rank) between percentage of time alert and the potential explanatory measures of the following factors were examined: (1) state dependent factors (male size, mass, or mass loss rate), (2) age, (3) colony attendance parameters (length of stay, arrival, or departure dates), (4) home range size, (5) rates of either sexual or aggressive interactions, (6) dominance rank, (7) mating success, and (8) reproductive longevity. Bonferonni corrections for multiple tests were applied, and for all ICCs $n_0 = 2$ (Bell et al., 2009).

Results

There was substantial within-season variability among the eight males in most parameters. Coefficients of variation for all parameters were greater than 15%, with the exception of body length (4%) and departure date in both years (11% and 12%, respectively), and starting mass in 1989 (8%). Despite this within-season variation, individual males showed strong interannual consistency in their time devoted to alert behaviour (Figure 1) with a high repeatability measure significantly greater than zero (ICC = 0.833, 95% CI = 0.415 to 0.963, $F_{7,8} = 10.95$, $p = 0.002$). Although based on a limited sample, these results clearly indicate individually specific behaviour patterns maintained over successive time points. This consistency cannot easily be explained by intrinsic or extrinsic factors that the individuals experience in each breeding season because males' alertness

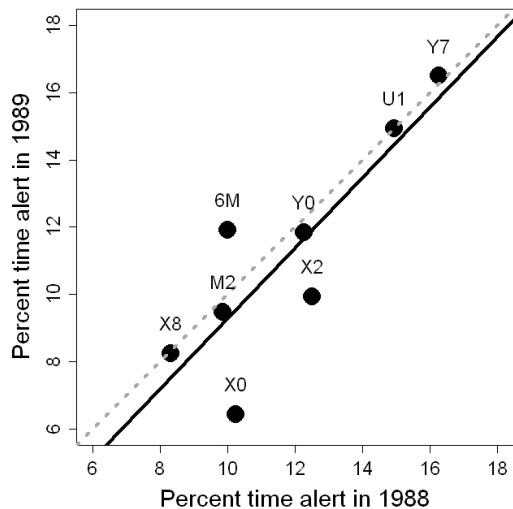


Figure 1. Interannual consistency in time spent alert by male grey seals present on North Rona in 1988 and 1989; solid line represents linear regression, and dashed line indicates the 1:1. Alphanumeric codes represent male identities.

tendencies showed no consistent relationship within seasons with any of our potential explanatory factors: (1) state dependent factors (male body size, mass, or mass loss rate), (2) age, (3) colony attendance parameters (length of stay, arrival or departure dates), (4) home range size, (5) rates of sexual or aggressive interactions, or (6) dominance rank (Table 1). Moreover, this consistent individual variation was unrelated to measures of within-season mating success or reproductive longevity (number of years males were present at the colony) and, therefore, was independent of short- or long-term fitness consequences (Table 1).

Discussion

This study shows clear interannual consistency in male grey seal behaviour patterns unrelated to age, size, indices of energy expenditure, patterns of colony attendance and utilisation, levels of sexual or aggressive behaviour, or dominance status. It may be argued that each individual experienced very similar social and physical local environmental conditions in both years of the study and responded accordingly in terms of time spent alert, leading to the correlation in alertness across years. This is an unlikely explanation, however, especially as four of the males in this study moved territorial

locations between years. The study area comprised an area of 27,491 m² compared to the mean male territory size of 420 ± 70 m² (Twiss et al., 1994). Although all the males in this study were site-faithful in that they were present at the study area in both years, only two returned to exactly the same geographical locations with a spatial overlap of their 1988 and 1989 territories of over 90%. Of the remaining six males, two had interannual territorial overlaps of 40% and 68%, respectively, while four males moved to new parts of the study area with no overlap of their 1988 and 1989 territories (Twiss et al., 1994). Those males that moved experienced different male neighbours and differing numbers and densities of females in their new locations (Pomeroy et al., 1994), and yet they retained their previous levels of alertness. These results indicate individually specific behaviour patterns maintained over successive time points (Sih & Bell, 2008) that cannot easily be explained by either intrinsic or extrinsic factors that the individuals experienced in each breeding season and, therefore, provide evidence of behavioural types in male grey seals.

This study examines male grey seals within the context of the breeding season. Grey seals are capital breeders, as are most phocid species, and therefore breeding is temporally separate from foraging. It is therefore possible that differing levels of alertness could be associated with differing foraging techniques and persist as behavioural "hang-overs" on the breeding grounds (Sih & Bell, 2008). However, the results presented here suggest that even if this is so, there is no net effect on males' behaviour, condition, energy utilisation, or ultimate success on the breeding colony. Irrespective of the causes, these results imply that for dominant, tenured male grey seals in the wild, differing behavioural types exist. Whether this constitutes evidence of individual personalities or not, the key point is that individuals behave differently and do so consistently. It also remains an open question whether these patterns are developed or learned by individuals during their life, how long such consistency persists (Sih et al., 2004a, 2004b; Dingemanse & Réale, 2005; Sih & Bell, 2008) or whether there is a heritable component to this variation (Sih & Bell, 2008; Smith & Blumstein, 2008).

Sih & Bell (2008) argue that to fully understand the evolutionary causes and ecological consequences of consistent individual differences in behaviour, it is important to quantify and then explain the patterns of variation in behavioral syndromes across populations and species. A first step towards this is to gather as much information as possible on behavioural correlations across many species. While many taxa are already represented in the literature, most marine mammals

Table 1. Summary data for Spearman's rank correlation tests between time spent alert in both 1988 and 1989 and potential explanatory variables; R = Spearman's Rank correlations and *p* = two-tailed significance. Sample size is 8 in all tests except for tests involving starting mass or rate of mass loss in 1989 (*n* = 6) and age in both years (*n* = 7). All tests are nonsignificant upon applying Bonferroni corrections for multiple tests (no tests significant at *p* < 0.001).

Year	Percent time spent alert			
	1988		1989	
Variable	R	<i>p</i>	R	<i>p</i>
Size	-0.31	0.46	-0.66	0.16
Starting mass	0.14	0.74	-0.54	0.27
Rate of mass loss	0.29	0.49	-0.89	0.02
Age	-0.51	0.24	-0.61	0.15
Length of stay	-0.48	0.23	0.29	0.49
Arrival date	0.39	0.33	0.32	0.44
Departure date	-0.12	0.78	0.46	0.26
Home range size	-0.67	0.07	0.10	0.82
Copulations/day	-0.10	0.82	-0.07	0.87
Aggressive interactions/day	0.07	0.82	-0.19	0.65
Dominance rank	0.29	0.49	0.17	0.69
Mating success	-0.30	0.47	0.00	1.00
Years present	0.39	0.34	0.11	0.80
Years known	0.41	0.32	0.65	0.08

are not represented (Réale et al., 2007; Smith & Blumstein, 2008). At the very least, the preliminary results presented here indicate a need to extend such studies to a broader spectrum of individuals to test for behavioural types among more subordinate (transient) males and, perhaps more importantly, among breeding females. It would also be instructive to extend such studies to other wild marine mammal species for which individuals can be reliably identified, observed, and relocated at differing time points or in different behavioural contexts. Although field-based studies of behavioural types are difficult, pinnipeds often lend themselves to repeated observational studies of individuals due to their annual site fidelity to breeding colonies. Such analyses can form a simple addition to ongoing observational studies but with the power to provide valuable insights into the nature and ecological consequences of individual variation in behaviour. Indeed, there are probably existing datasets that could readily be re-analysed from the perspective of individual consistencies in behaviour patterns.

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