Journal of
Bat Research & Conservation

OPEN ACCESS
www.secemu.org
DOI: 10.14709/BarbJ.14.1.2021.02

NATURAL HISTORY NOTE

A scale for quantifying behavior based on aggressiveness in bats

Julie Teresa Shapiro[1,2*†], Richard A. Stanton Jr.[1,2], Robert A. McCleery[1,2,4], Ara Monadjem[3,4]

[1] School of Natural Resources and Environment, University of Florida, 103 Black Hall, Gainesville FL USA

[2] Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville FL USA

[3] Department of Biological Sciences, University of Eswatini, Private Bag 4, Kwaluseni, Eswatini

[4] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa

[†] Present address: Department of Life Sciences, Ben-Gurion University of the Negev, Be'er Sheva, Israel

*Corresponding author:
julie.teresa.shapiro@gmail.com

DOI: https://doi.org/10.14709/BarbJ.14.1.2021.02

Keywords: Aggression, behavior, *Chaerephon pumilus*, Chiroptera, observer ratings, personality, traits

received: January, 22nd 2021
accepted: April, 13rd 2021

ABSTRACT

Behavior and personality play a crucial role in the evolution and ecology of animal species. We have limited knowledge of bat personality traits, partially due to the time, equipment, and facilities needed to measure them. To help fill this gap, we developed a scale for quantifying aggressiveness in bats that can be used during ordinary fieldwork and handling by researchers. This scale is based on observations of the following ecologically relevant and easily observed behaviors in wild-captured bats during routine handling: amount and intensity of physical struggling, teeth-baring, and biting. We then applied this scale to 35 wild-caught individual bats belonging to three different species or species groups (*Chaerephon pumilus*, n=29; *Scotophilus dinganii*, n=3; and pipistrelloid bats, n=3) and measured agreement between observers using intraclass correlation coefficients (ICCs). We found that agreement between observers was good to excellent. This scale of aggressiveness provides an important, practical tool for researchers to reliably quantify this personality trait in wild bats that requires no additional equipment and minimal additional handling time. Collecting data on aggressive behavior during handling has the potential to increase our understanding of both intra- and interspecific variation in aggressiveness in bats, as well as the influence of this trait on many aspects of bat ecology. Finally, collecting data using this scale can facilitate comparisons between studies and promote research at broader spatial and temporal scales than commonly used in behavioral ecology studies.

INTRODUCTION

Behavior plays a crucial role in the ecology and evolution of animal species (West-Eberhard 1989, Wong & Candolin 2015). Individuals display behavioral plasticity, which is the variability in behavior in reaction to exogenous or endogenous stimuli (West-Eberhard 1989) or the adjustment of behavior or traits to different situations, contexts, or environmental variation (Sih et al. 2004a, 2004b, Dingemanse et al. 2010, Couchoux & Cresswell 2012). However, despite the wide range of behaviors animals could exhibit, individuals often behave consistently in multiple situations, especially when compared to other individuals (Sih et al. 2004a, Wolf et al. 2007, Biro & Stamps 2008, Carter et al. 2013, Luna et al. 2019). This individual consistency and repeatability in behavioral traits, often classified or quantified with multiple measures, is a personality (Sih et al. 2004a, 2004b, Réale et al. 2007). Personalities often vary between individuals within a species or population (Gosling 2001, Sih et al. 2004a, Réale et al. 2007, Biro & Stamps 2008). The correlation of multiple behavioral traits across different situations or contexts forms a behavioral syndrome (Sih et al. 2004a, 2004b).

Several traits have been measured in order to classify or quantify personality and behavioral syndromes in animals (both wild and domestic), such as aggressiveness (Arnqvist & Henriksson 1997, Sinn et al. 2008, Melotti et al. 2011, Bertram & Rook 2012, Yuen et al. 2015), boldness (Bergvall et al. 2011, Couchoux & Cresswell 2012, Magnhagen et al. 2014, Yuen et al. 2015), or fearfulness (Martins et al. 2011, Lecorps et al. 2018). Aggressiveness often forms a behavioral syndrome together with boldness or willingness to explore and has implications for foraging, predation, intraspecies interactions, and reproduction (Huntingford 1976, Sih et al. 2004a, Réale et al. 2007, Biro & Stamps 2008, Smith & Blumstein 2008). For example, female aggressiveness was correlated with kit survival in North American red squirrels (*Tamiasciurus hudsonicus*) (Boon et al. 2007). Further, aggressiveness has previously been used to measure personality, quantify behavior, and determine behavioral syndromes in a wide range of species (Gosling 2001, Sih et al. 2004a, Réale et al. 2007, Biro & Stamps 2008), including honey bees (*Apis mellifera*) (Walton & Toth 2016), wild cod (*Gadus morhua*) (Villegas-Ríos et al. 2018), great tits (*Parus major*) (Thys et al. 2017), and spotted hyenas (*Crocuta crocuta*) (Yoshida et al. 2016). Finally, ratings of aggressiveness generally show high agreement between independent observers (Gosling 2001).

Bats are the second-most diverse group of mammals in the world with over 1400 species (Burgin et al. 2018) and display a variety of social structures (Wilkinson 2003), illustrated, for example, by lekking (Bradbury 1977, Toth et al. 2018), territoriality (Smarsh & Smotherman 2017), social information gathering from both conspecifics and heterospecifics (Lewanzik et al. 2019), and forming social foraging relationships (Carter & Wilkinson 2013, Harten et al. 2018). Furthermore, bats also exhibit personality traits, such as aggressiveness, boldness, competitiveness, activity, exploration, and ability to learn, that are stable over time (Kilgour & Brigham 2013, Menzies et al. 2013, Nachev & Winter 2019, Boyer et al. 2020, Webber & Willis 2020a). Aggressiveness in bats is generally characterized by vocalizations, pushing, teeth-baring, and biting (Ortega & Maldonado 2006, Ancillotto et al. 2012, Gadziola et al. 2012, Kilgour & Brigham 2013, Boyer et al. 2020). Aggressiveness is a socially and ecologically important trait in bats - aggression towards conspecifics is often tied to dominance and social position within colonies (Ortega & Maldonado 2006, Gadziola et al. 2012, Welch et al. 2020) and may be used to access better sites within roosts (Kilgour & Brigham 2013).

Previous research on bat personality has been largely based on the performance of wild-caught bats kept in captivity for at least 24 hours in behavioral assays (Kilgour & Brigham 2013, Menzies et al. 2013, Boyer et al. 2020, Webber & Willis 2020a), although behavioral studies have also used long-term observations of captive (Ancillotto et al. 2012, Gadziola et al. 2012, Carter et al. 2018, Harten et al. 2018, Welch et al. 2020) or wild colonies (Ortega & Maldonado 2006). Such approaches may require a substantial amount of time, equipment, or specialized facilities (Kilgour & Brigham 2013, Menzies et al. 2013, Boyer et al. 2020, Webber & Willis 2020a). Observational scales are an efficient tool for quantifying animal behavior and personality traits whose results are relatively easy to interpret (Meagher 2009). While they are often used to study animals in captivity (Meagher 2009), scales can be particularly useful in a field context when many animals are captured but time and personnel are limited. For example, in 1969, Burtt & Giltz (1969) developed a rating scale of aggressiveness for birds captured during routine banding. While birds were held in hand, they were presented with the hand of the handler in a "threatening" manner and then scored on a 10-point scale based on the amount and vigor of biting (Burtt & Giltz 1969). This scale has been applied to other studies involving personality in birds, such as canaries (*Serinus canaria*) (Amy et al. 2017, Lalot et al. 2017) and cowbirds (*Molothrus ater*) (Johnson et al. 1980). Similar scales of aggressiveness have also been used to study rodents in captive settings (Hall & Klein 1942, Ebert & Hyde 1976).

A scale of aggressiveness does not currently exist for bats but would enhance our understanding of their behavior and personality traits. To this end, we developed a scale of aggressiveness to quantify aggression in bats subjected to ordinary handling by researchers during field studies, including those that are not exclusively focused on studying behavior or personality. We also measured reliability, which is the consistency or level of agreement in scores (Trevethan 2017), between individual observers using this scale. This scale can be easily incorporated into any study in which bats are handled, including field-based studies, with no additional cost or equipment and thus greatly expand our knowledge of bat behavior and personality traits across species and geography. Our objectives were: 1) to describe this scale of aggressiveness in detail; and 2) to measure the reliability of observers using this scale to determine the most reliable and consistent way of using it.

METHODS

Study site

This study was carried out in northeastern Eswatini (26°S, 31°E), which is mostly comprised of open savanna or woodland (Roques et al. 2001, Monadjem & Reside 2008). Elevation ranges from approximately 150 to 600 m above sea level. The climate is warm, semi-arid subtropical (Matondo et al. 2004) with mean monthly temperatures of 26° C in January and 18° C in July (Monadjem & Garcelon 2005) and annual rainfall of 500-700 mm per year (Matondo et al. 2004, Knox et al. 2010). Twenty of Eswatini's 32 bat species have been recorded in this region (Monadjem & Reside 2008, Monadjem et al. 2021b).

Bat Capture and Handling

We captured bats using 12 m x 3 m mist nets (EcoTone, Poland) placed around suspected roosts and areas of likely bat activity, such as water bodies or pathways (Shapiro et al. 2020). We set mist nets before sunset (before bat emergence) and kept them open for four hours, during which time we checked nets at least every 10 minutes. We collected bats under a permit from the Eswatini National Trust Commission. Handling methods were approved by the University of Florida Institutional Animal Care and Use Committee (Protocol #201508751).

We placed captured bats in cloth holding bags and removed them individually. Routine handling and measuring was comprised of the following actions: measuring forearm length with calipers to the nearest 0.1 mm; taking mass with a spring balance; determining sex and reproductive status by visual examination of genitals and nipples; and determination of age (adult or juvenile) by examining ossification of the epiphyseal joints by shining a light behind a finger joint in the wing (Racey 1974). Bats were identified to species according to physical characteristics and measurements based on Monadjem et al. (2010, 2020, 2021a).

Scale of aggressiveness

Bat behavior was scored during routine handling and measuring. Each handled bat received two types of score: a mean of the scores given at each stage of handling and measuring (forearm measurement, sexing, aging, verification of reproductive status) (hereafter "mean score") (Lewis 1993) and a single, overall score given at the conclusion of all handling of the bat (hereafter "overall score"). Bats were scored simultaneously by the handler (JTS) and

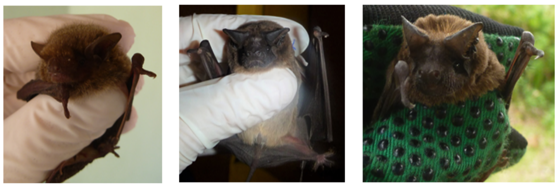
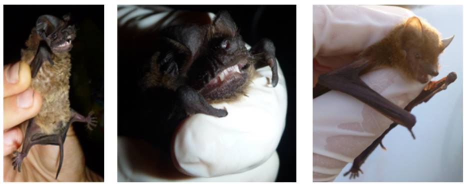
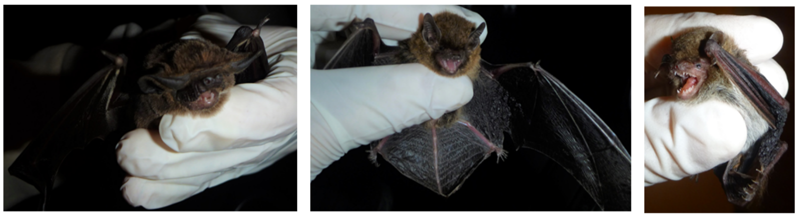
Level	Description	Illustration
Level 1	Bat is completely calm in the hand during manipulation and measurements, with little movement. It is not struggling, biting, or trying to escape. The bat's mouth is closed.	
Level 2	The bat exhibits some struggling, with movements on the body, arms, or wings, but does not attempt to bite. These movements are intermittent. The bat's mouth is closed.	
Level 3	In addition to struggling intermittently with movements of the body, arms, or wings, the bat opens its mouth and bares its teeth but does not actively try to bite.	
Level 4	The bat engages in continuous struggling during the period of handling with strong movements of the body, arms, and wings. In addition to baring its teeth, the bat occasionally gnashes its teeth or attempts to bite handler or equipment, such as calipers.	
Level 5	The bat continuously and aggressively struggles with the body, arms, and wings and continuously gnashes its teeth and bites throughout handling and manipulation .	

Fig. 1 - Illustration of typical bat behavior at each level of the scale of aggressiveness. Level 1: *Chaerephon pumilus*, *Scotophilus dinganii*, pipistrelloid sp.; Level 2: *Chaerephon pumilus*, pipistrelloid sp.; Level 3: *Chaerephon pumilus*, *Nycticeinops schlieffeni*; Level 4: *Chaerephon pumilus*, *Afronycteris nana*; Level 5: *Chaerephon pumilus*, *Scotophilus dinganii*, pipistrelloid sp., *Afronycteris nana*. Note: All pictures were taken in Eswatini from 2015 – 2016 but not all individuals pictured here were scored using the scale.

independently by a second observer. All bats received four final scores: a mean score and an overall score from both the handler and the observer.

Aggressiveness was scored using a scale that we developed based on a range of relevant, observed behaviors in handled bats (Gosling 2001). These behaviors were primarily the following: how much the bat struggled while being held by the handler; whether it bared its teeth or not; and whether it attempted to bite the handler's glove or calipers or not. Teeth baring and biting in particular are associated with aggression in bats in other contexts, such as establishing dominance and forming social groups (Ortega & Maldonado 2006, Ancillotto et al. 2012, Gadziola et al. 2012). The scores assigned were based on the following 5-point scale, with each level in the scale corresponding to specific behaviors exhibited by the bat. We illustrate these behaviors with photographs taken during handling in the field (Fig. 1):

Level 1: Bat is completely calm in the hand during manipulation and measurements, with little movement. It is not struggling, biting, or trying to escape. The bat's mouth is closed.

Level 2: The bat exhibits some struggling, with movements of the body, arms, or wings, but does not attempt to bite. These movements are intermittent. The bat's mouth is closed.

Level 3: In addition to struggling intermittently with movements of the body, arms, or wings, the bat opens its mouth and bares its teeth but does not actively try to bite.

Level 4: The bat engages in continuous struggling during the period of handling with strong movements of the body, arms, and wings. In addition to baring its teeth, the bat occasionally gnashes its teeth or attempts to bite the handler or equipment, such as calipers.

Level 5: The bat continuously and aggressively struggles with its body, arms, and wings and continuously gnashes its teeth and bites throughout handling and manipulation.

Statistical Analysis

We used intraclass correlation coefficients (ICCs) (Fisher 1954, Hallgren 2012, Koo & Li 2016, Trevethan 2017) to: 1) determine how closely scores from the handler and observer agreed; 2) assess the repeatability of this scale of aggressiveness and its generalizability to similar handlers and/or observers; and 3) determine the most reliable and consistent way to use this scale. We calculated ICCs based on scores of all bats in the study using the function "ICC" in the psych package (Revelle 2020) in the program R version 3.6.0 (R Core Team 2013).

We calculated ICCs for the different types of scores. We first calculated the two-way fixed average-measures ICC ($ICC_{3,k}$) based on absolute agreement to compare the mean scores from the handler and observer within the context of this specific study. Then we calculated the two-way random average-measures ICC ($ICC_{2,k}$) based on absolute agreement to determine how generalizable the scale of aggressiveness would be to similar handlers and/or observers using mean scores. In both cases we used average-measures ICC because the scores from the handler and observer were based on the mean of the scores assigned during handling each stage of of the bat (Koo & Li 2016, Trevethan 2017).

We then repeated this procedure with the overall scores from the handler and observer. Here, we calculated a two-way fixed single-measures ICC ($ICC_{3,1}$) to compare the handler and observers within this study, followed by a two-way random single-measure ICC ($ICC_{2,1}$) to determine how generalizable this scale would be. We used the single-measures type because the handler and observer each assigned a single overall score to each bat immediately after handling (Koo & Li 2016, Trevethan 2017).

We interpreted the quality of the ICC values as: excellent (≥0.75), good (0.60 – 0.74), fair (0.40 - 59), or poor (≤0.39) after Cicchetti (1994) and Hallgren (2012).

As an illustration of potential applications of this scale, we compared the mean scores of female (n=19) and male (n=10) bats of the species *Chaerephon pumilus*. We excluded *Scotophilus dinganii* and pipistrelloid bats from this analysis due to small sample sizes. We first calculated the mean of the mean scores given by each observer for each bat. We then compared the scores of males and females using the Mann-Whitney-Wilcoxon rank sum test using the function "wilcox.test" in the "stats" package of program R version 3.6.0 (R Core Team 2013).

Results

We used this scale to score the aggressiveness of thirty-five individual bats. The majority (n = 29) belonged to the species *Chaerephon pumilus*. We also scored three *Scotophilus dinganii* and three pipistrelloid bats (family Vespertilionidae) that were not identified to species but belonged to one of the three following genera: *Pipistrellus*, *Laephotis*, or *Neoromicia* (Monadjem et al. 2020). Thirteen of the bats were male and 22 were female. All bats were adults. Based on the mean of the mean scores given by the handler and the observer, scores ranged from 1.0 – 3.5 (Table 1).

Observers showed higher agreement in rating aggressiveness when using the mean score compared to the overall score. The specific handler and observers in this study showed good to excellent agreement when using mean scores (two-way fixed average-measures ICC = 0.80, 95% confidence interval: 0.65 – 0.89) while overall scores showed poor to good agreement (0.60, 95% CI: 0.39 – 0.76). Mean scores also appeared to be more generalizable to other similar handlers and/or observers because agreement was good to excellent based on two-way random average-measures ICC (0.79, 95% CI: 0.64 – 0.88), compared to the poor to moderate agreement of overall scores based on the equivalent two-way random single-measures ICC (0.55, 95% CI: 0.28 – 0.72) (Table 2).

We found no significant difference in the mean scores between male and female *C. pumilus* ($W = 101.5$, $p = 0.78$) (Fig. 2).

Table 1 - Summary of aggressiveness scores (based on the mean from two observers) for all bats in this study: mean ± standard deviation and maximum and minimum assigned scores.

Species	n	Mean Score (± SD)	Minimum Score	Maximum Score
Chaerephon pumilus	29	1.9 ± 0.64	1.0	3.5
Scotophilus dinganii	3	2.5 ± 1.06	1.4	3.5
Pipistrelloid spp.	3	2.5 ± 0.79	2.0	3.4

Table 2 - Summary of intraclass correlations (ICC) with 95% confidence intervals for mean and overall scores given by two independent observers, specifying ICC model and form.

Score Type	Model and Form Abbreviation	Model	Form	ICC (95% CI)
Mean score	$ICC_{3,k}$	Two-way fixed	Average measures	0.80 (0.65 – 0.89)
	$ICC_{2,k}$	Two-way random	Average measures	0.79 (0.64 – 0.88)
Overall score	$ICC_{3,1}$	Two-way fixed	Single measures	0.60 (0.39 – 0.76)
	$ICC_{2,1}$	Two way random	Single measures	0.55 (0.28 – 0.72)

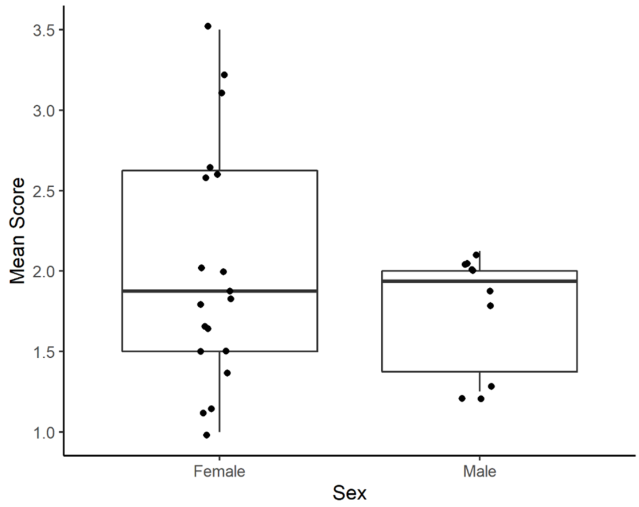


Fig. 2 - Boxplot comparing the mean of scores assigned by two observers using this scale of aggressiveness between female and male *Chaerephon pumilus*.

DISCUSSION

Here we provide a simple scale that can be used to quantify bat behavior based on aggressiveness. This scale is relatively easy to integrate into any study that involves trapping and handling individual bats. It does not require any additional equipment or specialized facilities, adds minimal time to handling, and avoids inducing further fear or anxiety in wild-caught bats, which may occur with behavioral assays (Meagher 2009). Collecting such data from bats can yield insights into many aspects of behavioral ecology that personality and behavior influence, such as dispersal (Luna et al. 2019), survival (Boon et al. 2008, Yoshida et al. 2016), habitat-use (Villegas-Ríos et al. 2018), foraging (Bergvall et al. 2011, Couchoux & Cresswell 2012, Nachev & Winter 2019), and pathogen transmission (Boyer et al. 2020, Webber & Willis 2020b).

We show that it is possible to quantify aggressiveness in bats using a standardized, repeatable method with generally high agreement between observers. This method can be employed by both experienced and inexperienced handlers or observers, as the behaviors and categories are easily observable and generally intuitive. While we found that agreement between the independent handler and the observers was generally good to excellent, further training and experience might increase the reliability and agreement. Increasing the number of observers may also improve the consistency of scores (Shrout & Fleiss 1979). Video recording bats during handling could improve this scale by reducing bias and allowing individual observers to score bats more than once and thus establish intra-rater reliability (Mugenda et al. 2019). Such recordings would also allow additional observers who were not present during the original experiment to score bats, thus increasing the total number of observers (Mugenda et al. 2019).

Agreement between the handler and observers was highest when using the mean score (averaged from the scores given at different stages of handling), compared to a single overall score assigned at the end of the handling session. The use of means is generally more reliable than a single score (Block 1961, Gosling 2001) and allows for variation in behavior over the course of handling to be factored in. An overall score could be biased by the behavior of the bat at the beginning or end of handling, which might be easier for observers to remember. Scoring behavior throughout handling also requires more attention from handlers and observers. We therefore recommend evaluating behavior using an average of scores given at each stage of handling (e.g., forearm measurement, sexing, aging, verification of reproductive status as in the present study) and employing multiple observers to score aggressiveness independently. The mean of multiple observers' mean scores provides a more reliable estimate for any further analysis using this data (Shrout & Fleiss 1979).

There are several limitations of this study. We tested and evaluated the scale of aggressiveness on a relatively small number of bats (n=35) belonging to only three species or species-groups of bats, and mostly one species – *Chaerephon pumilus*. However, the behaviors that we based the scale on are easily observable and common to all bats, although the intensity (such as the force or speed of biting) may vary between species (Santana & Dumont 2009). Further application of this scale to other bat species by other observers can confirm its utility. Because this scale of aggressiveness, particularly the use of mean scores, was designed for use during standard handling, we did not score bats a second time and therefore cannot make inference on the repeatability of individual bats' levels of aggressiveness. While aggressiveness generally has high repeatability across taxa (Bell et al. 2009), a study on big brown bats (*Eptesicus fuscus*) found it to be less repeatable than other traits due to high intra-individual variability (Boyer et al. 2020). Within the context of that study (competition trials with another conspecific), the limited repeatability may have been due to behavioral plasticity allowing bats to adjust their response to their current opponent (Wilson et al. 2011, Boyer et al. 2020, Briffa et al. 2015). However, behavioral plasticity depends not only on a specific context, but on personality at the scale of individuals (Betini & Norris 2012, Couchoux & Cresswell 2012, Dingemanse et al. 2012), populations (Briffa et al. 2008, Natarajan et al. 2009, Dingemanse et al. 2012), and species (Wong et al. 2017) and may be shaped by environmental conditions, genetics, development, and experience (Dingemanse et al. 2010). Currently, the general plasticity and repeatability of aggressiveness in bats within and across individuals, populations, and species is largely unknown and requires further research, which could incorporate the use of this scale. Finally, although the scale is based on behaviors, particularly teeth-baring and biting, that bats use when displaying aggression toward conspecifics (Ortega & Maldonado 2006, Ancillotto et al. 2012, Gadziola et al. 2012), we scored aggressiveness while bats were handled by humans, which differs from those more "natural" contexts. However, since bats were wild-caught and not repeatedly subjected to trials, their behavior could plausibly be interpreted as a response to a potential predator, and thus may still be ecologically relevant. In other species, behavior during handling appears to have a wider relevance: for example, Johnson et al. (1980) found cowbirds that were scored as more aggressive during handling (Burtt & Giltz 1969) were less likely to die during mortality events.

Nevertheless, using this scale in conjunction with further observations in the wild or behavioral experiments (Sih et al. 2004a, Réale et al. 2007, Carter et al. 2013) could both validate it and determine bat personalities and behavioral syndromes when recapturing or following individuals.

CONCLUSIONS

With this scale of aggressiveness, we provide a tool that is easily integrated into studies on any bats that are handled, including wild-captured or captive bats. It requires only additional observation and note-taking with minimal training and no extra cost, therefore allowing a broader range of bat researchers to collect behavioral data during standard data collection, e.g., while recording forearm size, age, sex, and reproductive condition. Although further validation of this scale is needed, we believe that developing it provides an important tool and first step to more widely quantifying aggressiveness in bats. Using this scale of aggressiveness could produce replicable, comparable datasets across the world and thus help us better understand the social and ecological factors that determine aggressiveness within and across bat species at broader spatial and temporal scales than previously favored in behavioral ecology studies.

ACKNOWLEDGEMENTS

We would like to thank Hervé Echecolonea, Mnqobi Mamba, Ashley Farley Shimota, and Jenny Howland for assistance in scoring bats. We thank Mandla Motsa, Smart Shabangu, Tal Fineberg and the staff at the Mbuluzi Game Reserve, Thea Litschka-Koen, Clifton Koen, Alan Howland and staff at the IYSIS Cattle and Game Ranch, The Savanna Research Center and Kim Roques and All Out Africa, for help with logistics. We also thank Jessica Laskowski for fruitful discussion on this topic. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138 (J.T.S), a Student Research Grant from Bat Conservation International (J.T.S), a National Geographic Young Explorer's Grant (J.T.S.) and a grant from The Explorers Club Exploration Fund – Mamont Scholars Program (J.T.S.).

REFERENCES

AMY, M., UNG, D., BÉGUIN, N. & LEBOUCHER, G. (2017). Personality traits and behavioural profiles in the domestic canary are affected by sex and photoperiod. *Ethology*, 123(12): 885-893. https://doi.org/10.1111/eth.12662

ANCILLOTTO, L., SERANGELI, M. T. & RUSSO, D. (2012). Spatial Proximity between Newborns Influences the Development of Social Relationships in Bats. *Ethology*, 118(4): 331-340. https://doi.org/10.1111/j.1439-0310.2011.02016.x

ARNQVIST, G. & HENRIKSSON, S. (1997). Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evol Ecol*, 11: 255-273. https://doi.org/10.1023/A:1018412302621

BELL, A. M., HANKISON, S. J. & LASKOWSKI, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim Behav*, 77(4): 771-783. https://doi.org/10.1016/j.anbehav.2008.12.022

BERGVALL, U. A., SCHÄPERS, A., KJELLANDER, P. & WEISS, A. (2011). Personality and foraging decisions in fallow deer, *Dama dama*. *Anim Behav*, 81(1): 101-112.https://doi.org/10.1016/j.anbehav.2010.09.018

BERTRAM, S. M. & ROOK, V. (2012). Relationship Between Condition, Aggression, Signaling, Courtship, and Egg Laying in the Field Cricket, *Gryllus assimilis*. *Ethology*, 118(4): 360-372. https://doi.org/10.1111/j.1439-0310.2011.02019.x

BETINI, G. S. & NORRIS, D. R. (2012). The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Anim Behav*, 83(1): 137-143. https://doi.org/10.1016/j.anbehav.2011.10.018

BIRO, P. A. & STAMPS, J. A. (2008). Are animal personality traits linked to life-history productivity?. *Trends Ecol Evol*, 23(7): 361-368. https://doi.org/10.1016/j.tree.2008.04.003

BLOCK, J. (1961). The Q-Sort Method in Personality Assessment and Psychiatric Research. ed.: Charles C Thomas. Springfield, USA, 107 pp.

BOON, A. K., RÉALE, D. & BOUTIN, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol Lett*, 10(11): 1094-1104. https://doi.org/10.1111/j.1461-0248.2007.01106.x

BOON, A. K., RÉALE, D. & BOUTIN, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, 117(9): 1321-1328.

BOYER, A., KAREVOLD, H., KREUGER, D. T., DOCHTERMANN, N. A. & GILLAM, E. H. (2020). Behavioural repeatability in the Big Brown Bat, *Eptesicus fuscus*. *Behaviour*, 157(8-9): 699-717. https://doi.org/10.1163/1568539X-bja10019

BRADBURY, J. W. (1977). Lek Mating Behavior in the Hammer-headed Bat. *Z tierpsychol*, 45(3): 225-255. https://doi.org/10.1111/j.1439-0310.1977.tb02120.x

BRIFFA, M., RUNDLE, S. D. & FRYER, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proc R Soc B*, 275(1640): 1305-1311. https://doi.org/10.1098/rspb.2008.0025

BRIFFA, M., SNEDDON, L. U. & WILSON, A. J. (2015). Animal personality as a cause and consequence of contest behavior. *Biol Lett*, 11(3). https://doi.org/10.1098/rsbl.2014.1007

BURGIN, C. J., COLELLA, J. P., KAHN, P. L. & UPHAM, N. S. (2018). How many species of mammals are there?. *J Mammal*, 99(1): 1-14. https://doi.org/10.1093/jmammal/gyx147

BURTT, H. E. & GILTZ, M. L. (1969). A statistical analysis of blackbird aggressiveness. *The Ohio Journal of Science*, 69(1): 58-62.

CARTER, A. J., FEENEY, W. E., MARSHALL, H. H., COWLISHAW, G. & HEINSOHN, R. (2013). Animal personality: what are behavioural ecologists measuring?. *Biol Rev*, 88(2): 465-475. https://doi.org/10.1111/brv.12007

CARTER, G. G. & WILKINSON, G. S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc R Soc B*, 280(1753): 20122573.https://doi.org/10.1098/rspb.2012.2573

CARTER, G. G., FORSS, S., PAGE, R. A. & RATCLIFFE, J. M. (2018) Younger vampire bats (*Desmodus rotundus*) are more likely than adults to explore novel objects. *PLoS ONE*, 13(5): e0196889. https://doi.org/10.1371/journal.pone.0196889

CICCHETTI, D. V. (1994). Guidelines, criteria, and rules of thumb for evaluating normed and standardized assessment instruments in psychology. *Psychological Assessment,* 6(4): 284-290. https://doi.org/10.1037/1040-3590.6.4.284

COUCHOUX, C. & CRESSWELL, W. (2012). Personality constraints versus flexible antipredation behaviors: how important is boldness in risk management of redshanks (*Tringa totanus*) foraging in a natural system?. *Behav Ecol*, 23(2): 290-301. https://doi.org/10.1093/beheco/arr185

DINGEMANSE, N. J., KAZEM, A. J. N., RÉALE, D. & WRIGHT, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends Ecol Evol*, 25(2): 81-89. https://doi.org/10.1016/j.tree.2009.07.013

DINGEMANSE, N. J., BOUWMAN, K. M., VAN DE POL, M., VAN OVERVELD, T., PATRICK, S. C., MATTHYSEN, E. & QUINN, J. L. (2012). Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *J Anim Ecol*, 81(1): 116-126. https://doi.org/10.1111/j.1365-2656.2011.01877.x

EBERT, P. D. & HYDE, J. S. (1976). Selection for agonistic behavior in wild female *Mus musculus*. *Behav Genet*, 6: 291-304. https://doi.org/10.1007/BF01065725

FISHER, R. A. (1954). Statistical methods for research workers 12th ed. ed.: Oliver and Body. Edinburgh, Scotland, 239 pp.

GADZIOLA, M. A., GRIMSLEY, J. M. S., FAURE, P. A. & WENSTRUP, J. J. (2012). Social Vocalizations of Big Brown Bats Vary with Behavioral Context. *PLoS ONE*, 7(9): e44550. https://doi.org/10.1371/journal.pone.0044550

GOSLING, S. D. (2001). From mice to men: What can we learn about personality from animal research?. *Psychological Bulletin*, 127(1): 45-86. https://doi.org/10.1037/0033-2909.127.1.45

HALL, C. S. & KLEIN, S. J. (1942). Individual differences in aggressiveness in rats. *J Comp Psychol*, 33(3): 371-383. https://doi.org/10.1037/h0056754

HALLGREN, K. A. (2012). Computing Inter-Rater Reliability for Observational Data: An Overview and Tutorial. Tutorials in Quantitative Methods for Psychology, 8(1): 23-34. https://doi.org/10.20982/tqmp.08.1.p023

HARTEN, L., MATALON, Y., GALLI, N., NAVON, H., DOR, R. & YOVEL, Y. (2018). Persistent producer-scrounger relationships in bats. *Science Advances*, 4(2): e1603293. https://doi.org/10.1126/sciadv.1603293

HUNTINGFORD, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus Aculeatus*. *Anim Behav*, 24(2): 245-260. https://doi.org/10.1016/S0003-3472(76)80034-6

JOHNSON, D. M., STEWART, G. L., CORLEY, M., GHRIST, R., HAGNER, J., KETTERER, A., MCDONNELL, B., NEWSOM, W., OWEN, E. & SAMUELS, P. (1980). Brown-Headed Cowbird (*Molothrus ater*) Mortality in an Urban Winter Roost. *The Auk*, 97(2): 299-320. https://doi.org/10.1093/auk/97.2.299

KILGOUR, R. J. & BRIGHAM, R. M. (2013). The Relationships between Behavioural Categories and Social Influences in the Gregarious Big Brown Bat (*Eptesicus fuscus*). *Ethology*, 119(3): 189-198. https://doi.org/10.1111/eth.12052

KNOX, J. W., RODRÍGUEZ DÍAZ, J. A., NIXON, D. J. & MKHWANAZI, M. (2010). A preliminary assessment of climate change impacts on sugarcane in Swaziland. *Agr Syst*, 103(2): 63-72. https://doi.org/10.1016/j.agsy.2009.09.002

KOO, T. K. & LI, M. Y. (2016). A Guideline of Selecting and Reporting Intraclass Correlation Coefficients for Reliability Research. *Journal of Chiropractic Medicine*, 15(2): 155-163.https://doi.org/10.1016/j.jcm.2016.02.012

LALOT, M., UNG, D., PÉRON, F., D?ETTORRE, P. & BOVET, D. (2017). You know what? I'm happy. Cognitive bias is not related to personality but is induced by pair-housing in canaries (*Serinus canaria*). *Behav Process*, 134: 70-77. https://doi.org/10.1016/j.beproc.2016.09.012.

LECORPS, B., KAPPEL, S., WEARY, D. M. & VON KEYSERLINGK, M. A. G. (2018). Dairy calves' personality traits predict social proximity and response to an emotional challenge. *Sci Rep-UK*, 8: 16350. https://doi.org/10.1038/s41598-018-34281-2

LEWANZIK, D., SUNDARAMURTHY, A. K. & GOERLITZ, H. R. (2019). Insectivorous bats integrate social information about species identity, conspecific activity and prey abundance to estimate cost-benefit ratio of interactions. *J Anim Ecol*, 88(10): 1462- 1473. https://doi.org/10.1111/1365-2656.12989

LEWIS, J. R. (1993). Multipoint scales: Mean and median differences and observed significance levels. *International Journal of Human-Computer Interaction*, 5(4): 383-392. https://doi.org/10.1080/10447319309526075

LUNA, Á., PALMA, A., SANZ-AGUILAR, A., TELLA, J. L. & CARRETE, M. (2019). Personality-dependent breeding dispersal in rural but not urban burrowing owls. *Sci Rep-UK*, 9: 2886. https://doi.org/10.1038/s41598-019-39251-w

MAGNHAGEN, C., WACKER, S., FORSGREN, E., CATS MYHRE, L., ESPY, E. & AMUNDSEN, T. (2014). Context Consistency and Seasonal Variation in Boldness of Male Two-Spotted Gobies. *PLoS ONE*, 9(3): e93354. https://doi.org/10.1371/journal.pone.0093354

MARTINS, C. I. M., SILVA, P. I. M., CONCEIÇÃO, L. E. C., COSTAS, B., HÖGLUND, E., ØVERLI, Ø. & SCHRAMA, J. W. (2011). Linking Fearfulness and Coping Styles in Fish. *PLoS ONE*, 6(11): e28084. https://doi.org/10.1371/journal.pone.0028084

MATONDO, J. I., PETER, G. & MSIBI, K. M. (2004). Evaluation of the impact of climate change on hydrology and water resources in Swaziland: Part I. *Physics and Chemistry of the Earth, Parts A/B/C*, 29(15-18): 1181-1191. https://doi.org/10.1016/j.pce.2004.09.033

MEAGHER, R. K. (2009). Observer ratings: Validity and value as a tool for animal welfare research. *Appl Anim Behav Sci*, 19(1-2): 1-14. https://doi.org/10.1016/j.applanim.2009.02.026

MELOTTI, L., OOSTINDJER, M., BOLHUIS, J. E., HELD, S. & MENDL, M. (2011). Coping personality type and environmental enrichment affect aggression at weaning in pigs. *Appl Anim Behav Sci*, 133(3-4): 144-153. https://doi.org/10.1016/j.applanim.2011.05.018

MENZIES, A. K., TIMONIN, M. E., MCGUIRE, L. P. & WILLIS, C. K. R. (2013). Personality Variation in Little Brown Bats. *PLoS ONE*, 8(11): e80230. https://doi.org/10.1371/journal.pone.0080230

MONADJEM, A. & GARCELON, D. (2005). Nesting distribution of vultures in relation to land use in Swaziland. *Biodivers Conserv*, 14: 2079-2093. https://doi.org/10.1007/s10531-004-4358-9

MONADJEM, A. & RESIDE, A. (2008). The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. *Acta Chiropterol*, 10(2), 339-348.https://doi.org/10.3161/150811008X414917

MONADJEM, A., TAYLOR, P. J., COTTERILL, F. P. D. & SCHOEMAN, M. C. (2010). Bats of Southern and Central Africa: A Biogeographic and Taxonomic Synthesis. ed.: Wits University Press. Johannesburg, South Africa, 608 pp.

MONADJEM, A., TAYLOR, P. J., COTTERILL, F. P. D. & SCHOEMAN, M. C. (2020). Bats of Southern and Central Africa: A Biogeographic and Taxonomic Synthesis, 2nd ed. ed.: Wits University Press. Johannesburg, South Africa, 640 pp.

MONADJEM, A., DEMOS, T. C., DALTON, D. L., WEBALA, P. W., MUSILA, S., PETERHANS, J. C. K. & PATTERSON, B. D. (2021a). A revision of pipistrelle-like bats (Mammalia: Chiroptera: Vespertilionidae) in East Africa with the description of new genera and species. *Zool J Linn Soc-Lond*, 191(4): 1114-1146. https://doi.org/10.1093/zoolinnean/zlaa087

MONADJEM, A., SIMELANE, F., SHAPIRO, J. T., GUMBI, B. C., MAMBA, M. L., SIBIYA, M. D., LUKHELE, S. M. & MAHLABA, T'A. A. M. (2021b). Using species distribution models to gauge the completeness of the bat checklist of Eswatini. *Eur J Wildlife Res*, 67: 21. https://doi.org/10.1007/s10344-021-01463-9

MUGENDA, L., SHREYER, T. & CRONEY, C. (2019). Refining canine welfare assessment in kennels: Evaluating the reliability of Field Instantaneous Dog Observation (FIDO) scoring. *Appl Anim Behav Sci*, 221: 104874. https://doi.org/10.1016/j.applanim.2019.104874

NACHEV, V. & WINTER, Y. (2019). Behavioral repeatability and choice performance in wild free-flying nectarivorous bats (*Glossophaga commissarisi*). *Behav Ecol Sociobiol*, 73: 24. https://doi.org/10.1007/s00265-019-2637-4

NATARAJAN, D., DE VRIES, H., SAALTINK, D-J., DE BOER, S. F. & KOOLHAAS, J. M. (2009). Delineation of Violence from Functional Aggression in Mice: An Ethological Approach. *Behav Genet*, 39: 73-90. https://doi.org/10.1007/s10519-008-9230-3

ORTEGA, J. & MALDONADO, J. E. (2006). Female interactions in harem groups of the Jamaican fruit-eating bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Acta Chiropterol*, 8(2): 485-495. https://doi.org/10.3161/1733-5329(2006)8[485:FIIHGO]2.0.CO;2

R CORE TEAM. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

RACEY, P. A. (1974). Ageing and assessment of reproductive status of Pipistrelle bats, *Pipistrellus pipistrellus*. *J Zool*, 173(2): 264-271. https://doi.org/10.1111/j.1469-7998.1974.tb03136.x

RÉALE, D., READER, S. M., SOL, D., MCDOUGALL, P. T. & DINGEMANSE, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol Rev*, 82(2): 291-318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

REVELLE, W. R. (2020). psych: Procedures for Personality and Psychological Research. R package version 2.0.12.

ROQUES, K., O'CONNOR, T. & WATKINSON, A. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J Appl Ecol*, 38(2): 268-280. https://doi.org/10.1046/j.1365-2664.2001.00567.x

SANTANA, S. E. & DUMONT, E. R. (2009). Connecting behaviour and performance: the evolution of biting behaviour and bite performance in bats. *J Evolution Biol*, 22(11): 2131-2145. https://doi.org/10.1111/j.1420-9101.2009.01827.x

SHAPIRO, J. T., MONADJEM, A., RÖDER, T. & MCCLEERY, R. A. (2020). Response of bat activity to land cover and land use in savannas is scale-, season-, and guild-specific. *Biol Conserv*, 241: 108245. https://doi.org/10.1016/j.biocon.2019.108245

SHROUT, P. E. & FLEISS, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychol Bull*, 86(2): 420-428. https://doi.org/10.1037/0033-2909.86.2.420

SIH, A., BELL, A. M. & JOHNSON, J. C. (2004a). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol*, 19(7): 372-378. https://doi.org/10.1016/j.tree.2004.04.009

SIH, A., BELL, A. M., JOHNSON, J. C. & ZIEMBA, R. E. (2004b). Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology*, 79(3): 241-277. https://doi.org/10.1086/422893

SINN, D. L., WHILE, G. M. & WAPSTRA, E. (2008). Maternal care in a social lizard: links between female aggression and offspring fitness. *Anim Behav*, 76(4): 1249-1257. https://doi.org/10.1016/j.anbehav.2008.06.009

SMARSH, G. C. & SMOTHERMAN, M. (2017). Behavioral response to conspecific songs on foraging territories of the heart-nosed bat. *Behav Ecol Sociobiol*, 71: 142. https://doi.org/10.1007/s00265-017-2370-9

SMITH, B. R. & BLUMSTEIN, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behav Ecol*, 19(2): 448-455. https://doi.org/10.1093/beheco/arm144

THYS, B., PINXTEN, R., RAAP, T., DE MEESTER, G., RIVERA-GUTIERREZ, H. F. & EENS, M. (2017). The Female Perspective of Personality in a Wild Songbird: Repeatable Aggressiveness Relates to Exploration Behaviour. *Sci Rep-Uk*, 7: 7656. https://doi.org/10.1038/s41598-017-08001-1

TOTH, C. A., SANTURE, A. W., HOLWELL, G. I., PATTEMORE, D. E. & PARSONS, S. (2018). Courtship behaviour and display-site sharing appears conditional on body size in a lekking bat. *Anim Behav*, 136: 13-19.https://doi.org/10.1016/j.anbehav.2017.12.007

TREVETHAN, R. (2017). Intraclass correlation coefficients: clearing the air, extending some cautions, and making some requests. Health Services and Outcomes Research Methodology, 17: 127-143. https://doi.org/10.1007/s10742-016-0156-6

VILLEGAS-RÍOS, D., RÉALE, D., FREITAS, C., MOLAND, E. & OLSEN, E. M. (2018). Personalities influence spatial responses to environmental fluctuations in wild fish. *J Anim Ecol*, 87(5): 1309- 1319. https://doi.org/10.1111/1365-2656.12872

WALTON, A. & TOTH, A. L. (2016). Variation in individual worker honey bee behavior shows hallmarks of personality. *Behav Ecol Sociobiol*, 70: 999-1010. https://doi.org/10.1007/s00265-016-2084-4

WEBBER, Q. M. R. & WILLIS, C. K. (2020a). Correlations between personality traits and roosting behaviours suggest a behavioural syndrome in little brown bats. *Behaviour*, 157(2): 143-183. https://doi.org/10.1163/1568539X-00003585

WEBBER, Q. M. R. & WILLIS, C. K. R. (2020b). Personality affects dynamics of an experimental pathogen in little brown bats. *Roy Soc Open Sci*, 7: 200770. http://doi.org/10.1098/rsos.200770

WELCH, M. J., SMITH, T., HOSIE, C., WORMELL, D., PRICE, E. & STANLEY, C. R. (2020). Social Experience of Captive Livingstone's Fruit Bats (*Pteropus livingstonii*). *Animals*, 10(8): 1321. https://doi.org/10.3390/ani10081321

WEST-EBERHARD, M. J. (1989). Phenotypic Plasticity and the Origins of Diversity. *Annu Rev Ecol Syst*, 20: 249-278. https://doi.org/10.1146/annurev.es.20.110189.001341

WILKINSON, G. S. (2003). Social and vocal complexity in bats. In: Animal social complexity: Intelligence, culture, and individualized societies. ed.: Harvard University Press. Cambridge, Massachusetts, USA, p.322-341.

WILSON, A. J., DE BOER, M., ARNOTT, G. & GRIMMER, A. (2011). Integrating Personality Research and Animal Contest Theory: Aggressiveness in the Green Swordtail *Xiphophorus helleri*. *PLoS ONE*, 6(11): e28024. https://doi.org/10.1371/journal.pone.0028024

WOLF, M., VAN DOORN, G., LEIMAR, O. & WEISSING, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447: 581-584. https://doi.org/10.1038/nature05835

WONG, B. B. M. & CANDOLIN, U. (2015). Behavioral responses to changing environments. *Behav Ecol*, 26(3): 665-673. https://doi.org/10.1093/beheco/aru183

WONG, M. Y. L., BEASLEY, A. L., DOUGLASS, T., WHALAN, S. & SCOTT, A. (2017). Some anemonefish lack personality: a comparative assessment of behavioral variation and repeatability in relation to environmental and social factors. *Coral Reefs*, 36: 1307-1316. https://doi.org/10.1007/s00338-017-1625-2

YOSHIDA, K. C. S., VAN METER, P. E. & HOLEKAMP, K. E. (2016). Variation among free-living spotted hyenas in three personality traits. *Behaviour*, 153(13-14): 1665-1722. https://doi.org/10.1163/1568539X-00003367

YUEN, C. H., PILLAY, N., HEINRICHS, M., SCHOEPF, I. & SCHRADIN, C. (2015). Personality does not constrain social and behavioural flexibility in African striped mice. *Behav Ecol Sociobiol*, 69: 1237-1249. https://doi.org/10.1007/s00265-015-1937-6