ORIGINAL ARTICLE

Agonism does not covary with territoriality in a gregarious reptile

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Abstract

Natural selection for territoriality is theorised to occur under conditions favouring intra-sexual phenotypic variation in physiology, morphology, and behaviour. In this context, certain suites of behavioural traits associated with territoriality are expected to consistently covary among individuals (sometimes referred to as 'behavioural syndromes') within sexes. Agonism (conflict-associated behaviours that may or may not be associated with physical aggression) and movement—for example, ranging, or relocation within or across seasons—are two behavioural components that are associated with territoriality and may be expected to covary in this context. Territorial males are expected to employ agonistic behaviours to actively establish and defend areas and resources and show more stability in their location across the landscape. However, the interaction between agonism and movement especially for wild reptiles has rarely been tested. We investigated whether agonistic and movement behaviours correlate at the individual level both within one year and across multiple years, in a wild population of Australian eastern water dragons, *Intellagama lesueurii*. Although both types of behaviours exhibited among-individual repeatability over year and multi-year scales, we found no evidence of an agonistic-movement behavioural syndrome. These findings indicate that agonistic and movement behaviours are likely independent traits, and thus, territoriality may not drive shared selective pressures for both. It is possible that other social behaviours and strategies are in place to maintain social structure in this wild population.

Significance statement

Males of many animals establish and maintain or defend territories. Territory defence is expected to be associated with behaviours associated with conflict or expressions of dominance, to signal territory boundaries to encroaching individuals, or more aggressive approaches for active defence. We investigated whether such agonistic behaviours correlated with the distances individuals ranged or dispersed within and between years, as an indicator of territoriality. Through thousands of observations of a wild population of Australian eastern water dragons, *Intellagama lesueurii*, we found that although individuals showed repeatable patterns of both agonistic and movement behaviours, we found no evidence that these were correlated. It appears that territory establishment and defence may therefore not rely on agonistic signals in this species in direct contrast to other taxa, indicating that other systems are in place to maintain social structures.

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Introduction

In animals, sexual selection often involves the use of an overarching strategy by individuals to obtain high-quality mates. This may appear relatively simple or straightforward, such as in species where female selection for elaborate ornamentation is obvious and ubiquitous (McLean et al. 2012). In many species of lizards, intra-sexual selection can be observed in the association between sexual size dimorphism, male territoriality, and reproductive success (Fairbairn et al. 2007). For species that tend towards

territoriality, males invest in monopolisation and primary access to mates (e.g. dominant, territorial, guarders, bourgeois). In some lizard species, alternative reproductive tactics may also evolve, for males that seek direct access to mates by capitalising on the investment of others (e.g. satellite, transient, roamers, parasitic) (Taborsky 1997).

The selective conditions under which territoriality emerges and persists in wild populations are still being investigated and understood. However, theory predicts that this mating strategy likely evolves under conditions favouring both inter- and intra-sexual phenotypic variation in morphology (as mentioned above), but also in physiology or behaviour (Taborsky et al. 2008; Engqvist and Taborsky 2016). This is commonly seen in fish. For example, Mediterranean wrasse *Symphodus ocellatus* demonstrates age- and size-dependent reproductive tactics, with older, larger males establishing and maintaining nests and smaller males successfully reproducing not by establishing territories, but rather by adopting a 'satellite' or 'sneaker' strategy (Alonzo et al. 2000).

Traits that are found to associate with territoriality include body size, colouration (Jensen et al., 2004), and behaviours such as agonism (any social behaviour related to fighting or aggression, including threats and displays) and movement patterns (Moczek and Emlen 2000; Ota and Kohda 2006; Oettler et al. 2010; Noble et al. 2013). Importantly, these traits often consistently differ among individuals (i.e. are repeatable) or, in extreme cases, can even be fixed (e.g. multiple traits making up male polymorphisms (Taborsky et al. 2008; Buzatto and Machado 2014)). Territorial behaviours may also covary (i.e. form a behavioural syndrome; (Dingemanse and Réale 2005; Sih et al. 2012)) and allow individuals to exploit different intra-specific niches, such as occupying hierarchical positions or filling social niches (Bergmüller and Taborsky 2010). As social environments can vary in their stability over time, behavioural syndromes may also manifest or become stable over different time scales (e.g. within years and between years for long-lived species). In the context of territoriality, agonism and across-landscape mobility (hereafter "movement behaviours") are expected to form a behavioural syndrome (Kortet and Hedrick 2007; Chang et al. 2012), with large, territorial males showing less movement (i.e. displacement or ranging) and more agonism as they establish, defend, and maintain stable territories.

Lizards provide an excellent study system to explore behavioural syndromes as many species employ territoriality as a reproductive strategy (Crews 1983; Noble et al. 2013). Further, they display a diverse array of individually repeatable agonistic behaviours (While et al. 2010; Horváth et al. 2017), and repeatable movement patterns have also been widely studied, as well as the extent to which these behaviours vary in time (van Berkum et al. 1989; Martin and Avery 1998; Clusella Tullas et al. 2007; Bowker et al. 2013; Michelangeli et al. 2017, 2018a, b). This gives us a solid foundation upon which to examine whether these two traits form a behavioural syndrome and therefore jointly capture an individual's territoriality.

Here, we test the hypothesis that agonistic behaviour and movement are concurrent and individually repeatable in a species that shows strong territoriality in a large subset of its male population (Baird et al. 2012). To do this, we use a longitudinal dataset including over 17,000 observations of Australian eastern water dragons, *Intellagama lesueurii* (hereafter water dragons), in a known population. We ask whether agonistic behaviour and three types of movement behaviour (successive distance, displacement, and site fidelity) are repeatable within and across years in male water dragons and whether individual movement forms a behavioural syndrome with agonistic behaviour. If aggression is associated with a territorial tactic, we would expect to see individuals remain in their defined territory (a negative correlation between overall distance measurements and agonism) with non-aggressive individuals moving further between territories both within and between seasons (Ota and Kohda 2006; Dennenmoser and Thiel 2008; Ota 2016). Alternatively, if territoriality is plastic and increases with age and experience, we may expect to see behavioural consistency and correlations within years, but not necessarily between years (Sakata et al. 2002).

Methods

Study species

Eastern water dragons are long-lived (> 10 years), sexually dimorphic, and social (Strickland et al. 2014). Approximately 336 adult individuals occupy the 16-ha study site (see below) at any one time, and population density varies with habitat features (e.g. water, complex vegetation); however, density (and thus competition for territories) is known to be high compared with equivalently-sized rural locations (Gardiner et al. 2014; Strickland et al. 2018). The species engages in polyandry, with females laying up to three clutches per season, with a mean of seven eggs per clutch (Kent et al. 2019). The breeding season lasts from August to March, and males demonstrate alternative reproductive tactics including the establishment and defence of territories that can be held across years, as well as satellite behaviour (Kent et al. 2019). The relative reproductive success of each of these tactics (either within seasons or across lifetimes), especially in this population, is currently unknown.

Behavioural survey data (agonism)

We utilised data taken as part of a longitudinal study (2010–2020) conducted at Roma Street Parklands, Brisbane, Australia (− 27.462315, 153.019052). Between August and May each year, behavioural surveys were recorded 3 days per week, twice each day (07:30–10:30 and 13:00–16:00), with the survey route capturing approximately 85% of the water dragon population (Strickland et al. 2014). For every individual encountered, a profile photograph was taken using a Canon EOS 600 digital camera, their GPS coordinates were recorded using a GARMIN eTREX10 handheld device, and any agonistic behaviour being exhibited was recorded. Water dragons perform a number of discrete visual and physical behaviours that are considered agonistic or aggressive towards conspecifics. We noted whether, during the survey, the focal individual demonstrated any of the following: head bob, arm wave, tail slap, chasing, or fighting. We did not include fighting data for our subsequent analyses, since directionality could not be inferred (i.e. if another individual had begun a fight and the focal individual was acting in defence, rather than demonstrating agonistic behaviour). All other behaviours were pooled, such that an encounter would have recorded an agonistic behaviour, or not (i.e. a binary response variable). This was done in order to test the likelihood of a male to display any antagonism towards others, without introducing confounding external or internal variables that might influence the 'level' of antagonistic behaviour (Baird and Timanus 1998). Individual ID of each dragon was determined subsequently; thus, these observations were done blind to ID.

Individual sex was determined based on known sexual dimorphic characteristics: males present a red ventral colouration which the females lack and are larger in size than females (Cuervo and Shine 2007). Individuals could then be identified via their photographs in the I3S Manta software using the unique scale patterning around their ear (Gardiner et al. 2014). In addition, once or twice each year, a morphological catch took place where we measured individual snout-to-vent length (SVL) from the tip of the snout to the posterior edge of the anal scale, as a measure of body size (Littleford-Colquhoun et al. 2017). All work was done with the approval of the University of the Sunshine Coast Animal Ethics Committee.

Over the 10-year period, we collected 68,452 observations of water dragons with 1414 unique individuals identified. The data used for these analyses only included adult males that had body size measurements and therefore consisted of 17,207 observations made for 303 individuals. On average, individuals were observed 32 times per season, with most individuals being observed across two successive seasons (Supplementary material 8).

Distance measurements (movement)

We converted GPS points of each individual sighting into x-y coordinates using the adehabitatHR package (Calenge 2006) in the R statistical environment (R Development Core Team 2010). We then calculated two types of distance measures: successive and displacement. Successive distance was defined as the number of meters between each successive sighting (with time between each, minimum 1 day, maximum 205 days). Displacement was the number of meters between an individual's first adult sighting of the season and each subsequent sighting (Fig. 1). Successive distance tends to reveal more about an individual's daily activity or patrolling (i.e. tendency to always be found in the same place) whereas displacement reflects territory shifts (or the lack of territory) within a season—something that may occur to submissive, younger, or transient males. Both traits, however, may be positively correlated with territory size.

In order to determine individual site fidelity between seasons, we calculated the centroid of each home range using the kernel utilisation distribution for each adult male (minimum 20 sightings) at the 95% home range class (Strickland et al. 2017). Following methods from Gardiner et al. (2014), we applied a smoothing parameter of seven meters optimised for this species. We then took the centroid coordinates from the projected polygons for each individual per year and measured the distance the centroid had moved between years. This would reveal whether individuals remained in the same area across years or whether they moved their home range site. Since territory space is of high value in this population, we expect agonistic individuals to move little across years, in order to maintain their space within the site (Strickland et al. 2018). Site fidelity was then log-transformed, while other movement behaviours were scaled (mean = 0; SD = 1) in order to improve model convergence.

Statistical analyses

To estimate repeatability for each trait, we first fitted univariate mixed models using the 'MCMCglmm' package (Hadfield 2010) in R (R Development Core Team 2021). Error structure was specified for each response variable with agonistic behaviour (a binary response) fitted as threshold and the three movement measures fitted as Gaussian. In all models, we fitted individual identity (ID) to estimate among-individual variance between years (VID). Additionally and following Araya-Ajoy et al. (2015), a combination of identity and year (ID_Year) was fitted for agonistic behaviour, successive and displaced movement, in order to estimate among-individual variance within years (VID_Year). This was not done for site fidelity, as individuals only had one measure per year for this trait. All models included SVL as a fixed effect, as size

Fig. 1 Example of successive and displaced distance measurements, with the successive distance measured between an individual's successive sightings on the left and the displaced distance measured from an individual's first adult sighting (A) and their subsequent sightings thereafter on the right
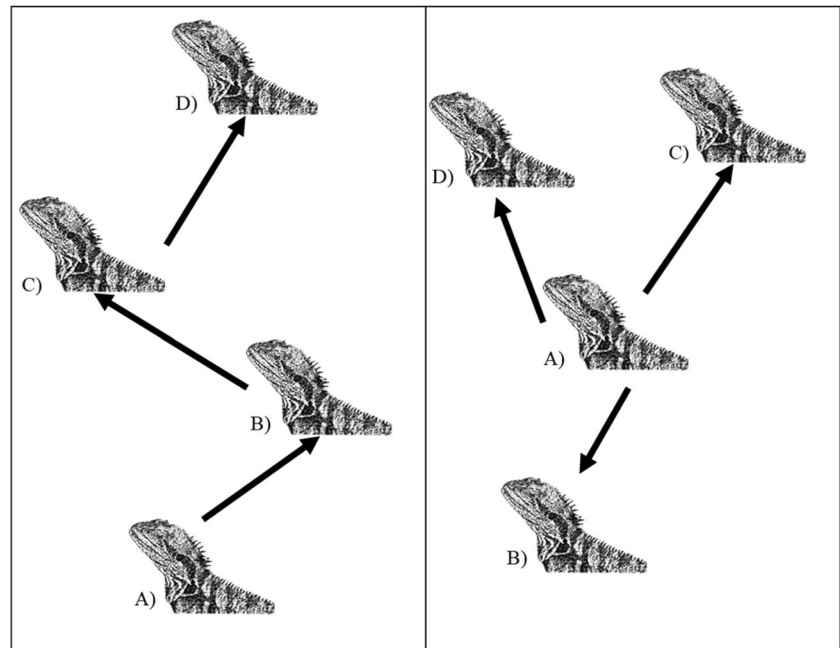
is known to be correlated with agonism in this species (Littleford-Colquhoun et al. 2019). Seasonal effects were also accounted for by fitting season (the period from September to January being the breeding season and the rest of the field season being the non-breeding season) as a categorical fixed effect for agonistic behaviour, successive and displaced movement. Finally, successive distance was corrected for time between sightings (hours) and displacement distance was corrected for the observation order within the field season. These univariate models were run at 710,000 iterations with a burn-in period of 10,000 and a thinning of 700 iterations. For agonistic behaviour, successive and displaced movement models, we used a prior approaching chi-squared distribution. The Heidelberger and Welch's diagnostic were performed on each model to check convergence as well as trace checks for chain mixing. All univariate model scripts can be found in the Supplementary materials (Supplementary materials 1, 2, 3 and 4).

We calculated adjusted repeatability (and covariances in subsequent correlational analyses) in the short and long-term as

$$R = VG/(VG + VR)$$

where VG is the among-individual variance either within-year (VID + VID_Year) or between years (VID) and VR the residual variance (Nakagawa and Schielzeth 2010). For agonistic behaviour (binary trait), R represents the latent scale repeatability, which is why we also calculated repeatability on the raw scale, using the function QGicc from the QGglmm package (de Villemereuil et al. 2016).

Correlations between traits

To test whether an individual's agonistic and movement behaviours were correlated, we fitted multivariate mixed models in MCMCglmm using similar fixed effects and error structures as described above for each trait. We first fitted a trivariate model for agonistic behaviour, successive and displaced movement, in which random effects included ID and ID_Year to estimate both their within-year and among-year covariances. We then fitted a series of bivariate models to estimate the among-individual covariance between each of these traits and site fidelity. In these bivariate models, both responses had different levels of replication which is why only ID was fitted as a random effect. We calculated among-individual correlations between each pair of traits by dividing the posterior of their covariance by the square root of the product of their variance posteriors (Houslay and Wilson 2017). We used the posterior mean and credible intervals to infer statistical significance (CIs not overlapping zero). The multivariate model was run at 510,000 iterations, with a burn in period of 10,000 and a thinning of 500 iterations. The multivariate model script (for trivariate and all bivariate analyses) can be found in the Supplementary material 5.

Once all models were run, we produced covariance-correlation matrices iterating all results (Supplementary material 6 and tested for non-linear effects by extracting BLUPs (best linear unbiased predictions), calculating the mean BLUP for each individual trait and running linear models for each pair of traits (Supplementary material 7.

This test was to capture any less predictable or nuanced correlations that might exist in the dataset. Finally, we estimated the variance explained by fixed effects, ID, and ID_Year (akin to an *R*-squared value).

Results

We noted that mean, minimum, and maximum distances were consistent with our assumption that movement measurements were likely capturing movement across the landscape between territories rather than simply establishing larger territories, since they far exceeded the mean 'territory size' previously calculated in this population (~ 6.0-m radius; Strickland et al. 2014) (displacement mean = 42.7 m, 0–321 m; distance mean = 17.7 m, 0–323 m; centroid distance moved mean = 14.0 m, 0.4–197 m).

Long-term and short-term repeatability estimates

Agonistic behaviour was not repeatable across years but showed low to moderate repeatability within years. On the raw scale, its within-year repeatability was low (mean [95%CI] = 0.16 [0.09, 0.24]). In contrast, all movement behaviours were repeatable within years (moderate for successive distance, high for displacement, Table 1) and between years (low for successive distance, moderate for

site fidelity, and high for displacement, Table 1). There was a positive effect of size on agonistic behaviour in males (mean = 0.58 [0.40, 0.77]) and a negative effect on centroid distance moved (mean = − 0.10 [− 0.12, − 0.07]). All fixed effects and variance estimates for univariate models can be found in the Supplementary materials (Supplementary material 8).

Among-individual correlations

We found no evidence of covariation between an individual's agonistic behaviour and our three distance measures either between or within years (Tables 2 and 3), with the exception of agonism weakly covarying negatively with successive distance within years only (Table 2). However, we did find low but significant positive correlations between successive distance and displacement at the long-term individual and residual (within-individual within years) levels (Table 2). Additionally, the bivariate mixed models showed that individuals that moved more between successive sightings (within and between years) also moved the centroid of their home range further between years (Table 3). Finally, displacement was negatively correlated with centroid distance moved (site fidelity) between years at the residual level (within individuals, Table 3). No non-linear effects

Table 1 Among-individual repeatability (and 95%CI) calculated in the long-term and short-term levels for each trait

Trait	Between years	Within years
Successive distance	0.10 [0.35;0.18]	0.33 [0.29;0.38]
Displacement	0.51 [0.45;0.59]	0.82 [0.80;0.85]
Agonistic behaviour	0.00 [0.00;0.09]	0.17 [0.13;0.20]
Site fidelity	0.28 [0.04;0.49]	

Table 3 Correlations (and 95%CI) between site fidelity (centroid distance moved) and the other movement and agonistic behaviours at the among-individual and residual levels. These estimates were obtained by fitting bivariate mixed models. Bold values indicate confidence intervals that did not encompass zero, likely indicating an important or significant effect

	Among individual	Residual
Agonistic behaviour	− 0.04 [− 0.13;0.04]	0.03 [− 0.34;0.37]
Successive distance	**0.69 [0.49;0.84]**	0.01 [− 0.12;0.12]
Displacement	0.20 [− 0.05;0.46]	**− 0.15 [− 0.26; − 0.03]**

Table 2 Variance-covariance matrices (and 95%CI) derived from the trivariate model fitting the three traits repeatedly measured with years. A 3 by 3 matrix is presented for the among-individual long-term, short-term, and residual components. Variances are presented in the diagonal, covariances in the upper triangle, and correlations in the lower triangle. Bold values indicate confidence intervals that did not encompass zero, likely indicating an important or significant effect

Level		Successive distance	Displacement	Agonistic behaviour
Between years	Successive distance	**0.14 [0.05;0.25]**	**0.12 [0.06;0.19]**	− 0.01 [− 0.06;0.04]
	Displacement	**0.55 [0.35;0.70]**	**0.38 [0.29;0.46]**	0.00 [− 0.05;0.05]
	Agonistic behaviour	− 0.08 [− 0.79;0.97]	0.07 [-0.59;0.89]	0.03 [0.00; 0.09]
Within year	Successive distance	**0.28 [0.21;0.36]**	0.03 [-0.01;0.08]	**− 0.07 [− 0.13; − 0.01]**
	Displacement	0.14 [− 0.01;0.31]	**0.21 [0.18;0.26]**	0.01 [− 0.04;0.06]
	Agonistic behaviour	− 0.03 [− 0.00;0.07]	0.06 [-0.21;0.30]	**0.20 [0.12;0.28]**
Residual	Successive distance	**0.82 [0.80;0.83]**	**0.08 [0.07;0.08]**	0.03 [0.00;0.06]
	Displacement	**0.08 [0.07;0.08]**	**0.25 [0.23;0.26]**	0.02 [0.00;0.03]
	Agonistic behaviour	0.04 [0.00; 0.07]	0.04 [0.01;0.08]	**1.00 [1.00;1.00]**

were identified when correlational models were run on the extracted BLUPs for each trait (Supplementary material 8). Variances in each behavioural response variable explained by the predictive variables can be found in Supplementary material 8.

Discussion

We investigated the potential correlation of agonistic behaviour and movement in a long-lived agamid. Firstly, we found movement and agonistic behaviours to display various levels of repeatability in male water dragons. Secondly, multivariate mixed models revealed that movement behaviours were correlated with each other among individuals, but not with agonistic behaviour. We conclude that agonistic and movement behaviours are independent traits in male eastern water dragons and therefore do not together form what might be perceived as a behavioural syndrome. This is significant, as our findings provide evidence against the theory that males in a system with territoriality should demonstrate particular behavioural syndromes that include agonism and movement. Namely, we do not see that highly agonistic individuals remain in their defined territory while non-agonistic individuals move further between territories. Furthermore, the independence of these behaviours suggests they may be affected by different selective pressures. On the one hand, we can hypothesize territoriality to be determined more by space use (i.e. distance measures) than by agonism, which may explain the higher repeatability and among-individual correlation between the different distance measures. On the other hand, only agonism and not within-year movement behaviours were affected by size, which is often a determinant of territoriality. Indeed, site fidelity across years was associated with size, indicating that smaller males likely move more between years, and larger males maintain territory locations between years. It should be noted that we did not find any non-linear relationships between agonism and movement behaviours. Although agonism has been previously shown to confer fitness benefits under certain conditions (Piza-Roca et al. 2020), it remains unclear which of these behaviours (movement or agonism) relates more to reproductive success in this population.

Another aim of this study was to simultaneously estimate long-term and short-term among-individual variation for agonism and movement behaviours. These analyses showed that the time period over which repeatability was assessed appeared to affect how consistently different individuals behaved compared to one another. Notably, all behaviours were more repeatable within than between years, which is in line with previous studies showing that short-term repeatability is generally stronger than long-term repeatability

(Bell et al. 2009; Boulton et al. 2014). We note, however, that short-term repeatability was expected to be similar to, or stronger than, long-term repeatability simply because of the way it was calculated (Araya-Ajoy et al. 2015). Here, agonistic behaviour was only repeatable within years, which indicates that this trait is highly dependent on temporally variable current social and/or physical environments. For example, previous research showed that individuals can adjust their level of agonism based on previous encounters and number of surrounding males (Adamo and Hoy 1995; Andino et al. 2011). Social environments may change drastically between years due to individuals shifting territories, and even the location in which a dragon is found within its territory can affect its level of agonism (Piza-Roca et al. 2018). Similarly, this is a species with a strong annual cycle for breeding, and territoriality is much stronger during the breeding season. The level of agonism that may be displayed could also therefore be influenced by how 'established' a territory might be—whether there are current territorial disputes, or whether territories (especially for that season) are widely recognized in the population, etc. This low consistency also likely contributes to the lack of observable correlation with movement behaviours highlighted above. Thus, while a tendency for agonism may be an individual trait, it is likely flexible based on social conditions and not necessarily a determinant of what reproductive strategy an individual may use throughout its life—although specific studies into the reproductive success of agonistic individuals in this population have not yet been completed and would be a fruitful line of inquiry.

In contrast, movement behaviours were moderately to highly repeatable across years, with displacement showing the highest level of longer-term repeatability. This means that some individuals consistently shift territories while others consistently retain their territory. It also reveals that the distance over which an individual patrols or searches is repeatable. Previous studies on this population have highlighted complex social networks (Strickland et al. 2014; Piza-Roca et al. 2018); it would thus follow that a level of philopatry would help to maintain these social networks through familiarity of the local environment and local individuals (Jaeger 1981). Furthermore, we observed a strong positive correlation between movement behaviours, especially between successive distance and site fidelity: highly displaced individuals were less likely to remain in the same area. This may be representative of territoriality and alternative reproductive tactics, whereby some individuals gain territories, and those that do not shift more across years. This may be further subject to positive reinforcement: if an individual's residency status significantly impacts their likelihood of winning territorial contests, then it would follow that individual movement would be consistent between and across years (Umbers et al. 2012).

Although residual covariances often need to be interpreted with caution, we can see that some residuals appear to covary between traits. Again, it is possible that social environment is playing a large role in contributing to how these traits manifest at different times. We suggest investigating this as a potential next step in determining how movement, agonism, size, and reproductive strategy might be displayed. It is possible that flexibility itself in some of these traits is in fact being selected for, rather than consistency or repeatability: the mechanisms of selection (increasing reproductive success or survival across an individual's lifetime) need further study in this context.

To conclude, our work demonstrates that c repeatable behaviours used to define territoriality do not always constitute behavioural syndromes. Finally, we provide evidence that movement behaviour may be an individually repeatable trait with multiple correlated components, yet requires further study of its interaction with social and environmental variables.

Declarations

Ethics approval Data collection was approved under animal ethics approval numbers ANS1858 and ANA20161 granted by the University of the Sunshine Coast and adhered to the Australian Animal Welfare Standards and Guidelines Model Code of Practice (Australian Government: Department of Agriculture, Fisheries and Forestry).

Conflict of interest The authors declare no conflict of interest.

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