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Towards informed metrics for examining the role of human-induced animal responses in tag studies on wild animals

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Abstract

Two prime issues can detrimentally affect animals that have been equipped with tags; (i) the effect of the capture and restraint process and (ii) the effect of the tag itself. This work examines some of the issues surrounding quantification of tag effects on wild animals for both restrained and free-living animals. A new method to quantify stress effects based on monitoring ventilation rates in relation to activity is suggested for restrained animals which may help improve the practice of handling animals. It is also suggested that various metrics, many derived from accelerometers, can be examined in tagged wild animals to examine the change in behaviours over time with a view to having a better understanding of welfare issues, assuring the quality of recorded data and informing best practice.

Introduction

Unlike plants, most animals can move, and this allows them to execute behaviours, and position themselves within the environment so that they have enhanced lifetime fitness. This explains why the study of animal behaviour is so important for understanding animal ecology and life history strategies. But it is challenging to acquire robust data on animal behaviour because the process of doing so often affects the animal concerned. This 'measurement affects outcome' conundrum (cf. (Wilson et al. 1986)) is manifest in a variety of ways. For example, in the simple observation of animals, the presence of an observer may elicit a variety of responses from the study subject, from ostensibly no response, to a marked behavioural escape reaction (Fig. 1). Although such responses are usually a function of observer stimulus, such as distance (Beale and Monaghan 2004) or environment (Recarte et al. 1998), at no time can the observer be sure that the animal is unaware of his/her presence since reaction may be physiological, involving a change of state (Gross and Levenson 1995) but with no external manifestation of change (Gross and Levenson 1997).

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Understanding the extent to which our procedures affect animals is key to being able to interpret the validity of any data we collect. This issue is far-reaching and covers research across time and space scales as well as from autoecology to community ecology.

In this paper, we consider a particular branch of wild animal research that uses animal-attached devices (also called biologging) (Ropert-Coudert and Wilson 2005) to study animal behaviour and ecology. The issue of measurement affecting outcome is particularly germane in this field since it is essentially impossible to ‘tag’ an animal without changing its ‘state’. This occurs because it is normally necessary to capture and restrain the study animal in order to equip it, and because animals can be affected by tags in many different ways, including manifestation of aberrant behaviour (Vandenabeele et al. 2011), compromised performance (Wilson et al. 1986), and increased energy expenditure (Bannasch 1995).

Given that a tag-equipped animal is subject to all this, we consider here, the extent to which we can use tag technology itself to help define how animals react to the process of being tagged. Our specific aim is to; consider the applicability of some tag-based metrics that could be used to assess the extent to which a tagged animal is affected by our procedures. For this, we present data stemming from both animal and human-derived data using animal-attached devices. We use humans because (i) we expect them to respond less to other humans interfering with them than most animals while still displaying reactions that can be likened to those of animals and (ii) we can ask human subjects about the qualitative effects of stress. The work is opportunistic and concentrates around accelerometry- and magnetometry-based metrics, working across scales of both space and time, with the specific intent to find cross-cutting metrics to facilitate both intra- and inter-specific comparison.

Methods and results

Changes in behaviour and state over time manifest via acceleration-based metrics

Animal behaviour

Many studies examining human-induced animal responses typically consider the prevalence of particular behaviours such as attempts to remove an attached tag (Vandenabeele et al.

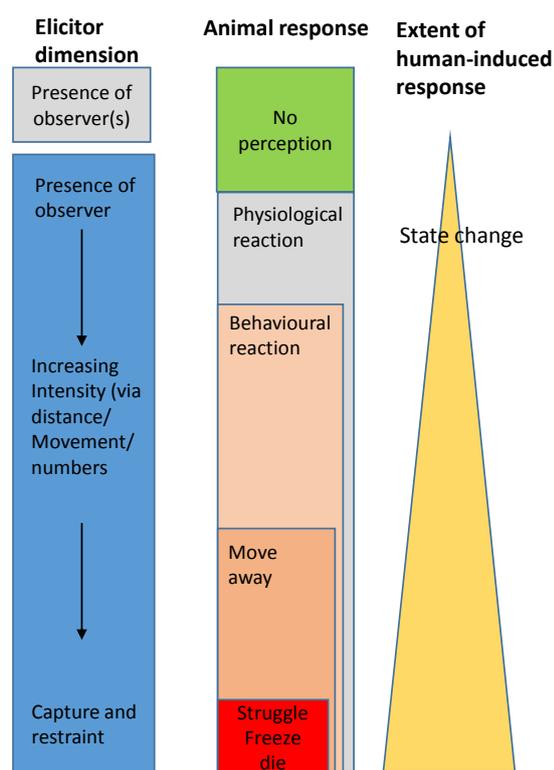


Fig. 1 – Interaction between stimuli and human-induced responses by animals showing increasing intensity of response.

2011) or the incidence of vigilance behaviours (Kröschel et al. 2017) as metrics for human-induced animal responses. In view of the difficulty in standardizing these across taxa, we suggest that the integration of orthogonal, tri-axial accelerometers within tags can help (cf. Kröschel et al. 2017). Specifically, we suggest tri-axial acceleration is particularly powerful since, via the calculation of dynamic body acceleration (DBA) (Wilson et al. 2006) and posture (Shepard et al. 2008b), behaviour can be specifically and generally quantified (Shepard et al. 2008b, Wilson et al. 2016).

The most used method of calculating animal posture is to smooth the acceleration channels from an animal-attached tag to provide the ‘static’ acceleration, ie the value that is nominally due to the earth’s gravitational field (Shepard et al. 2008a, Shepard et al. 2008b). For this, the static element of any acceleration (A) data point i ($SA_{c,i}$) is given by:

$$S_i = \frac{1}{w} \sum A_j$$

where w is the smoothing window. The sine or cosine of this can be used to determine the angle of the tag with respect to gravity (pitch and roll) and thereby the posture of the animal (Wilson et al. 2016).

In order to derive the dynamic body acceleration per orthogonal axis channel (DA_c), the smoothed values (SA_c) should be subtracted from the raw values per channel (A_c) following;

$$DA_c = A_c - SA_c$$

All 3 dimensional axes of acceleration need to be added to provide a summed acceleration metric. The most used form of this is the vectorial sum of the dynamic body acceleration ($VeDBA$) which uses the dynamic components of acceleration (DA_x , DA_y and DA_z) to take the vectorial length of the dynamic acceleration vector (Qasem et al. 2012) via;

$$VeDBA = \sqrt{DA_x^2 + DA_y^2 + DA_z^2}$$

Use of DBA alone is a powerful metric for general animal activity, as manifest by Fig. 2, which shows the $VeDBA$ of a European badger *Meles meles* tagged in northern Ireland over 6 full days and the gradual increase in movement dynamism following initial capture, sedation with ketamine, and release.

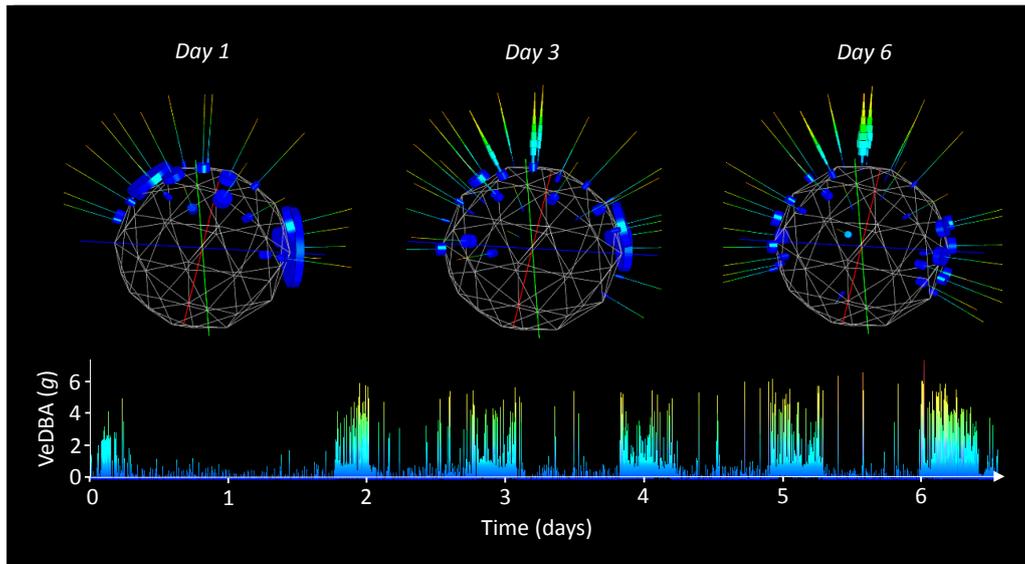


Fig. 2 – Changes in activity of a wild-caught, sedated and released European badger over the first 6 days post-release. The lower graph illustrates VeDBA over time and shows generally reduced VeDBA activities initially, followed by increasing VeDBA values over time. The ‘urchin’ plots above this represent 3 days within this period to provide more information on activity. This spherical plot represents body angle by spine position (spines on the North pole show periods when the animal was horizontal, with increasing proximity to the equator showing the animal lying more completely on its side). Increased activity allocated to body angle is shown by discs on the spines, with disc thickness indicating VeDBA bins (starting from low [blue] VeDBA values close to the disc surface to increasing VeDBA values farther away from the sphere [warmer colours]) while disc diameter indicates time at VEDBA and posture. Note the extended times spent essentially immobile (body postures indicate most likely sleeping) and the slow return to higher VeDBA values at the North pole of the sphere, an indication of the animal was moving about on all fours.

The same data can be interrogated by using visualisations that incorporate both the static and the dynamic accelerations. Here, a tri-axial plot of the static acceleration will tend to have the data all lie on the surface of a sphere that has a radius of 1 g, with the position on the surface being dependent on the animal body posture. The nominal limits (in g) to the co-ordinates of this sphere (following a y-, x- and z-axis system) are: 1, 0, 0 (North Pole); -1, 0, 0 (South Pole); and 0, 0, 1; 0, 0, -1; 0, 1, 0; and 0, -1, 0 for the 4 equatorial limits. This ‘g-sphere’ representation (Wilson et al. 2016) allows all postures to be visualised intuitively within one plot, with some idea of the representation of time to posture. However, much data in one locality hide other data in this locality so the visualisation cannot represent, in this format, large quantities of data, and nor does it incorporate the dynamic component of acceleration.

Both these problems are dealt with by dividing the surface of the g-sphere into facets (for details see (Wilson et al. 2016)) and the number of data points within each facet summed. The VeDBA values of all points within any given facet are then classified into frequency bins. The distribution of the VeDBA frequencies per facet is then represented by discs on a spine emanating from the centre of the facet and projecting into space. The width of the discs represents the width of the VeDBA bin while the diameter represents the proportion of the data residing in any given bin. The process is conducted for all facets of the sphere. This ‘urchin plot’ gives an immediate picture of time and dynamism allocated to posture, highlighting modes which may constitute particular behaviours (Fig. 2).

In the case of data acquired from a badger *Meles meles* (Fig. 2), the urchin plots illustrate both variation of time and energy allocated to various postures over the 6 days the animal was monitored following capture, sedation and release. The urchin visualisation shows how the first days involved much sleeping in positions for long periods (without changing position) with little normal locomotion, slowly giving way to normal activities. Closer inspection of the urchin provides more specific data. Importantly, irrespective of the details manifest by the particular individual in Fig. 2, the technology provides valuable quantification of activity.

Animal state

But urchin plots are also theoretically valuable for manifesting animal ‘state’ (Wilson et al. 2016) and this was investigated by asking 20 human participants equipped with back-mounted accelerometers to watch two 4 minute films, one which was considered to elicit feelings of happiness (a clip of two people drinking beer supposedly laced with helium, which gave them high pitched voices) while the other was chosen to elicit sadness (a death scene from Disney’s ‘Bambi’). Following each film, participants were asked to walk down an empty 40 m corridor to rate their reaction to the films on a piece of paper. Their data sets were then processed by being allocated to urchin plots, within which facet dispersion (320 facets were used to cover the g-sphere) and VeDBA allocation to facet were examined.

This showed a significant effect of film type (Happy or Sad) ($\chi^2_{(2,1)} = 17.99$, $p < 0.0001$), time spent walking ($\chi^2_{(1,1)} = 6.69$, $p = 0.009$), and facet dispersion ($\chi^2_{(1,1)} = 6.54$, $p = 0.011$), on mean (log) VeDBA. (Fig. B1).

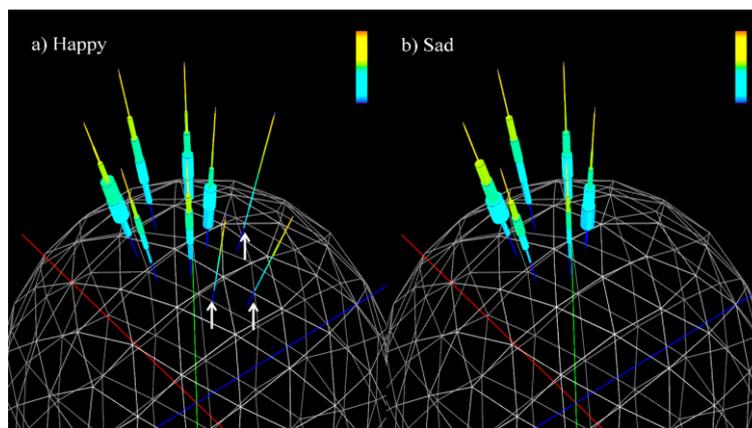


Fig. 3 - Example walks of a male participant after having watched the (a) happy and (b) sad film clips. Note the decrease in the number of facets ‘occupied’ by the acceleration data in the ‘sad’ condition indicating reduced ‘facet dispersion’ (data in the facets indicated by the arrows are missing) manifesting reduced ‘swagger’.

State effects manifest in movement patterns may also be observable in micro-movements of the body’s external surface (Flavel et al. 2012). As part of a study to investigate the effects of nicotine, we attached tri-axial accelerometers sampling at 800 Hz to the fingernails of 20 smokers and looked at the manifestation of tremor prior to, and during, smoking. Analysis of the accelerometer outputs using a fast Fourier transformation showed a marked increase in the intensity (signal strength) of tremors across all individuals (e.g. Fig. 4), demonstrating that the change in chemical state was readily detected using the accelerometry approach.

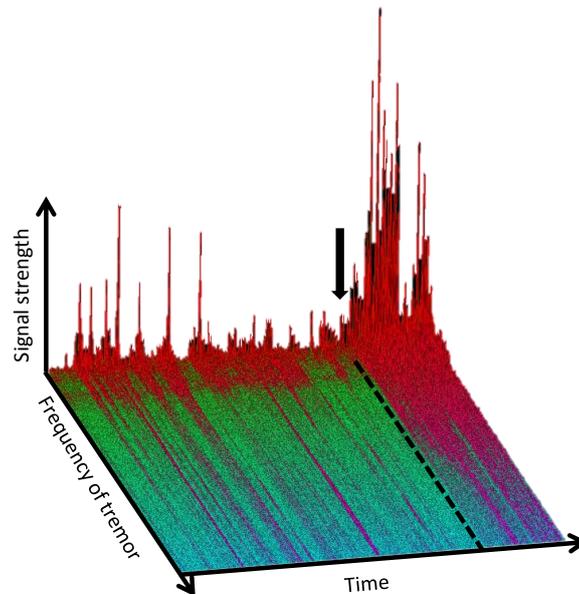


Fig. 4 – Change in tremor over time manifest in a tri-axial accelerometer mounted on the fingernail of a smoker at the moment of the first inhalation of tobacco smoke of the day (black arrow and dashed line). The graph has a base of green, with signal strengths that depart significantly from 0 shown in red. Note how, following the first inhalation, the strength of the tremor increases dramatically, indicated by the higher red peaks, and how it does so across both low frequencies (which make up most of the signal prior to inhalation) and high frequencies (cf. the right-hand corner of the graph).

Changes in physiology manifest via magnetometry-based metrics;

Ventilation rates

Based on the observation that animal ventilation rates change with stress (Brown et al. 2005, Barreto and Volpato 2011), we constructed, and tested, a simple system designed to be attached to restrained (or perhaps free-living) wild animals for easy measurement of ventilation rates. It was initially tested on humans before being trialled on penguins.

A custom magnet-driven magnetometer (MDM) was constructed, consisting of a tri-axial magnetometer (Honeywell HMC5883L, supplied by <http://www.wildbyte-technologies.com/>), which recorded (at 40 Hz) the proximity of a distant neodymium boron magnet (10 X 7 mm dia) *via* changes in magnetic field intensity. The basic principal of functioning relied on having a circum-thoracic strap containing an inbuilt system whereby the magnet-sensor distance varied with expansion of the rib change and thereby with lung volume. For this, both magnetometer (encased in a tightly fitted plastic case) and magnet were placed *ca.* 5 cm apart, on a circum-thoracic cotton and velcro strap except for the material between magnet and magnetometer, which was made of elastic. The relationship between magnetic signal and inspirational volume and breath frequency was ascertained by asking 8 participants lying in three different positions (on both sides and on their back) wearing the magnet-driven magnetometer to breathe into a face mask connected to a Vyntus IOS, a device with a clinically proven lung function testing device frequently used in medicine for determining tidal volume and breathing rates with high accuracy

(<http://www.carefusion.com/our-products/respiratory-care/pulmonary-function-testing/spirometers/pc-based-spirometers/vmax-vyntus-spiro>).

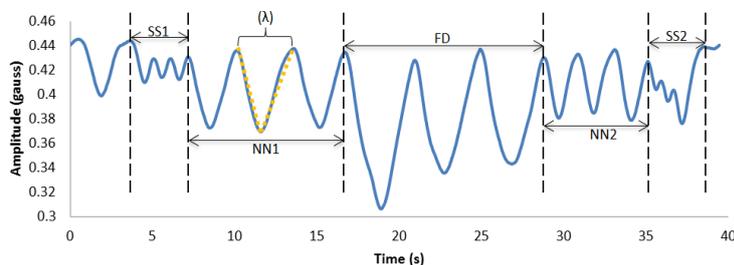


Fig. 5 – Example of how a simple magnet-driven magnetometer on an elasticated circum-thorax strap can code for ventilation rates in humans. The trace shows the raw signal in relation the breathing. For this exercise, the participant was asked to lie and then execute three types of breathing patterns; SS1 & SS2 – Short, sharp breaths, NN1 & NN2 – Normal breaths, and FD – Full, deep breaths. λ indicates the wavelength (and hence the ventilation rate). That all breaths represented by the system corresponded to real breaths was ascertained by independent equipment (see text).

The system showed breathing patterns extremely clearly with obvious time and amplitude differences between breathing regimes according to different tidal volumes and respiration rates (Fig. 5). Indeed, peak-to-peak analysis of data was successful in identifying all 654 of 654 breaths executed when magnetometer signals were compared to the breath-by-breath data of the Vyntus IOS. Individual correlations between tidal volume and amplitude were very clear for all participants (e.g. Fig. 6) as well as between participants and positions, including all positions and participants combined, and were highly significant ($p < 0.001$) (Table 1) although variation is high. Specifically, use of ANOVAs to compare GLMs with and without terms (positions and participants) showed that tidal volume had a significant effect on amplitude (Estimate = 6.26, Std Error = 0.15, $t = 42$, $p < 0.001$) and that body position (1 = On back, 2 = on right side, 3 = on left side) also had a significant interaction with volume and its effect on amplitude ($\chi^2_{(2,1304)} = 81.23$, $p < 0.001$).

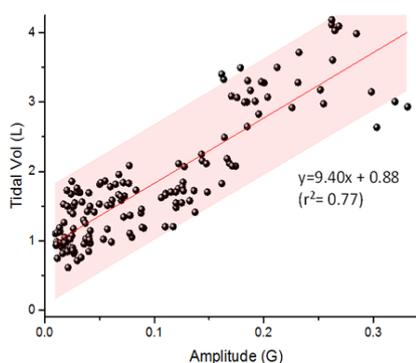


Fig. 6 – Example of how the amplitude in the breathing signal (cf. Fig. V1) from a simple magnet-driven magnetometer on an elasticated circum-thorax strap can code for tidal volume (ascertained by independent means – see text) in humans across body positions. The pink shaded area shows 95% confidence limits.

Table 1 – Best fit linear relationships ($y = mx + c$) between y (the magnetometer signal amplitude (gauss)) and x (the tidal volume (L) for participants lying in three different positions (1 = on back, 2 = on right side, 3 = on left side). The SEM² is the standard error of the mean and * shows statistical significance at the shown level.

Participant	Position	Gradient	Intercept	r ²	P-value	SEM ²
1	1	13.16	0.33	0.96	<0.001*	0.21
	2	12.15	0.99	0.90	<0.001*	0.11
	3	9.17	0.77	0.79	<0.001*	0.09
	All	9.40	0.89	0.77	<0.001*	0.07
2	1	33.31	0.26	0.91	<0.001*	0.09
	2	35.46	0.24	0.89	<0.001*	0.08
	3	29.17	0.34	0.90	<0.001*	0.07
	All	32.76	0.28	0.89	<0.001*	0.05
3	1	9.16	0.60	0.92	<0.001*	0.16
	2	6.85	0.61	0.87	<0.001*	0.14
	3	5.13	0.56	0.89	<0.001*	0.14
	All	6.09	0.68	0.80	<0.001*	0.10
4	1	14.61	0.03	0.95	<0.001*	0.08
	2	14.74	0.11	0.96	<0.001*	0.06
	3	13.82	0.14	0.92	<0.001*	0.05
	All	13.97	0.09	0.93	<0.001*	0.04
5	1	22.16	0.00	0.96	<0.001*	0.14
	2	11.15	0.01	0.93	<0.001*	0.09
	3	6.37	0.24	0.96	<0.001*	0.13
	All	13.63	0.12	0.61	<0.001*	0.07
6	1	26.03	0.39	0.93	<0.001*	0.13
	2	14.66	0.40	0.72	<0.001*	0.09
	3	9.62	0.42	0.91	<0.001*	0.10
	All	12.28	0.54	0.64	<0.001*	0.06
7	1	9.35	0.38	0.91	<0.001*	0.10
	2	8.49	0.25	0.94	<0.001*	0.11
	3	4.96	0.31	0.85	<0.001*	0.08
	All	5.76	0.44	0.70	<0.001*	0.06
8	1	15.41	0.12	0.94	<0.001*	0.27
	2	5.69	0.31	0.87	<0.001*	0.12
	3	5.01	0.16	0.83	<0.001*	0.13
	All	5.35	0.40	0.62	<0.001*	0.09
ALL	P1	11.42	0.50	0.75	<0.001*	0.004
ALL	P2	6.65	0.63	0.60	<0.001*	0.005
ALL	P3	4.96	0.50	0.75	<0.001*	0.006
ALL	ALL	6.26	0.65	0.57	<0.001*	0.003

Deployment of this same magnet-driven magnetometer system on 8 wild Magellanic penguins *Spheniscus magellanicus* held in darkened boxes showed that breathing patterns were reflected very well in magnetometer signal amplitude so that breathing rate could readily be determined according to condition (Fig. 7). Importantly, the respiration rates could be examined with respect to activity, as manifest by VeDBA (Fig 7). Under these conditions it was notable in all 8 individuals that the respiration rate was not simply dependent on activity with, for example, appreciable variation in respiration rate even during constant conditions of exercise (e.g. Fig. 7) indicating that ‘stress’ is an important element modulating ventilation rates.

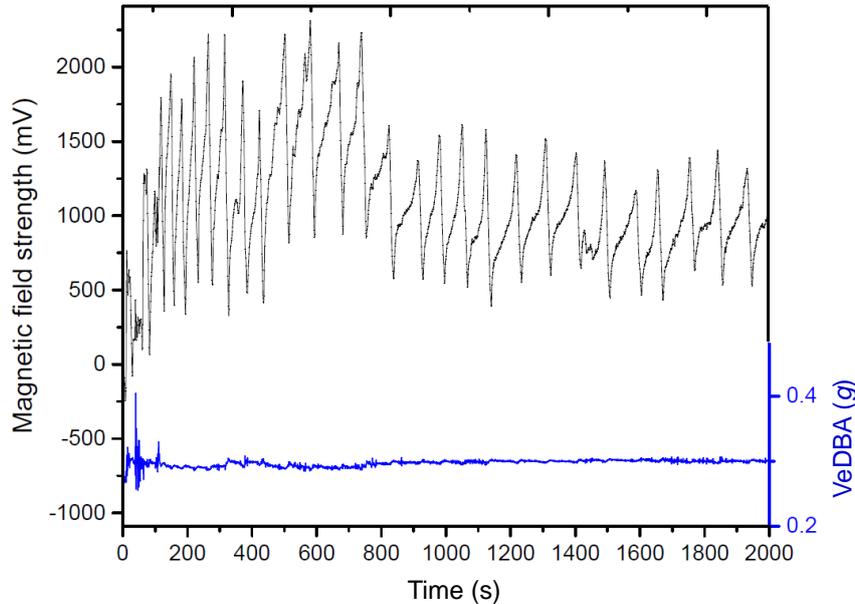


Fig. 7 - Example of how a simple magnet-driven magnetometer on an elasticated circum-thorax strap can code for ventilation rates in wild animals. The example here is from a Magellanic penguin, placed in a darkened box. Note how, even though there is no change in activity (as indicated by the VeDBA), the respiration rate following stress at time 0 decreases. The VeDBA values here (*ca.* 0.3 g) indicate that the animal is predominantly 'still' whereas, for comparison, the VEDBA for a walking penguin with an upper back-mounted tag would be *ca.* 1.4 g.

Changes in physiology manifest via movement-corrected ventilation metrics;

Since activity is the main modulator of ventilation rates (Thomas et al. 2015), activity must be known, and corrected for, in order to examine environmentally induced ventilation rates. In a brief attempt to demonstrate this, one of us (RG), used a combined tri-axial accelerometer (see above) in tandem with a system for determining breathing rate (Zephyr bio-harness) while undertaking various tasks (sitting, standing, walking) and being submitted to different stimuli (exposure to calm music, loud music and horror films).

This pilot work confirmed other studies that link ventilation rate to extent of activity (Thomas et al. 2015 and refs therein) (Fig. 8) but also showed convincingly that breath rates for particular activities preceded those activities in an anticipatory manner (Fig. 8) both in terms of increases in breathing rates preceding higher activities and decreases in breathing rates preceding lower activities. Indeed, the changes between standing and walking, and *vice versa*, suggest that there may be two components to this response; (i) a mentally mediated response (typically of smaller magnitude) and (ii) a physiological response (of larger magnitude). Importantly though, even anticipation of activity appears to be enough to change ventilation rates. Beyond that, for particular activities (all of which have defined VeDBAs alluding to metabolic rate (Halsey et al. 2011), and thus likely ventilation rate), breathing rate and variance changed according to perceived stress. This was apparent because, in a sitting, immobile subject, we observed changes in ventilation rates associated with different environmental stimuli (Fig. 9).

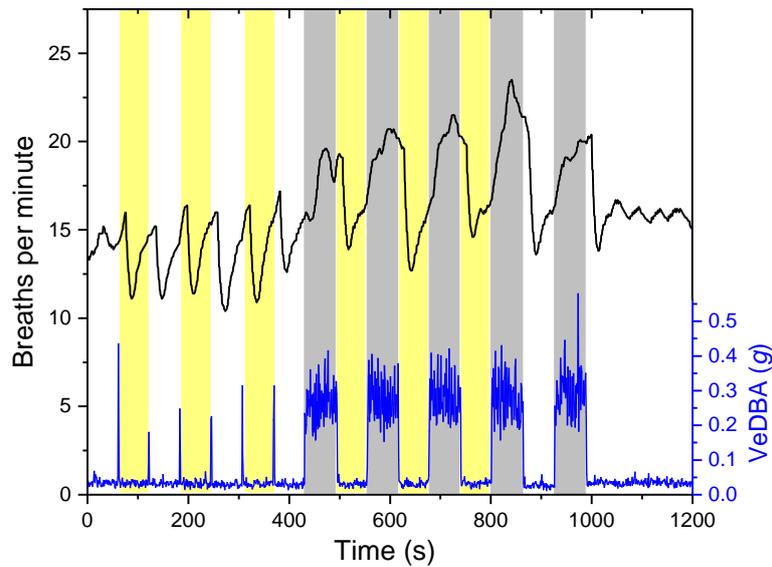


Fig. 8 – Change in breathing rate according to activity of a person engaged in defined periods (each lasting for 1 minute) of sitting (white panels), standing (yellow panels) and walking (grey panels). The VeDBA is shown to indicate the level of activities and only shows a spike between sitting and standing, the subject otherwise being motionless (even ostensibly completely motionless people have some residual movement, which is why the VeDBA is not 0 at this time). Note, how the breath rate uncouples from activity in anticipation of activity to come some 30 s before the new activity is undertaken.

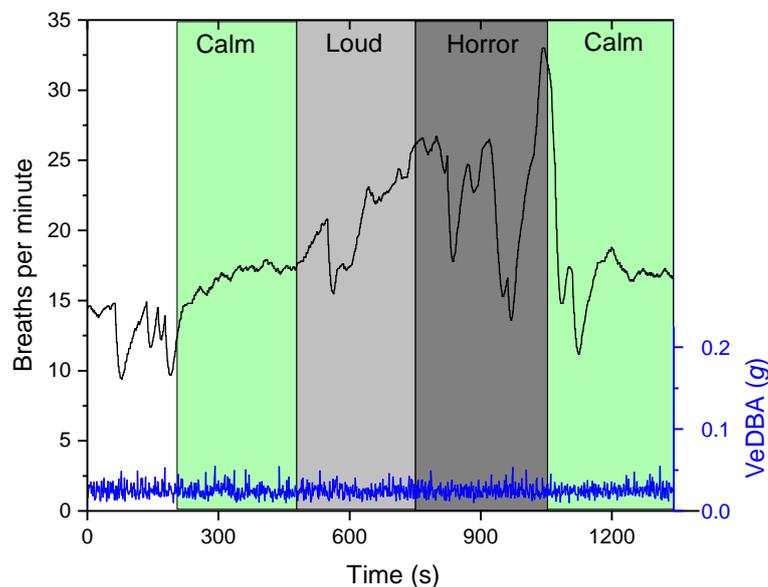


Fig. 9 – Change in breathing rate according to exposure to different stimuli for a sitting person. The green panel shows when the person was exposed to relaxing music (Toto; 'Africa' and Rusted Root; 'Send me on my way'), the light grey when exposed to loud music (Aerosmith; 'Don't want to miss a thing') and the dark grey panel shows when the person watched a horror sequence (a baboon eating a live impala). The VeDBA is shown for the same period to demonstrate that the changes in breathing rate are not a consequence of activity. For comparison, the mean VeDBA value for someone walking with an upper back-mounted accelerometer is approximately 0.35 g (cf. Fig. 10).

This effect was not just manifest during minimal exercise conditions because, in our pilot trials, environmentally elicited breathing rates were additive to exercise-linked breathing rates (Fig. 10) irrespective of whether the metric for exercise was speed (Fig. 10a) or the more general activity metric, VeDBA (Fig. 10b).

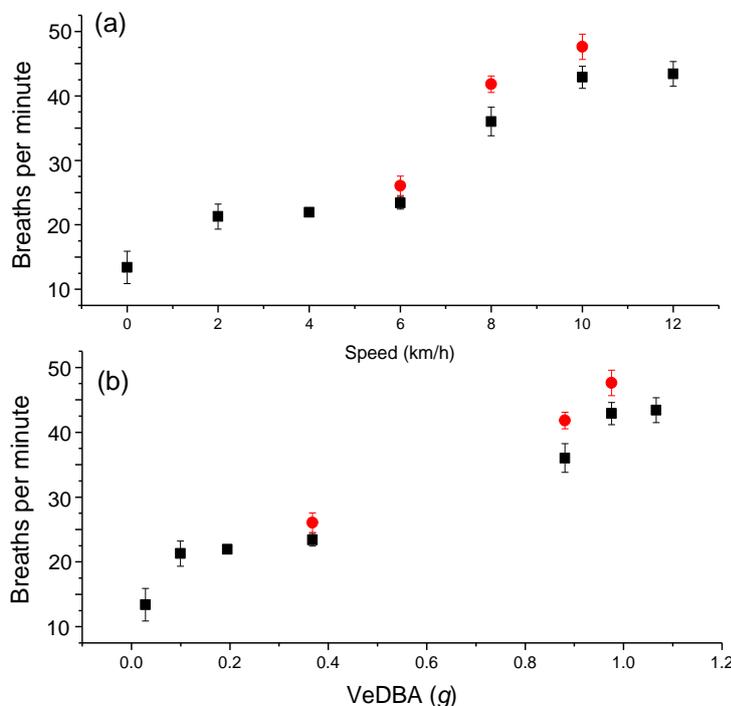


Fig. 10 – Breathing rate of a person moving on a treadmill at (a) different speeds and (b) at different VeDBAs (corresponding to those speeds). The black squares show the stabilized breathing rates (with SD error bars) while the red circles show the breathing rates for the same conditions but with the person listening to loud music. Note how the breathing rates between the two conditions dissociate, with the ‘music’ conditions being consistently higher than ‘expected’.

Discussion

Effects of interaction with humans

There are a few ways of using tags to study animals without affecting them at all (as far as we can tell). A notable example of this is the egg in the nest for monitoring heart rate (Borneman et al. 2014). Critically, the dummy egg containing heart rate monitoring technology has to be switched for a real egg while the adult to be monitored is away and its partner is incubating. Only one of the pair is thus obviously impacted by the process, the study animal being essentially naïve. This does not preclude some inter-partner transmission of stress or that the study bird might not react to the fake egg as it would to a real one, but the procedure goes a long way to monitoring genuinely naïve animals even though no tags are actually properly ‘attached’.

At the next level, it is possible to attach tags to some animals without restraint, whale sharks and whales being examples of this (Baumgartner et al. 2015, Rohner et al. 2018). Here, some

clamping or suction mechanism is employed to make the tag adhere to the animals as they swim past a human who deploys the units (Rohner et al. 2018). Reactions to this process vary but are sometimes not discernible (Gleiss et al. 2013), which is as much as could be hoped for. Notably though, this procedure is only used because it is difficult, or impossible, to restrain the study animal. Given the obvious advantages in precluding restraint and associated stress on the study animal, it is surprising that more of this type of approach is not attempted with animals that are currently restrained. The attachment procedure could even take the form of drones attaching tags (perhaps most obviously starting with larger animals) or, as tags get smaller, might extend to using static movement-triggered systems to shoot ‘sticky’ systems to animals as they move within range. While such processes are obviously challenging, and such speculation might seem futuristic, smart technology, including with respect to drones navigating and executing complex manoeuvres in cluttered airspace, is ever more competent (Vanegas and Gonzalez 2016). An obvious advantage to such systems is that they might prevent the study animal from associating humans with the procedure. In this respect, it is notable that animals, including humans, are generally very discerning with respect to the form of other vertebrates in their vicinity (cf. Yorzinski et al. 2014) and attention to humans is usually particularly prioritized (Le Pelley et al. 2016).

Inevitably though, many tagged animals will have to be restrained, and it is expected that this will constitute the most extreme form of stress they are likely to have experienced since capture and restraint can be likened to predation; the worst thing that can happen to a wild animal. Accordingly, observers have noted extreme heart rates in restrained animals (Meijer et al. 2006) and reactions to restraint so extreme that it can result in death. This is clearly highly undesirable, either for the period that the animal is restrained, or for the period following this, when the animal’s behaviour is expected to be highly modified as a consequence (Marin et al. 2007). Two approaches help; one is to employ means to reduce the effects of stress, which includes sedatives (although these come with their own problems (Ross and Ross 2009)), sensory deprivation, such as covering the eyes and minimizing noise, while the other seeks to use methods to define the extent of animal stress during the period of restraint. We would advocate, where possible, that restrained animals be fitted with systems that record metrics that readily allude to stress, notably movement-corrected ventilation rates. Depending on the animal, it takes a few moments to place an elasticated band around the animal’s torso within which a magnet-driven magnetometer-based system and accelerometer is embedded. Mirroring work done by multiple authors for a variety of animals, we noted in our pilot study, that stress in humans was accompanied by an increase in ventilation rates and increased variation (Figs 9 & 10) and our work with penguins indicates that this is likely to be true for them too. Consideration of movement-corrected ventilation rates during restraint procedures should not only serve to highlight the extent of the stress but also to make good practice apparent *post hoc* to aid in future studies. Thus, for example, the ventilation rates of all 8 penguins indicated a decreasing response after birds were placed in a darkened box, with, however, momentary increases in ventilation rates to speech outside the box under otherwise silent conditions (cf. Fig. 7). In general, a key challenge in this approach though, will be to determine how, exactly, ventilation rates relate to movement metrics, such as VeDBA, in unstressed animals so that the degree of stress can be couched in terms of ‘ventilation rates above expected’. Studies of captive animals may help here but, until substantive work is undertaken for different species, we may have to work with comparative data where it is generally accepted that the lower the ventilation rate for a given activity, the less stressed the study animal would appear to be (cf. Fig. 7).

Post-tagging effects

‘Bad experiences’ for tagged animals are almost inevitable (McMahon et al. 2011) so we should expect to see changes in the behaviour stemming from the capture and restraint process as well as the effect of the tag itself manifest in the sort of data that tags record. Across effect scales, we may expect to see, and therefore look for (in an attempt to quantify), changes in general activity (Fig. 2) as well as changes in the incidences of specific behaviours (Fig. 2). These are not only important for us to be able to put the behaviours into context with respect to ‘the expected norm’, but they will also help us examine the decay in adverse reaction across time (Fig. 11). This will be complicated by the varying half-lives of differing adverse reactions (Fig. 11) but a real advantage of the increasingly sophisticated logging systems that are being deployed on wild animals, is that they may store data from a multitude of sensors (Ropert-Coudert and Wilson 2005) and thus data may be examined in detail across domains. This is a real departure from older studies where hard-worked-for visual observations could relate to few parameters and then, as often as not, be improperly quantified.

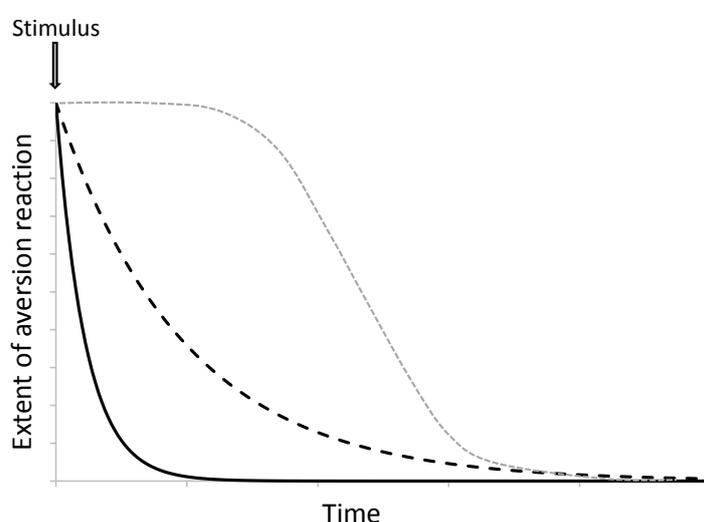


Fig. 11 – Depending on the metric chosen to quantify the extent of the aversion reaction to the stimulus, the value is expected to decay with time at different rates. Thus, for example, the solid black line might represent heart rate while the dashed black line might indicate the frequency of vigilance behaviours. The simplest examples take the form of half lives, which are easily expressed by time constants. However, depending on the species concerned, the form of the elicitor, and the aversion metric taken, the reaction could decay negligibly for a period before dropping in a more conventional manner (grey dashed line). Cognisance of variability in response across metrics is important for us to be able to quantify detriment more completely.

How far might we go in our interpretation of tag data in attempting to quantify human-induced detriment? The fact that humans change their gait according to emotional state, as manifest in our short study (Fig. 3), suggests that animals may do the same and one study has already demonstrated this for elephants (Wilson et al. 2014)). State expression most likely has its roots in sociality (cf. Roether et al. 2009) but has great potential for studies of wildlife, not just with respect to determining half-lives of reactions to tagging, but also with respect to examining whether certain conditions, or localities, elicit state changes. Avoidance of an area by animals because they have experienced perceived detriment will presumably be more subtle than a binary response, with state changes becoming more apparent as the animal

approaches the area. Acceleration metrics lend themselves to examination of state because the variability in the signal over time and across axes provides an almost limitless source with which to signal-process and distil out ‘fingerprints’ which define states. This is particularly apparent in the study on how nicotine affects tremor (Fig. 4), where the fast Fourier transformation analysis over time effectively provides a fingerprint for both the pre- and the post-nicotine conditions. The complexity of the output suggests that important state-dependent cues may be hidden within the matrix with, once identified, potential to extend the process of fingerprint identification to other states. This is no trivial task but deep-machine learning could be put to good use here. Importantly, we should not be lulled into thinking that small physical changes in micro-movements reflect small changes in state condition. There need be no direct relationship.

The sophistication that tags and refined processing give us can also help us quantify the (multiple) reactions to multiple, and potentially additive, stressors (Fig. 12). Indeed, functional relationships for responses across variables should perhaps be moving towards n-dimensions. It may seem impossibly complex to do this at the moment, but with increasing environmental data (Avouris and Page 2013), increasingly diverse and powerful ways to document our role within it, and increasing tag sensing and storage capacities, we will be doing our ethics approaches a disservice if we did not consider this.

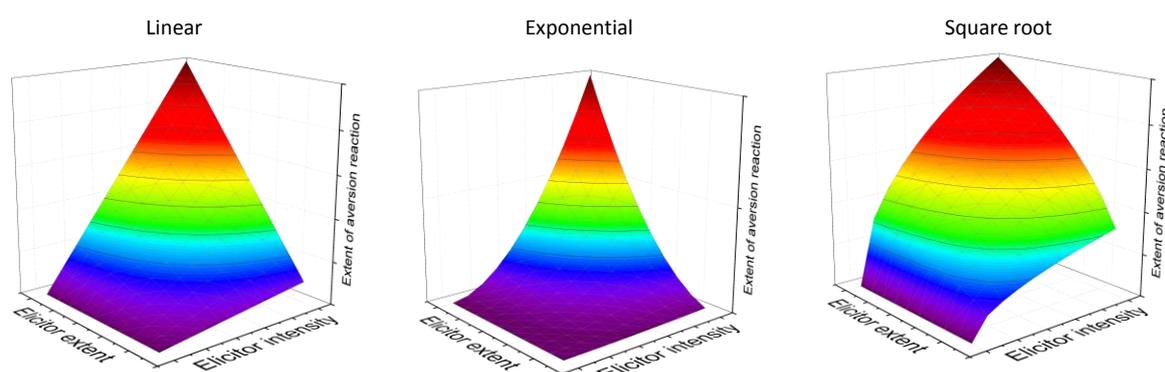


Fig. 12 – Examples of how animals might react to adverse elicitors due to human intervention showing different functional responses. The intensity of the elicitor may be, for example, the distance between a human and the study animal while the extent might be the number of humans or the number of times to which the animal is exposed to a single human. In reality, elicitor intensity and extent are just convenient descriptors of two dimensions of an n-dimensional matrix where multiple factors interact to produce an overall response. This response is typically manifest in some metric such as heart rate or the frequency of vigilance behaviour. Note that the form of the functional relationship with respect to the extent or intensity of different stimuli profoundly affects the degree of response. In the examples, all reactions assume that both intensity and extent have equal weighting and have a multiplicative effect. Note the difference between interacting linear effects, exponential (reaction = $f(\text{elicitor})^{1.8}$) [where the animal is increasingly disproportionately stressed by the stimuli] and square-root (reaction = $f(\text{elicitor})^{0.5}$) [where the animal shows signs of habituation]. Any information on such functional responses will help inform us on how best to minimize aberrant man-induced effects.

The expected decay in adverse reaction across time (though not necessarily to zero) is analogous to the suggestion made to assess tag effects by measuring changes in a given parameter as a function of tag size/mass so as to be able to regress the relationship to a tag of zero mass (Wilson et al. 1986). This should help indicate the situation of an untagged animal although it should only work for physical, rather than mental, detriment. Animal memory, particularly with regard to substantive stressors, may have a decay rate that means the animal may never return to the naïve state over the course of its lifetime (cf. Yorzinski 2017).

The future

This work compliments many others that have attempted to quantify the impact of human intervention on study animals but has hopefully demonstrated that we can do much more to learn about the short-term and long-term effects of capture, restraint and tagging on our study animals if we exploit the complex sensors that we now use more completely. The change in parameters over time (or not) will be pivotal to interpretation of the primary data (rather than the tag effects *per se*) and should also help examine the time-based dynamics of rehabilitated animals. Finally, the process should enable us to refine our procedures for dealing with animals so that, at once, we have minimum impact on our study animals and a more grounded ethical approach.

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